

The role of seed limitation and resource availability in the recruitment of native perennial grasses and exotics in a South Australian grassland

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Abstract We investigated what factors lead to invasion of exotics or re-colonization of native perennial grasses in the South Australian mid-north grasslands. We manipulated 160 experimental quadrats by clipping, irrigation and seed addition and assessed recruitment by exotics in an area dominated by perennial grasses and perennial grass recruitment in an area dominated by exotics. Treatment effects differed with season for exotics: their biomass increased with irrigation in autumn and seed addition in winter. However, in both periods other factors, probably soil properties, also had a strong effect. We detected no perennial grass seedlings in the quadrats over 1 year, possibly due to unsuitable environmental conditions or persistent high competition levels. Under controlled conditions the presence of the invasive annual *Avena barbata* had a strong negative effect on the recruitment of the native perennial *Austrodanthonia caespitosa* at any moisture and nutrient availability. *Avena* also germinated faster and more frequently than *Austrodanthonia*, especially at low soil moisture. During an imposed drought *Austrodanthonia* seedlings survived longer in the absence of *Avena*. The results suggest that annual exotics are highly responsive to resources and can quickly invade areas, while the re-colonization of invaded areas by native grasses requires a complex (and less likely) rainfall regime.

Key words: *Austrodanthonia caespitosa*, *Avena barbata*, perennial grass, recruitment, South Australia.

INTRODUCTION

The largest threat to the remaining temperate grasslands in Australia is the invasion of exotic plant species (Kirkpatrick *et al.* 1995). In South Australian grasslands, approximately half of the 20 most abundant species are introduced (Hyde 1995; Robertson 1998). A variety of models have been used to explain or predict the occurrence of these invasions. Initially, invasions were viewed either from the perspective of the invader or the perspective of the invaded systems almost exclusively. Certain plant characteristics (Baker 1965) or ecosystem characteristics, such as disturbance or low diversity (Fox & Fox 1986; Rejmánek 1989; Hobbs & Mooney 1991; Tilman 1997), can promote plant invasion. However, they are not required for invasions to occur (Huenneke *et al.* 1990; Kolar & Lodge 2001) or may relate to other invasion-promoting factors (Van der Putten *et al.* 2000; Dukes 2001; Foster *et al.* 2002). Newer theoretical frameworks explicitly take species interactions and stochastic events into account, regardless of climate,

productivity, diversity or disturbance regimes. Thus, these models do not predict system- or species-specific characters that promote invasion. The ‘fluctuating resource availability theory’, for example, states that plant communities become more susceptible to invasion when the amount of unused resources increases, propagules are present and the characteristics of the species are suitable for this particular habitat (Davis *et al.* 2000). The model predicts that systems are more likely to be invaded when they experience resource fluctuations, or after an abrupt change in the rate of supply of a limiting resource, or when the interval between an increase in resource supply and capture of resources by present vegetation is large. While direct experimental evidence for this model is uncommon (cf. Davis & Pelsor 2001), several recent experimental studies on invasions have directly or indirectly supported the importance of interactions between resource fluctuations and species identities (Pérez-Fernández *et al.* 2000; Buckland *et al.* 2001; Thompson *et al.* 2001; Troumbis *et al.* 2002).

The initial stage of invasion of a system by a new plant species is the emergence, survival and recruitment from newly arrived propagules. In temperate grasslands, recruitment dynamics can be driven by propagule availability (dispersal and seed bank dynamics), abiotic conditions, resource competition,

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interference via litter accumulation, herbivory and fire regimes. Species-specific and source-population-specific properties, environmental fluctuations and microclimates are responsible for the high variability observed 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 grasslands in general, both invasive and native species are 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). Localized seed bank limitation is an important factor, especially in unmanaged or overgrown grasslands (Kalamees & Zobel 1998; Zobel *et al.* 2000; Kalamees & Zobel 2002) and in particular for perennial species (Peco *et al.* 1998). 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). Restoration efforts in European grasslands are as much limited by propagule availability as by unsuitable abiotic conditions (Bakker & Berendse 1999) and increasing seed availability has increased the abundance of native species in perennial seminatural grassland in northern Europe (Zobel *et al.* 2000) and Californian grasslands (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 1986; 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-seeded 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 (Hobbs & Atkins 1988; Huenneke *et al.* 1990; Hobbs & Atkins 1991; Pérez-Fernández *et al.* 2000; Buckland *et al.* 2001; Thompson *et al.* 2001). Exotic annuals in particular are favoured by high soil moisture or nutrient availability (Huenneke *et al.* 1990; Hobbs & Mooney 1991;

Nicholson & Hui 1993; Morgan 1998b; Paschke *et al.* 2000).

The theory of fluctuating resource availability suggests that the success of an invasion depends on the interactions between resource uptake of resident vegetation, resource supply, propagule availability and species identity. Natural rainfall variability, accidental seed dispersal and standard management activities such as grazing and seeding are known to play a major role in the recruitment dynamics in grasslands and also can result in resource fluctuations and propagule availability. To explore the potential of further invasion by exotics or re-invasion by perennial grasses in ungrazed (and unburnt) grasslands of the South Australian mid-north, we aimed to determine the importance of soil moisture and propagule availability for the recruitment of exotic species in perennial grass stands and perennial grasses into stands dominated by exotics.

METHODS

Field site

The experiments were carried out 1 km north of Burra, South Australia (138°55'E, 33°41'S, 500 m a.s.l.). Burra has a Mediterranean-type climate with hot summers, mild winters and an average annual rainfall of 439 mm. Rainfall in summer is more variable than in winter (Table 1). Rainfall in 2001, the year of the experiment, was 413 mm (Bureau of Meteorology). Fire is not used as a management tool in this area (Robertson 1998). The pre-European settlement fire regime is unknown (Nicholson 1981). A range of semiarid grasslands in south-eastern Australia are self-sustaining in the absence of fire (Nicholson 1981), and the absence of woody vegetation in long-time ungrazed and unburned mid-north grasslands (T. Lenz, unpubl. data, 2001) suggests that this is the case in the mid-north region.

The 2-ha study site was a south-east facing hillside grassland that was destocked in January 1999 after long-term medium to heavy sheep grazing (J. Agnew, R. Williams, pers. comm., 2000). The soil is a sandy loam, ranging from skeletal to more than 0.5 m deep (T. Lenz & J. M. Facelli, unpubl. data, 2000). The pre-European vegetation of the study site is unknown. A

Table 1. Long-term seasonal rainfall averages (41 years) and coefficients of variation (CV) for Burra South Australia (Bureau of Meteorology)

	Summer (Dec–Feb)	Autumn (Mar–May)	Winter (Jun–Aug)	Spring (Sep–Nov)	Total
Mean	68.57	88.92	159.05	118.22	434.76
CV (%)	75.77	60.18	34.58	47.51	28.81

grassland 1 km west, unstocked for more than 30 years, is a *Lomandra multiflora* (R. Br.) Britten tussock complex (Hyde 1995). Some *Lomandra* individuals occur at the study site. However, short lived or geophytic exotic species (*Avena barbata* Pott ex Link, *Bromus diandrus* Roth, *B. hordeaceus* L., *B. rubens* L., *Echium plantagineum* L., *Gynandris setifolia* (L.f.) Foster, *Poa bulbosa* L., *Romulea* spp. Maratti and *Salvia verbenaca* L.) dominate the lower slope positions. The higher slope positions are 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 and *Austrostipa nodosa* (S.T.Blake) S.W.L. Jacobs & J. Everett), with some exotics in the interstitial spaces. Nomenclature follows Jessop and Toelken (1986), with *Danthonia* and *Stipa* updated to *Austrodanthonia* and *Austrostipa*.

Emergence and survival under field conditions

To test for the effects of seed availability and changes in resource uptake and resource supply on the recruitment of exotics into perennial stands and of perennial grasses into exotic stands, we set up a blocked three-way factorial experiment in each stand. The exotic stand was the base of the slope (80–100% exotic annual grass cover) and the perennial-grass stand was at the top of the slope (40–60% perennial grass cover, plus lichens, rocks and bare ground). In each stand we established two rows of 15 blocks, each 4 m × 2 m and with 1 m spacing between each. We randomly selected 10 blocks for the experiment and in each block established eight 0.5 m × 0.5 m quadrats, with 0.5 m spacing between each, resulting in 80 quadrats per experiment. The eight combinations of the three experimental factors were randomly allocated to the quadrats. The three factors were seed addition (seed addition *vs.* control), decreased resource competition (removal of standing biomass *vs.* control), and increase resource availability (watering *vs.* control).

Seed addition

We used the most frequent introduced species, the Mediterranean annual grass *Avena barbata* (origin: field site) (Hyde 1995; Robertson 1998) as a potential invader for the perennial-grass stand, and *Austrodanthonia caespitosa* (origin: 138°41'E, 34°1'S), a common native perennial grass, as a potential invader for the exotic stand. Subsequently we will refer to the species by their generic names. To check for seasonal differences, we planted seeds twice: on 6–10 March 2001 for the autumn season (March–May) and 30 May–6 June 2001 for the winter season (June–August).

We created 1 cm deep holes with nails set at 3 cm intervals in a 7 × 7 grid on a 0.22 m × 0.22 m board in an area in both control quadrats and seed addition quadrats. In the seed addition quadrats we planted one seemingly viable (i.e. large and swollen) floret in each of the 49 holes. To assess seed viability we also randomly selected three preprepared 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 until no further germination occurred.

Reduced competition

Based on the positive relationship between plant size and soil moisture uptake in both *Avena* and *Austrodanthonia* (T. Lenz & J. M. Facelli, unpubl. data, 2003), we assumed that clipping would increase light availability and soil moisture to the remaining species. We thus treated 'reduced competition' 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, we 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 exotic stand ($181.10 \text{ g m}^{-2} \pm 64.47 \text{ SD}$) than in the perennial-grass stand ($245.98 \text{ g m}^{-2} \pm 84.00 \text{ SD}$) (ANOVA: $P = 0.009$). We re-clipped quadrats again approximately fortnightly.

Increased resource supply

At fortnightly intervals we watered quadrats if the soil water content of any quadrat was below field capacity, by sprinkling the equivalent of 10 mm rainfall slowly over the quadrats. We had previously determined field capacity by flooding three 0.25 m × 0.25 m quadrats with 3 L each in the centre and on each side of each transect and measuring volumetric soil moisture with a thetaprobe ML2x (Delta-T Devices) 12 h later. The field capacity was $14.33 \pm 1.99\%$ volumetric moisture (mean ± SE) in the perennial-grass stand and $12.53 \pm 1.70\%$ in the exotic stand transect.

Harvest

We harvested exotic species in the perennial-grass stand quadrats on 30 May and 31 August 2001 by clipping the 0.22 m × 0.22 m inner quadrats at ground level and discarding native plant material and litter. Exotic plant material (annual grasses, *Gynandris setifolia* and *Medicago* spp.) was dried at 80°C for 72 h and weighed.

We examined the quadrats within the stand dominated by exotics for the presence of perennial grass seedlings (defined as those less than 1 cm in basal diameter) on both dates but could not detect any seedlings within the dense cover of live exotic annual grasses and *Poa bulbosa*. We 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. In addition, we examined 24 1 m × 1 m permanent quadrats from another study, eight each in an annual-grass-dominated area, a perennial-grass-dominated area and a mixed area on 27 September 2002 for the presence of perennial grass seedlings.

Emergence and survival of *Austrodanthonia* under controlled conditions

Due to the lack of perennial grass recruitment in the field we ran a glasshouse experiment to determine the effect of exotic annual grass competition, soil moisture and nutrient availability on the emergence and survival of *Austrodanthonia* under controlled conditions. The experiment was a fully factorial experiment with three factors: *Avena* competition (24 viable *Avena* seeds per tray, origin: 138°11'E, 33°47'S, versus no *Avena* seed added), soil moisture (watered to 100% field capacity three times a week vs. misting the top layer (30 squirts with hand mister) three times a week) and nutrient availability (15 squirts with hand mister containing 1 g l⁻¹ Hortico Aquasol (23% N, 4% P, 18% K + trace elements) in tap water versus 15 squirts tap water fortnightly). Based on previous pot experiments we estimate that the low watering treatments averaged less than 8% field capacity.

Each combination was applied to eight replicates of 1 L plastic trays (9–11 cm wide, 14.2–16.5 cm long, 6 cm deep, six drainage holes), that contained Nu-Erth Special Native Plant mix (20% sand, 80% composted pine bark, trace elements). Each tray was seeded with 0.1 g (± 0.0005) *Austrodanthonia* caryopses (origin: 139°8'E; 35°1'S, containing 418 ± 7.7 seed (mean \pm SE)) on 2 May 2003. We counted seedling numbers of both species per tray weekly and removed any dicot seedlings. After 8 weeks, when little further recruitment was recorded, we discontinued watering and nutrient addition and terminated the experiments 10 weeks later, when no more recruits survived. We also assessed initial seed viability by germinating three batches of both species in Petri dishes as described above.

Statistical analyses

Field data conformed to assumptions of normality (Shapiro-Wilk W, JMP 3.1.4) and homoscedasticity

(Brown-Forsythe, JMP 3.1.4) at $P < 0.05$ after log-transformation. We analysed the data using repeated-measures MANOVA, followed by separate ANOVAs on the two harvests and Tukey-Kramer Honest 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 we repeated the test after pooling factors that were not significant in the ANOVA.

The majority of the glasshouse data distributions, where more than one tray contained living seedlings, conformed to the assumption of normality, but not homoscedasticity. 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). We thus performed repeated-measures MANOVAs.

RESULTS

Emergence and survival under field conditions

Rainfall (daily readings 1 km west of the field site; Bureau of Meteorology) was 58.6 mm during autumn and 154.6 mm during winter. The watering quadrats received an additional 20 mm during both autumn and winter.

Recruitment of exotic annuals

Under laboratory conditions $70.89 \pm 3.15\%$ (mean \pm SE) *Avena* seeds of the autumn run and $80.25 \pm 4.23\%$ (mean \pm SE) of the winter run germinated. In the field the mean dry weight of exotics harvested was 7.07 ± 0.46 g m⁻² (mean \pm SE) at the end of autumn and 36.63 ± 0.148 g m⁻² at the end of winter. Treatment effects differed with season. Watering strongly increased dry weight of exotics during autumn and seed addition slightly increased dry weight of exotics during winter (Table 2, Table 3, Fig. 1). However, the significant effect of block in both periods suggests that further small-scale factors, such as soil properties, have a strong effect on the recruitment of exotics. Plotting the initial quadrat biomass harvested against final harvest of exotics of the same quadrat showed a marginally non-significant positive relationship (log autumn harvest = $-5.5 + 1.0 \times \log$ initial biomass, $r^2 = 0.31$, $P = 0.09$; log winter harvest = $-2.7 + 0.8 \times \log$ initial biomass, $r^2 = 0.40$, $P = 0.05$), suggesting that recruitment of exotics may be more likely in higher productivity sites.

Table 2. Repeated-measures MANOVA of the effects of seed addition, clipping & watering on log-transformed DW of exotics during autumn and winter 2001 in a grassland in the South Australian mid-north

Factor	Numerator DF	F
Seed addition (S)	1	3.71 ^{ns}
Clipping (C)	1	0.59 ^{ns}
Watering (W)	1	11.44**
Block (B)	9	3.53**
Time (T)	1	836.30***
T × S	1	0.15 ^{ns}
T × C	1	0.03 ^{ns}
T × W	1	16.30***
T × B	9	2.12*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$; ^{ns} $P > 0.05$. Denominator DF = 67. Higher interactions not significant at $\alpha = 0.05$.

Table 3. ANOVAs of the effects of seed addition, clipping & watering on log-transformed DW of exotics during autumn & winter 2001 in a grassland in the South Australian mid-north

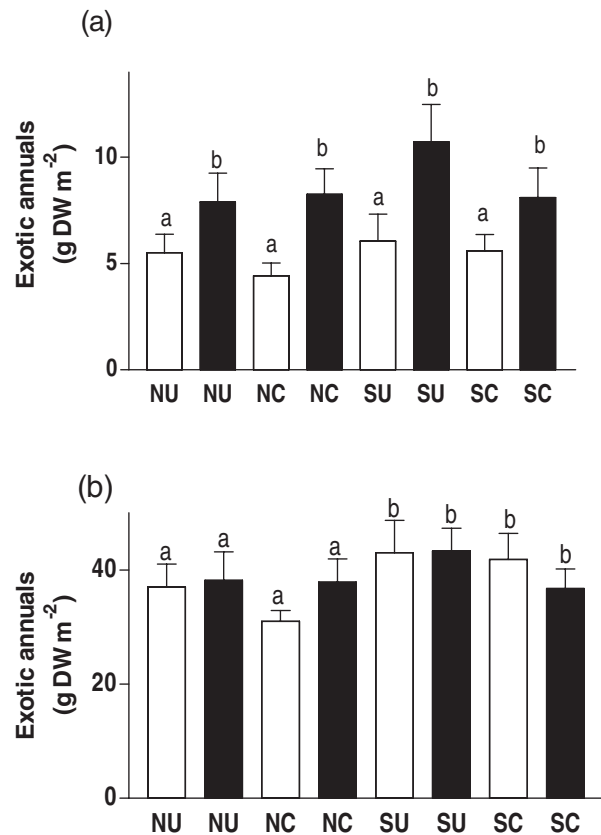
Factor	ANOVA Autumn ($r^2 = 0.63$)		ANOVA Winter ($r^2 = 0.76$)	
	DF	F	DF	F
Seed addition (S)	1	1.74 ^{ns}	1	6.62**
Clipping (C)	1	0.14 ^{ns}	1	2.03 ^{ns}
Watering (W)	1	14.72**	1	0.27 ^{ns}
Block (B)	9	2.33*	9	7.23***
S × C	1	0.42 ^{ns}	1	0.13 ^{ns}
S × W	1	0.07 ^{ns}	1	1.68 ^{ns}
S × B	9	0.66 ^{ns}	9	1.72 ^{ns}
C × W	1	0.14 ^{ns}	1	0.01 ^{ns}
C × B	9	0.95 ^{ns}	9	1.41 ^{ns}
W × B	9	1.23 ^{ns}	9	1.53 ^{ns}

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$; ^{ns} $P > 0.05$. Higher interactions not significant at $\alpha = 0.05$.

Recruitment of native perennial grasses

Under laboratory conditions $40.52 \pm 4.90\%$ SE *Austrodanthonia* seeds of the autumn run germinated. The same batch of seed was used for both runs and we assumed seed viability was similar in the second run.

There was no evidence of perennial grass recruitment in the field. We could not locate any perennial grass seedlings in the 40 quadrats we examined intensively within the annual grass litter or in the remaining 40 quadrats we examined briefly in March 2002. When surveying other permanent quadrats in September 2002, we located no perennial grass seedlings in the area dominated by exotic annual grasses, $0.38 \pm 0.18 \text{ m}^{-2}$ (mean \pm SE) *Austrostipa* seedlings in the area codominated by annual and perennial grasses

**Fig. 1.** Above-ground biomass of exotic annuals after 3 months under different experimental manipulations (□, not irrigated; ■, irrigated; N, no seed added; S, seed added; U, unclipped; C, clipped) 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). Note different scales for both graphs.

and $1.00 \pm 0.38 \text{ m}^{-2}$ *Austrostipa* seedlings in the perennial-grass-dominated area. During extended fieldwork at this site and other sites we 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 exotic annual grasses.

Emergence and survival of *Austrodanthonia* under controlled conditions

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 the emergence or survival of *Austrodanthonia* in the repeated-measures MANOVA model of the complete data set (data not shown) and hence nutrient addition was removed as a

Table 4. Repeated-measures MANOVA of the effects of water availability and competition by *Avena barbata* on *Austrodanthonia caespitosa* seedling numbers

Source	Test	Exact F	Numerator DF	Denominator DF
All between	F	109.56**	3	60
Water (W)	F	315.68**	1	60
<i>Avena</i> (A)	F	10.15*	1	60
W \times A	F	2.84 ^{ns}	1	60
All within	Wilks' λ	15.89**	54	128.94
T (Time)	F	128.75**	18	43
T \times W	F	123.59**	18	43
T \times A	F	7.50**	18	43
T \times W \times A	F	4.26**	18	43

* $P < 0.01$; ** $P < 0.0001$; ^{ns} $P > 0.05$.**Table 5.** Repeated-measures MANOVAs of the effects of nutrient addition and competition by *Avena barbata* on *Austrodanthonia caespitosa* seedling numbers in (a) low watering treatments and (b) high watering treatments

	Source	Test	Exact F	Numerator DF	Denominator DF
(a)	All Between	F	5.77**	3	28
	Nutrients (N)	F	5.63*	1	28
	<i>Avena</i> (A)	F	11.45**	1	28
	N \times A	F	0.24 ^{ns}	1	28
	All Within	Wilks' λ	1.10 ^{ns}	54	33.59
	Time (T)	F	3.16*	18	11
	T \times N	F	0.69 ^{ns}	18	11
	T \times A	F	2.31 ^{ns}	18	11
	T \times N \times A	F	0.70 ^{ns}	18	11
(b)	<i>Avena</i>	F	6.28*	1	30
	Time	F	86.77***	18	13
	Time \times <i>Avena</i>	F	5.16**	18	13

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.0001$; ^{ns} $P > 0.05$. No further interactions significant at $\alpha = 0.05$.

factor from this analysis. The resulting MANOVA (Table 4) 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.

In the high watering treatment 80–100 *Austrodanthonia* seedlings emerged in the first 2 weeks while in the low watering treatments 10–20 *Austrodanthonia* emerged over 7 weeks (Fig. 2a). While the presence of *Avena* seedlings appeared to decrease *Austrodanthonia* seedling numbers in both watering treatments, *Avena* had a relatively larger negative effect in the low watering treatment, where it halved the number of seedlings compared with a 10% decrease in the high watering treatment. *Avena* emerged much faster than *Austrodanthonia*, 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* (Fig. 2a,b). In both watering treatments *Avena* decreased the survival of *Austrodanthonia* seedlings by 2–3 weeks after water and nutrient addition ceased.

To investigate the results in further detail, we analysed high watering and low watering treatments separately. In the low watering treatments, the number of *Austrodanthonia* seedlings tended to be reduced by nutrient addition and by the presence of *Avena* between Week 6–13 (Table 5a, Fig. 2). In the high watering treatments, neither nutrient addition 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 5b). Initially *Avena* had no effect on *Austrodanthonia* seedlings, but after Week 11 *Avena* increasingly decreased the number of *Austrodanthonia* seedlings surviving.

DISCUSSION

Recruitment of exotics

Exotic species were able to recruit under all experimental conditions and their biomass was considerably

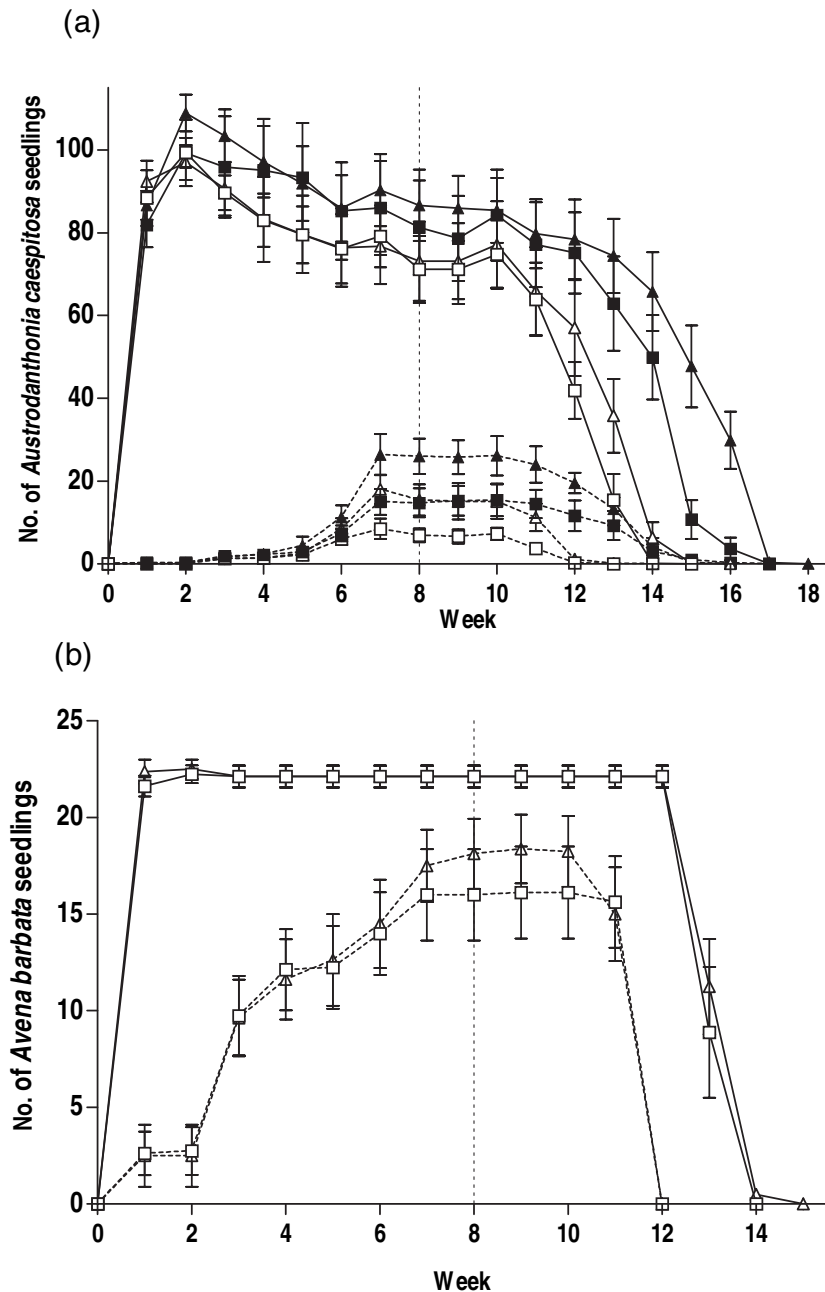


Fig. 2. (a) Effect of water availability (\cdots , low; $-$, high), nutrient availability (\blacktriangle , low; \blacksquare , high) and competition by *Avena barbata* (open symbols, *Avena* present; closed symbols, *Avena* absent) on number of *Austroanthonia caespitosa* seedlings; (b) effect of water availability (\cdots , low; $-$, high) and nutrient availability (\triangle , low; \square , high) on number of *Avena barbata* seedlings acting as competitors. Dashed lines indicate final water and nutrient addition. Note different scales for both graphs.

increased by watering in autumn, and slightly increased by seed addition in winter. Although soil water content in all quadrats fell below field capacity in winter and received as much additional water as during autumn, soil moisture was not as limiting for recruitment or initial growth as seed availability. However, it is most likely that the increased rainfall in winter resulted in fewer opportunities of soil moisture

being limiting to growth. Thus, overall, the recruitment of exotics was not strongly affected by any of the experimental treatments during winter. This suggests that propagules of exotics are present and that they can recruit well in areas still dominated by perennial grasses. Their recruitment is mainly limited by lack of soil moisture supply rather than strong resource uptake by perennial grasses. The large effect of block

on the results suggests that soil properties are a further important aspect in the recruitment of exotics, possibly due to differences in resource input, and requires further research. In south-eastern Australia invasive exotics, such as annual grasses, generally increase in abundance with soil nutrient availability (Prober *et al.* 2002).

Not only does *Avena* strongly increase in germination, recruitment and growth with soil moisture (Pérez-Fernández *et al.* 2000), but it is also 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 regardless of climate (Young & Evans 1989) annual grasses like *Avena* tend to be adapted to the driest possible conditions rather than to 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* seeds are also unaffected by drying out during germination (Pérez-Fernández *et al.* 2000). Overall, it is thus unlikely that annual grasses decrease significantly less in density than perennial species during periods of drought.

Recruitment of native perennial grasses

Given that suitable moisture and temperature conditions were provided during at least the winter period, perennial grass seeds from both the natural seed bank, if any, and experimental seed bank should have been able to germinate. There are two possible reasons why there was no survival of any perennial grass seedlings. First, recruitment in native grasses may be naturally rarer than in annual grasses. Compared with annual species, perennial grass species are more adapted to long-term survival rather than annual recruitment. In *Austrodanthonia caespitosa* for example, 50% of seedlings survive to between 15 and 30 months, with some plants reaching an age of 18 years (Williams 1970; Williams & Roe 1975). However, *Austrodanthonia* recruitment can occur annually (Williams & Roe 1975). In grasslands near Deniliquin (New South Wales, 400 mm annual rainfall) *Austrodanthonia* can recruit in densities up to 700 seedlings m⁻². Still, few of those seedlings survived the first summer and most overall recruitment was aided by summer rainfall (Williams 1968). In this study, 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 vegetation may have changed the biotic and abiotic environment to such a degree that it was not suitable for perennial grass seedlings any more. Events of a more extreme magnitude, such as

extreme rainfalls combined with pulses of grazing that reduce standing biomass and litter may be required to encourage perennial grass recruitment. In the grasslands near Deniliquin *Austrodanthonia* develops into pure and highly competitive stands only under summer irrigation (Williams 1961).

Without further research neither of these possibilities can be negated or confirmed. The results are consistent with findings from studies in most other temperate grasslands showing that sexual perennial grass recruitment is relatively rare. In Victorian grasslands, in south-eastern Australia the recruitment of native species is rare, especially on unmanaged sites (Morgan 2001). In Californian grasslands, the recruitment of *Nassella pulchra* is strongly limited by low moisture and seed availability, the former 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 good soil moisture (Maze *et al.* 1993), as confirmed by our glasshouse experiment.

Seed predation by ants can limit recruitment in perennial grasses. While viable seed was added to half the quadrats, predation of both annual and perennial grass seeds by ants has been concluded to be 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). We 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 reduce seed presence in the seed bank to levels that result in strong recruitment limitation.

However, the glasshouse results also indicate that even low levels of annual grass biomass 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 remained after fortnightly clipping in the field quadrats could have had a strong negative effect on any perennial grass seedlings that emerged. 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 perennial grasses, which tend to 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 regrew to some extent. Longer continuation of the clipping treatments or the complete removal of exotics may have been required to allow the survival of any perennial grasses that emerged.

CONCLUSIONS

The results suggest that successful recruitment of perennial grasses in unmanaged areas dominated by exotics is either extremely unlikely due to changes in abiotic conditions and/or is dependent on specific rainfall regimes or disturbance events. The extent of recruitment limitation for the native perennial grasses in this system also remains unknown. Soil moisture appears to drive the recruitment of exotics and is likely to be important for the recruitment of native perennial grasses, but their responses to and their effects on soil moisture are very different. The relatively low soil moisture uptake of perennial grasses compared with annual grasses (T. Lenz & J. M. Facelli, unpubl. data, 2003) may leave more resources unused in perennial grass stands than in stands dominated by exotics, resulting in low invasibility of the latter. Invasibility of exotic stands by perennial grass may increase during years with high warm-season rainfall. However, years with high warm-season rainfall are uncommon at this site. In the last 42 years four summer seasons and two autumn seasons had twice the average amount of rainfall and only once did a wet autumn follow a wet summer (Bureau of Meteorology).

The results stand in contrast to recent findings by Seabloom *et al.* (2003), who were able to restore a field site in California with native perennial grasses through more extreme treatments such as 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 resist 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 our study a more extreme disturbance, such as ploughing, heavier seed addition or longer experimental periods may well

have led to the recruitment of perennial grasses in the field. However, unlike in Seabloom *et al.* (2003), our results showed that annual grasses in the South Australian mid-north grassland are able to recruit in stands dominated by perennial grasses in certain conditions and later compete to some degree with perennial grasses (Lenz *et al.* 2003). Species-specific or environmental differences may be responsible for this difference between these similar species groups in quite similar systems. This lends further indirect evidence to the models that suggest invasions 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 propagule availability.

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REFERENCES

- 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. 147–69. Academic Press, New York.
- Bakker J. P. & Berendse F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends Ecol. Evol.* **14**, 63–8.
- Bischoff A. (2002) Dispersal and establishment of floodplain grassland species as limiting factors in restoration. *Biol. Conserv.* **104**, 25–33.
- Buckland S. M., Thompson K., Hodgson J. G. & Grime J. P. (2001) Grassland invasions: effects of manipulations of climate and management. *J. Appl. Ecol.* **38**, 301–9.
- Burke M. J. W. & Grime J. P. (1996) An experimental study of plant community invasibility. *Ecology* **77**, 776–90.
- Capon M. H. & O'Connor T. G. (1990) The predation of perennial grass seeds in Transvaal (South Africa) savanna grasslands. *S. Afr. J. Bot.* **56**, 11–15.
- Davis M. A. & Pelsor M. (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecol. Lett.* **4**, 421–8.
- Davis M. A., Grime J. P. & Thompson K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* **88**, 528–34.
- Dukes J. S. (2001) Biodiversity and invasibility in grassland microcosms. *Oecologia* **126**, 563–8.
- Foster B. L. (1999) Establishment, competition and the distribution of native grasses among Michigan old-fields. *J. Ecol.* **87**, 476–89.
- Foster B. L. (2002) Competition, facilitation, and the distribution of *Schizachyrium scoparium* along a topographic productivity gradient. *Écoscience* **9**, 355–63.

- Foster B. L. & Gross K. L. (1998) Species richness in a successional grassland: Effects of nitrogen enrichment and plant litter. *Ecology* **79**, 2593–602.
- 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**, 300–7.
- Fowler N. L. (1988) What is a safe site?: Neighbor, litter, germination date, and patch effects. *Ecology* **69**, 947–61.
- 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.
- Gurevitch J. (1986) Competition and the local distribution of the grass *Stipa neomexicana*. *Ecology* **67**, 46–57.
- Haase P., Pugnaire F. I. & Incoll L. D. (1995) Seed production and dispersal in the semi-arid tussock grass *Stipa tenacissima* L. during mast. *J. Arid Environ.* **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**, 518–26.
- 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**, 530–4.
- Heady H. F., Bartolome J. W., Pitt M. D., Saville G. D. & Stroud M. C. (1992) California prairie. In: *Natural Grasslands: Introduction and Western Hemisphere* (ed. R. T. Coupland) pp. 313–35. Elsevier, Amsterdam.
- Hobbs R. J. & Atkins L. (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the western Australian wheatbelt. *Aust. J. Ecol.* **13**, 171–80.
- Hobbs R. J. & Atkins L. (1991) Interactions between annuals and woody perennials in a Western Australian nature reserve. *J. Veg. Sci.* **2**, 643–54.
- Hobbs R. J. & Mooney H. A. (1991) Effects of rainfall variability and gopher disturbance on serpentine annual grassland dynamics. *Ecology* **72**, 59–68.
- 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**, 478–91.
- 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. *Aust. J. Bot.* **47**, 221–35.
- Hyde M. K. (1995) *The Temperate Grasslands of South Australia: Their Composition and Conservation Status*. World Wide Fund for Nature Australia, Sydney.
- 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 Oecol.* **7**, 191–212.
- Jain S. K. (1982) Variation and adaptive role of seed dormancy in some annual grassland species. *Bot. Gaz.* **143**, 101–6.
- 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. *Am. J. Bot.* **67**, 1342–6.
- Jessop J. P. & Toelken H. R., eds (1986) *Flora of South Australia*. South Australian Government, Adelaide.
- Kalamees R. & Zobel M. (1998) Soil seed bank composition in different successional stages of a species rich wooded meadow in Laelatu, Western Estonia. *Acta Oecol.* **19**, 175–80.
- Kalamees R. & Zobel M. (2002) The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology* **83**, 1017–25.
- 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.
- Kolar C. S. & Lodge D. M. (2001) Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.* **16**, 199–204.
- 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 Ecol.* **28**, 23–32.
- 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. *J. Arid Environ.* **53**, 467–77.
- Maze K. M., Koen T. B. & Watt L. A. (1993) Factors influencing the germination of six perennial grasses of central New South Wales. *Aust. J. Bot.* **41**, 79–90.
- 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**, 520–31.
- Morgan J. W. (1998a) Importance of canopy gaps for recruitment of some forbs in *Themeda triandra*-dominated grasslands in south-eastern Australia. *Aust. J. Bot.* **46**, 609–27.
- Morgan J. W. (1998b) Patterns of invasion of an urban remnant of a species-rich grassland in southeastern Australia by non-native plant species. *J. Veg. Sci.* **9**, 181–90.
- Morgan J. W. (2001) Seedling recruitment patterns over 4 years in an Australian perennial grassland community with different fire histories. *J. Ecol.* **89**, 908–19.
- 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**, 185–95.
- O'Connor T. G. (1991) Local extinction in perennial grasslands: a life-history approach. *Am. Nat.* **137**, 753–73.
- Paschke M. W., McLendon T. & Redente E. F. (2000) Nitrogen availability and old-field succession in a shortgrass steppe. *Ecosyst.* **3**, 144–58.
- Peco B., Ortega M. & Levassor C. (1998) Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model. *J. Veg. Sci.* **9**, 815–28.
- 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 Oecol.* **21**, 323–36.
- 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. *Aust. J. Bot.* **50**, 699–712.
- 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. *J. Appl. Ecol.* **40**, 65–77.
- Rejmánek M. (1989) Invasibility of plant communities. In: *Biological Invasions: a Global Perspective* (eds J. A. Drake, H. A. Mooney, F. Di Castri et al.), pp. 369–88. John Wiley and Sons, New York.
- 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**, 230–5.
- Robertson M. A. (1998) *A Biological Survey of Grasslands and Grassy Woodlands of the Lofty Block Bioregion South Australia 1995–96*. Department of Environment, Heritage and Aboriginal Affairs, Adelaide.
- 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. *Proc. Nat. Acad. Sci. USA* **100**, 13384–9.
- 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. *J. Ecol.* **89**, 1054–60.
- Tilman G. D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81–92.
- Troumbis A. Y., Galanidis A. & Kokkoris G. D. (2002) Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos* **98**, 239–50.
- Underwood A. J. (1997) *Experiments in Ecology*. Cambridge University Press, Cambridge.
- Van der Putten W. H., Mortimer S. R., Hedlund K. *et al.* (2000) Plant species diversity as a driver of early succession in abandoned fields: a multi-site approach. *Oecologia* **124**, 91–9.
- 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*. Mediterranean shrublands. *J. Ecol.* **88**, 479–91.
- Warren J., Christal A. & Wilson F. (2002) Effects of sowing and management on vegetation succession during grassland habitat restoration. *Agric. Ecosyst. Environ.* **93**, 393–402.
- Williams O. B. (1961) Studies in the ecology of the riverine plain. III. Phenology of a *Danthonia caespitosa* Gaudich. grassland. *Aust. J. Agric. Res.* **12**, 247–59.
- Williams O. B. (1968) Studies in the ecology of the riverine plain. IV. basal area and density changes of *Danthonia caespitosa* Gaudich. in a natural pasture grazed by sheep. *Aust. J. Bot.* **16**, 565–78.
- Williams O. B. (1970) Population dynamics of two perennial grasses in Australian semi-arid grassland. *J. Ecol.* **58**, 869–75.
- Williams O. B. & Roe R. (1975) Management of arid grasslands for sheep: plant demography of six grasses in relation to climate and grazing. *Proc. Ecol. Soc. Aust.* **9**, 143–56.
- 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.
- 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**, 3274–82.