COMMUNITY ECOLOGY - ORIGINAL PAPER

# Early emergence and resource availability can competitively favour natives over a functionally similar invader

Jennifer Firn · Andrew S. MacDougall ·
Susanne Schmidt · Yvonne M. Buckley

**Abstract** Invasive plant species can form dense populations across large tracts of land. Based on these observations of dominance, invaders are often described as competitively superior, despite little direct evidence of competitive interactions with natives. The few studies that have measured competitive interactions have tended to compare an invader to natives that are unlikely to be strong competitors because they are functionally different. In this study, we measured competitive interactions among an invasive grass and two Australian native grasses that are functionally similar and widely distributed. We conducted a pair-wise glasshouse experiment, where we manipulated both biotic factors (timing of establishment, neighbour identity and density) and abiotic factors (nutrients and timing of water supply). We found that the invader significantly suppressed the performance of the natives; but its suppression ability was contingent on resource levels, with pulsed water/low nutrients or continuous watering reducing its competitive effects. The native grasses were able to suppress the performance of the invader when given a 3-week head-start, suggesting the invader may be incapable of establishing unless it emerges first, including in its own understorey. These findings provide insight for restoration, as the competitive effect of a functionally similar invader may be reduced by altering abiotic and biotic conditions in favour of natives.

**Keywords** Competitive effect and response · Facilitation and suppression · Pulsed water regime · Inter- and intraspecific competition · Nutrient availability

Communicated by Scott Collins.

J. Firn (✉) · Y. M. Buckley
CSIRO Sustainable Ecosystems, 306 Carmody Rd,
St Lucia, QLD 4067, Australia
e-mail: jennifer.firn@csiro.au

A. S. MacDougall
Department of Integrative Biology, University of Guelph,
Guelph, ON N1G 2W1, Canada

S. Schmidt · Y. M. Buckley
School of Biological Sciences, The University of Queensland,
Brisbane, QLD 4072, Australia

## Introduction

Invasive plant species can be widely distributed and highly abundant in their introduced range. This observed dominance has been used incorrectly as anecdotal evidence for their competitive superiority (Levine et al. 2003). Mechanisms of community assembly other than competition can interact to explain the dominance of one species over others including environmental filters, propagule pressure and multi-trophic level interactions (e.g. herbivory and parasitism) (Chapin et al. 1996; Chesson and Kuang 2008; MacDougall et al. 2009; McNaughton and Wolf 1970). These mechanisms can alter abiotic and biotic conditions in a manner that also alters competitive interactions between plant species. This makes the competitive superiority of an invader difficult to declare based on observational data alone and also difficult to measure in the field because of confounding factors. Despite these difficulties, measuring competitive interactions between an invader and more desirable native species can provide key insights for restoration efforts, including the conditions needed to provide a competitive advantage to native species.

Glasshouse and field studies comparing the competitive ability of invaders to natives have generally found invasive species to be superior at acquiring limiting resources (Vila and Weiner 2004). These studies, however, tend to examine invaders and natives that are functionally dissimilar in terms of life history, life-form, size and taxonomic relatedness (MacDougall et al. 2009; Vila and Weiner 2004). However, based on the predictions of classical niche theory, and more specifically the concept of limiting similarity, species that differ functionally might never compete for similar resources.

The limiting similarity concept suggests that functionally similar species are more likely to compete and, because of competitive exclusion, may not co-exist (Abrams 1983; MacArthur and Levins 1967). Several field and mesocosm studies have shown that native plant communities can resist invasion by a functionally similar species (Dukes 2001; Emery 2007; Fargione et al. 2003; Turnbull et al. 2005). If an invader and a native are functionally similar, the invader may lack the competitive advantage needed to increase its abundance from rarity, unless other mechanisms, such as disturbance, facilitate an opportunity for establishment (Davis et al. 2000). Recommendations for restoring invaded sites with functionally similar natives have been made based on this concept (Funk et al. 2008). However, there is extensive scientific evidence that the competitive ability of a plant species will vary depending on resource availability, and the identity and density of the neighbour species it is competing with (Goldberg and Landa 1991; Goldberg 1996; Goldberg and Novoplansky 1997; Keddy 2001; Novoplansky and Goldberg 2001). This evidence suggests that individual species have different competitive abilities and that these abilities vary depending on the abiotic and biotic conditions. Therefore, selecting functionally similar natives to restore ecosystems dominated by an invader requires a consideration of the characteristics of the individual species, as well as a consideration for how each species performs when competing for resources at different levels of availability.

In this study, we measured competitive interactions between a widespread invasive grass, *Eragrostis curvula* (African lovegrass, hereafter Lovegrass) and two widespread Australian native grasses, *Bothriochloa decipiens* (hereafter Pitted bluegrass), and *Themeda triandra* (hereafter Kangaroo grass). Given the predictions of limiting similarity and its supposed connection to invasion success (Rout and Callaway 2009; Strauss et al. 2006), we seek to test the competitive interactions among these functionally similar grasses, and whether competitive outcomes are contingent on abiotic and biotic conditions. These grasses share many similar characteristics in terms of their life-history, photosynthetic pathway, and morphological characteristics (Table 1). Lovegrass has invaded in climatic regions where these native species also grow and in some cases used to dominate. However, despite Lovegrass having been described as a highly competitive grass species, supporting experimental evidence is equivocal (Firn 2009; Firn et al. 2010). We established a pair-wise competition experiment where we varied resource levels (water and nutrients), neighbour densities, and establishment time (concurrent or delayed sowing of target individuals). We then use the results of this experiment to address the following questions:

1. Is the functionally similar invader able to suppress the performance of the native grasses and how do these interactions vary depending on the abiotic and biotic conditions?
2. Are the native grasses able to suppress the performance of the functionally similar invader and how do these interactions vary depending on the abiotic and biotic conditions?

**Table 1** General characteristics of the invasive grass species Lovegrass *Eragrostis curvula* in comparison to the two native grasses, *Bothriochloa decipiens* and *Themeda australis*, included in the study

| Characteristics | *Eragrostis curvula* African lovegrass Invasive | *Bothriochloa decipiens* Pitted bluegrass Native | *Themeda australis* Kangaroo grass Native |
|---|---|---|---|
| Growth habit | Bunch grass perennial[a] | Bunch grass perennial[a] | Bunch grass perennial[a] |
| Photosynthetic pathway | $C_4$[b] | $C_4$[b] | $C_4$[b] |
| Height (cm) | Up to 120[b] | Up to 100[c] | Up to 200[c] |
| Growth season | Summer[a] | Summer[c] | Summer[c] |
| Flowering time | Spring to autumn[b] | Spring to summer[b] | Summer to autumn[d] |
| Response to fertility | Increased growth[e] | Increased growth[c] | Decreased growth[d] |
| Palatability to livestock | Low[e] | Low to moderate[c] | Moderate to high[d] |
| Native continental distribution | Africa[c] | Australasia[c] | Africa, Asia, Australasia and Pacific[c] |

Pitted bluegrass and Kangaroo grass are generally replaced by Lovegrass in the Millmerran region of Queensland Australia

[a] Mitchell (2002), [b] Anderson (2003), [c] Sharp and Simon (2002), [d] Henry et al. (1995), [e] Voight et al. (1970)

3.  Are there a set of abiotic and biotic conditions that could give the native grasses a competitive advantage?

## Methods

We conducted a 24-week competition trial from December 2007 to May 2008 in a temperature-controlled (29°C day, 18°C night) glasshouse at the University of Queensland, Brisbane. The temperature regime we used emulated the average summer temperatures where Lovegrass has invaded grasslands within the Millmerran region of Queensland, Australia. The duration of the experiment matched the 6-month summer growing period of the region. Generally two-thirds of rainfall occurs during the summer from October to April, averaging 600 mm/year, but is highly variable and the region is prone to drought (Biggs et al. 1999). In the 2006 growing season (7-month period), the total rainfall was 215 mm (growing season monthly average of $38 \pm 11$ mm SE) versus 475 mm in 2007 (growing season monthly average of $79 \pm 11$ mm SE). All seeds were collected in the summer of 2006 from this region.

Experimental design

The experiment had a split-plot additive design, where one target individual of each species was sown in the centre of a pot with 0, 2 or 6 neighbour individuals sown around either the same species (intraspecific interactions) or another species (interspecific interactions). All pots were over-sown and then weeded to the intended densities. The pots (150 mm in diameter PVC pipe) were 1.2 m high to allow unrestricted root growth and development, with a PVC cap fitted to the bottom and several drilled holes to ensure water drainage. We used a low nutrient soil media of composted pine bark fines (70%), peat (20%), sand (10%), dolomite (3 kg/m³), lime (1.5 kg/m³), FeSO₄ (1 kg/m³), and urea (0.75 kg/m).

Several treatments were applied in all combinations: (1) establishment time: concurrent and delayed sowing of target individuals; (2) water: pulsed and continuous (daily) supply but the same total amount; and (3) nutrients: high and low. In the concurrent treatment, we sowed the target individuals at the same time as the neighbours to mimic germination post-disturbance. In this treatment, all competition pairs (target species plus neighbour species) and neighbour densities were established except interspecific interactions between the natives (total of 17 competition pairs; see Electronic Supplementary Material, ESM, Table 1 for details). In the delayed treatment, we sowed the neighbour communities first and 3 weeks later sowed the target individuals. In this treatment, all competition pairs

were included and neighbour densities, except intra- and interspecific interactions between the natives (total of 13 competition pairs; see ESM, Table 1 for details). Because of limited space in the glasshouse the effect of delayed establishment time on intraspecific interactions with the native grasses was not investigated.

The water treatments were applied with an automated drip irrigation system, as either a daily supply of 5 ml of water (hereafter called continuous supply), or a pulsed supply of 20 ml of water added every 4 days—both treatments totalled 20 ml every 4 days. The nutrient treatments were either low (no added nutrients) or high [N–P–K (N 21.6%, P 1.1%, K 4.1%) added every 2 weeks]. A chemical injector pump (MixRite Proportional Injector Pump), fitted to the automated irrigation system, was used to mix and apply the liquid fertilizer to the pots (1% active ingredient per 5 ml of water per pot).

After sowing, the pots were arranged on six benches (i.e. six blocks). Water treatments (continuous or pulsed) were implemented at the block level. Within each block, there was one replicate of the establishment time and nutrient treatments. In total, this experiment was made up of 360 pots including: two water treatments × [30 competition pairs (17 concurrent + 13 delayed) × two nutrient treatments] × three replicates. Pots were randomized within each block weekly to account for the possibility of variable light levels within the glasshouse. After 24 weeks, we harvested all aboveground biomass from each pot keeping targets and neighbours separate. Samples were then dried for 48 h at 70°C and weighed to the nearest 0.1 g. We also measured the height of each target individual every 6 weeks or four times over the course of the 24-week experiment. We measured height as a surrogate for plant performance to capture the changing growth dynamics over time. We then calculated the relative change in height between each measurement time and found the average relative change in height.

To measure the intensity of competition between species under different environmental conditions, we used the logarithm of the response ratio (Goldberg et al. 1999; Weigelt and Jolliffe 2003):

$$\ln RR = \ln \left( \frac{\text{mass of target species } (i) \text{ with neigbour species } (k)}{\text{mass of target species } (i) \text{ without neighbours}} \right).$$

For each treatment, this index standardises the biomass of the target species grown without neighbours in comparison to the growth of the target with neighbours (Goldberg et al. 1999). The log ratio is affected equally by changes to the numerator or denominator (Weigelt and Jolliffe 2003) and does not set an upper limit on the intensity of competition. A negative value for ln RR

indicates a competitive effect or suppression of the target by the neighbours, while a positive value indicates a competitive response by the target or facilitation by the neighbours.

Data analysis

The results were analysed using linear mixed effects models (hereafter LMEM) to account for problems of non-independence and pseudo-replication that characterise spatially nested split-plot data (Crawley 2002). In the model, we treated block as a random effect to account for spatial variation, because the watering treatments were set up on different benches in the glasshouse. This allowed us to model the covariance structure introduced by grouping the data (Buckley et al. 2003; McMahon and Diez 2007). We created separate LMEMs for interspecific and intra-specific competition because intraspecific interactions for the native grasses were not included in the delayed estab-lishment treatment. In the interspecific competition LMEM, the fixed effects included competition pairs, den-sity and the treatments applied: water, nutrients and establishment time; while in the intraspecific competition LMEM the fixed effects included competition pairs, den-sity, water treatment and nutrient treatment. We also used LMEMs to analyse average height differences and the average relative change in height. In both cases, the ran-dom effects were again block and the fixed effects were water, nutrients, species and survey time.

We then found the best fit model by removing the fixed explanatory variables one at a time from the complete model and then comparing the simpler model to the more complex model using a likelihood ratio test and maximum likelihood. We tested the adequacy of random effects using likelihood ratio tests and restricted maximum likelihood (Ives and Zhu 2006; Pinheiro and Bates 2000). We then used diagnostic plots to check model assumptions (Pinheiro and Bates 2000). There was no evidence of correlation of observations within groups in any of the models. We used an ANOVA to assess the significance of fixed effects in the best fit model (Pinheiro and Bates 2000). All analyses were conducted using R 2.8.1 (R Foundation for Statistical Computing).

## Results

### Effect of abiotic treatments on the growth of the grasses without competition

The heights of the target individuals grown without neighbours across water and nutrient treatments show how these species grow in the absence of competition (Fig. 1). We first measured heights 6 weeks after the pair-wise combinations were sown, and then every 6 weeks for a total of 24 weeks. We found that species, nutrients and time had a significant three-way interacting effect on height ($F_{2,122} = 4.11$, $P < 0.02$; ESM, Table 2). The average height of all three grass species was reduced in the low nutrient relative to the high nutrient treatment, but this reduction was most pronounced for Kangaroo grass in the later measurement times (Fig. 1). Water, nutrients and



Fig. 1 Average height values for Lovegrass, Kangaroo grass and Pitted bluegrass targets grown without neighbours over time. Time *1* 6 weeks, *2* 12 weeks, *3* 18 weeks, *4* 24 weeks
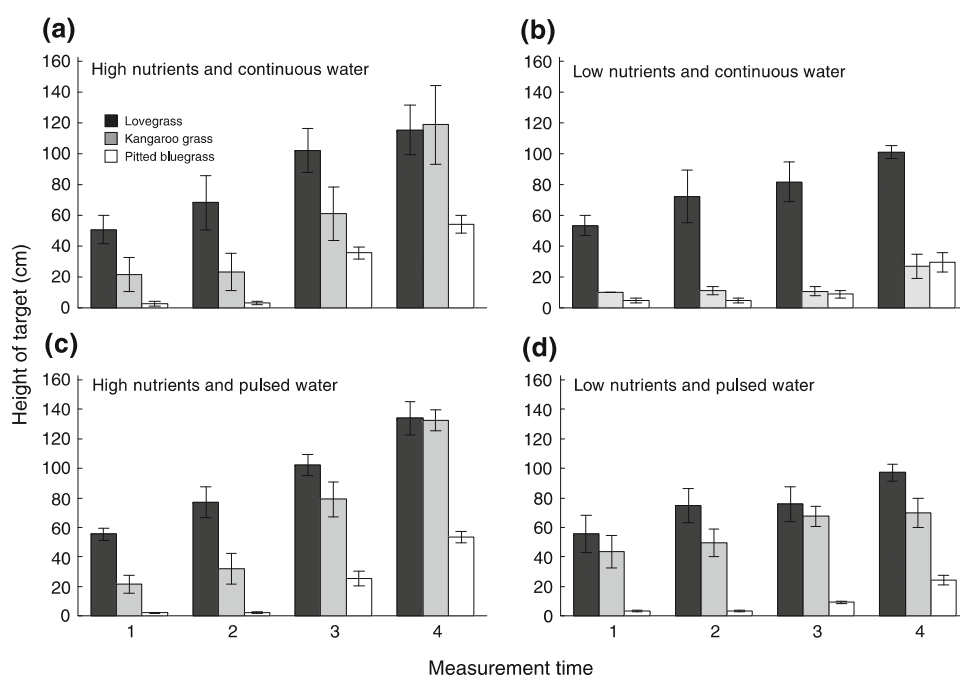
**Table 2** The average relative change in height (%) over the 24 weeks of the experiment (±SE)

| Treatment combination | Lovegrass: invasive | Kangaroo grass: native | Pitted bluegrass: native |
|---|---|---|---|
| High nutrients and continuous water | 31.67 (9.71) | 112.5 (36.7) | 354 (158) |
| Low nutrients and continuous water | 26.63 (7.90) | 42.6 (19.2) | 124.5 (42.7) |
| High nutrients and pulsed water | 36.18 (8.08) | 106.8 (35.9) | 345 (146) |
| Low nutrients and pulsed water | 21.3 (10.3) | 25.14 (9.59) | 71.5 (45.9) |

These values are based on the height measurements taken of each species grown without neighbours under the different treatment combinations. These values were calculated by averaging the relative change in height between each 6-week measurement time

**Table 3** Results from two ANOVAs conducted to assess the significance of the fixed effects on the simplest linear mixed effects model for the competition index values (ln RR), one ANOVA was conducted with interspecific competition pairs and one with intraspecific competition pairs, which is referred to as species in the table and text

| Fixed effect | Interaction type | Num $df$ | Den $df$ | $F$ value | $P$ value |
|---|---|---|---|---|---|
| Water | Interspecific | 1 | 4 | 8.24 | <0.05 |
| Nutrients | Interspecific | 1 | 168 | 6.07 | <0.015 |
| Competition pairs | Interspecific | 3 | 168 | 10.78 | <0.0001 |
| Timing | Interspecific | 1 | 168 | 258.12 | <0.0001 |
| Water: nutrients | Interspecific | 1 | 168 | 0.32 | <0.60 |
| Nutrients: competition pairs | Interspecific | 3 | 168 | 8.78 | <0.0001 |
| Water: competition pairs | Interspecific | 3 | 168 | 17.56 | <0.0001 |
| Competition pairs: timing | Interspecific | 3 | 168 | 40.36 | <0.0001 |
| Water: nutrients: competition pairs | Interspecific | 3 | 168 | 4.02 | <0.009 |
| Water | Intraspecific | 1 | 4 | 20.34 | <0.015 |
| Species | Intraspecific | 2 | 67 | 5.01 | <0.01 |
| Density | Intraspecific | 1 | 67 | 9.84 | <0.003 |
| Water: species | Intraspecific | 2 | 67 | 32.62 | <0.0001 |

Timing refers to the establishment treatment (concurrent or delayed sowing of the target)

*Num df* numerator degrees of freedom, *Den df* denominator degrees of freedom

species also had a significant three-way interacting effect on height ($F_{2,122} = 6.64$, $P < 0.002$; ESM, Table 2). The average height of Kangaroo grass was reduced in the low nutrient/continuous water treatments relative to all high nutrient treatments, while the average height of Pitted bluegrass and Lovegrass were reduced in the low nutrient/pulsed water treatment relative to all high nutrient treatments (Fig. 1). We also calculated the average emergence time using 60 seeds per species. We found Lovegrass had the earliest emergence time at 6.8 days (±1.1 SE), followed by Pitted bluegrass at 7.8 (±2.3 SE) days and Kangaroo grass at 9.3 days (±1.4 SE), although these mean values were not significantly different (Turkey's test). At time 1, Lovegrass was taller than the other species except under the low nutrient and pulsed water, where Kangaroo grass had a similar height.

We found nutrient treatments and species ($F_{2,97} = 3.69$, $P < 0.03$) had a significant interacting effect on the average relative change in height. Lovegrass had the most consistent relative increase in height across all treatments (Table 2). Both Kangaroo grass and Pitted bluegrass more than doubled

their average rate of increase in height in the high nutrient treatment in comparison to the low nutrient treatment, although these averages were highly variable (Table 2). In the high nutrient treatment by 24 weeks, Kangaroo grass grew to a similar height to Lovegrass (Fig. 1a, c).

### Effect of abiotic and biotic treatments on competitive interactions between the grasses

We found a significant three-way interacting effect of water, nutrients and competition pairs on the interspecific suppression of target plants ($F_{3,168} = 4.02$, $P < 0.009$; Table 3). Lovegrass suppressed the performance of both native species under most treatment combinations (Fig. 2). The exceptions occurred when Pitted bluegrass was grown with low nutrients and pulsed watering (Fig. 2a, b) and when Kangaroo grass was grown with continuous watering (Fig. 2c, d). Density (number of neighbours) had no significant effect on interspecific competition (Table 3).

Competition pairs and establishment time ($F_{3,168} = 40.36$, $P < 0.0001$; Table 3) had a significant interacting

**Fig. 2** Interspecific competitive effect of Lovegrass neighbours on target individual of **a**, **b** Pitted bluegrass and **c**, **d** Kangaroo grass under different water and nutrient treatments for the (**a**, **c**) concurrent establishment time and (**b**, **d**) delayed establishment time. Values are mean ± SE, $n = 3$
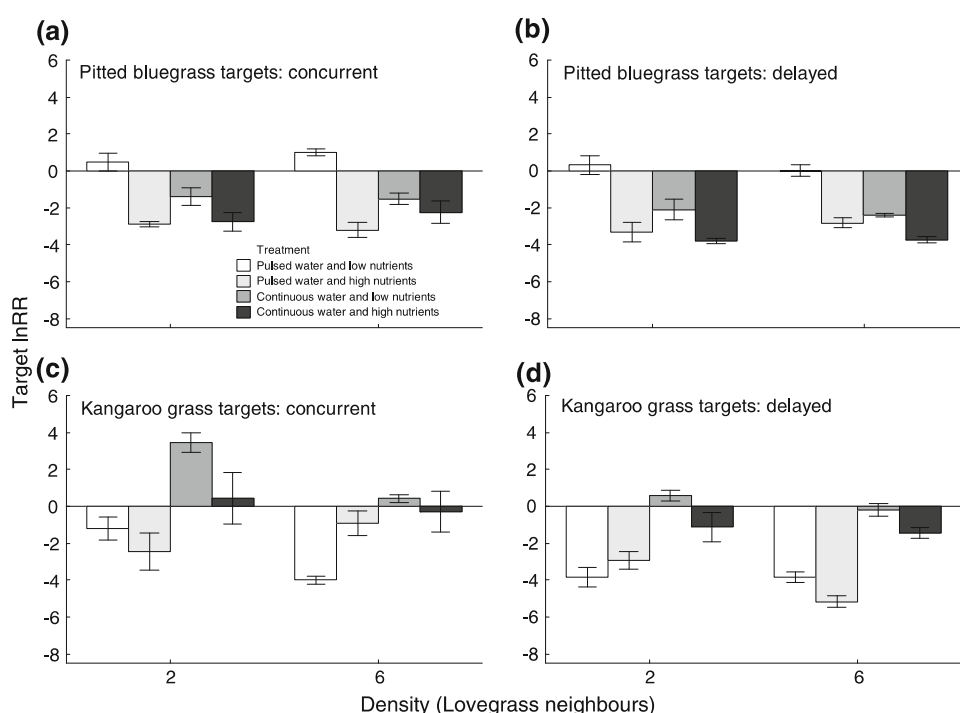


effect on the performance of the targets. When Lovegrass targets were sown at the same time as the native grass neighbours there was little effect on performance (Fig. 3a, c), but when grown amongst native grasses that were sown 3 weeks ahead of time, the performance of Lovegrass targets was suppressed (Fig. 3b, d). These outcomes did not vary with resource levels or neighbour density.

With intraspecific competition and concurrent establishment, we found that water and species had a significant interacting effect on the performance of the targets ($F_{2, 67} = 32.62$, $P < 0.0001$; Table 3; Figs 2e, f, and 3). Lovegrass targets responded differently to intraspecific competition than competition with natives, such that Lovegrass targets were suppressed when sown at the same time as Lovegrass neighbours (Fig. 3e). The performance of Kangaroo grass was reduced by intraspecific competition when watering was pulsed, but was facilitated with continuous watering (Fig. 4b). A similar trend was observed for Kangaroo grass when grown with Lovegrass neighbours (Fig. 2c). We verified this trend by conducting a LMEM to compare just the biomass of Kangaroo targets when grown with Lovegrass and Kangaroo grass neighbours. The only factor that had a significant effect was the water treatment ($F_{1,97} = 31.60$, $P < 0.0050$). Pitted bluegrass showed no significant effect of intraspecific competition across treatments, except where pulsed watering facilitated the performance of Pitted bluegrass targets (Fig. 4a). Lovegrass was significantly self-limited when the

sowing of targets was delayed, regardless of the water and nutrient treatments and neighbour density (Fig. 3f).

## Discussion

Functionally similar plant species are more likely to compete for the same resources (Abrams 1983; MacArthur and Levins 1967), but the victor can vary depending on the abiotic and biotic conditions (Goldberg 1996; Grime 2001; Tilman 1988). We found strong evidence that abiotic variability can affect the performance of the functionally similar invader and native species when grown with and without competition. Without competition, heights of all species were reduced in the low nutrient treatment. Lovegrass showed the most consistent relative increase in height across the different treatment combinations, while the relative increase in heights of the native grasses were the most responsive to the nutrient treatment. We found that the invader suppressed the performance of the natives, but this competitive effect was contingent on resource availability (water timing and nutrient quantity), which points to the importance of environmental drivers on competitive outcomes. We also found that the natives suppressed the performance of the invader, but this competitive effect was contingent on establishment time, which points to the importance of attributes that favour the ability to colonise rapidly (e.g. following disturbance and/or because of niche differences). Overall, the key finding for restoration was

**Fig. 3** Competitive response (tolerance) of Lovegrass target individuals to neighbours of **a, b** Pitted bluegrass, **c, d** Kanagroo grass and **e,f** Lovegrass under different water and nutrient treatments. **a, c, e** show results for concurrent establishment time and **b, d, e** for the delayed establishment time. Values mean ± SE, *n* = 3
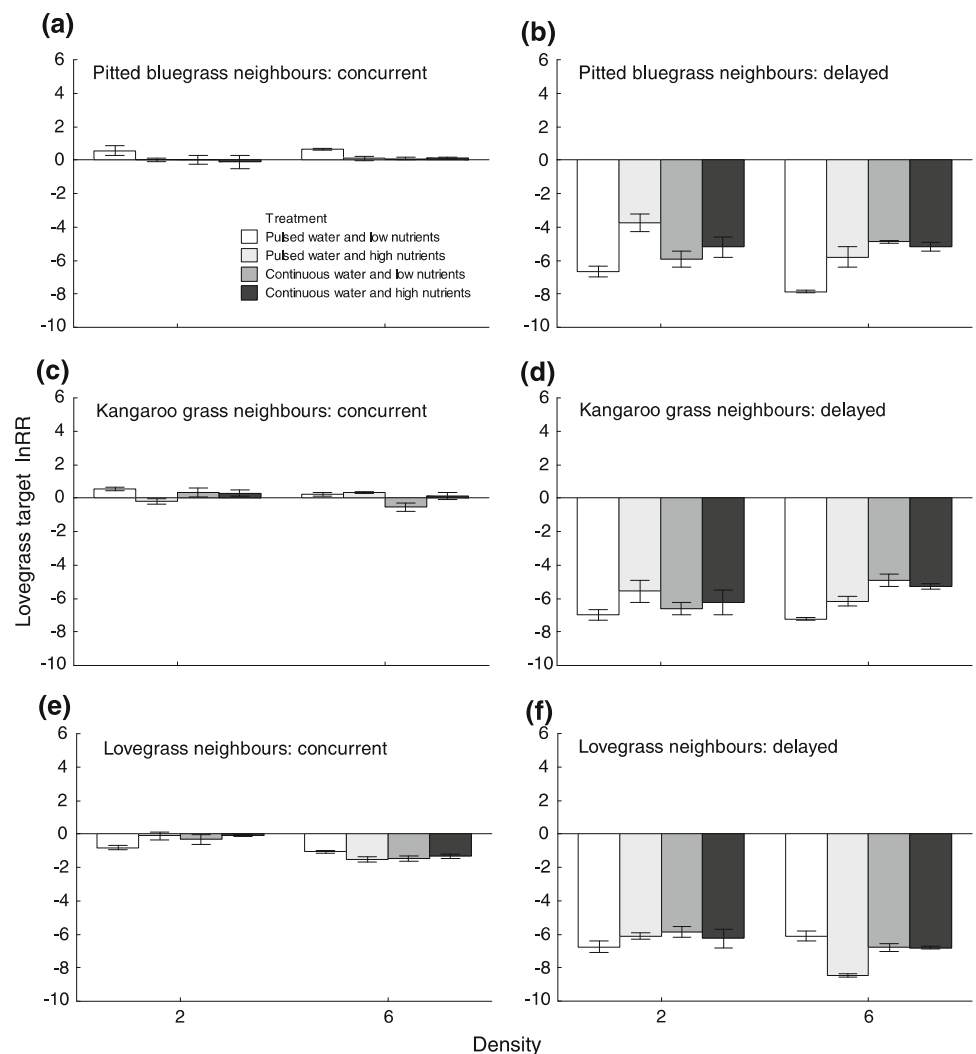


that the invader was not competitively superior to the native grasses across all the abiotic and biotic conditions.

## Does the functionally similar invader suppress the growth of the native grasses?

Lovegrass demonstrated characteristics typical of many suppression-based competitors, including rapid post-germination growth rates (Goldberg and Landa 1991) and significant intraspecific suppression, to the degree that Lovegrass appears incapable of recruiting from seed in its own understorey (Goldberg and Landa 1991; Grime 2001; MacDougall and Turkington 2004).

Lovegrass did not, however, suppress the growth of the native grasses under all water and nutrient treatments. The performance of Pitted bluegrass was facilitated when grown with Lovegrass neighbours under low nutrients and pulsed water supply, whereas the performance of Kangaroo grass was facilitated when grown with Lovegrass neighbours under continuous water supply. This result indicates

that the timing of water supply influences the competitive effect of the invader on the natives. This trend did not vary between the concurrent and delayed sowing treatments, suggesting the potential for the native grasses to recruit amongst previously emerged Lovegrass plants when environmental conditions are favourable.

Other studies have shown that resource availability can affect competitive interactions (Jankju-Borzelabad and Griffiths 2006; Novoplansky and Goldberg 2001). Novoplansky and Goldberg (2001) found that fast-growing competitive dominants from productive regions, were better able to utilise frequent pulses of resources, whereas conservative growers from less productive regions were more efficient at capturing infrequent pulses. Pulsed resources have also been found to affect competitive interactions between juvenile and adult individuals of the same species (Jankju-Borzelabad and Griffiths 2006). In a study by Jankju-Borzelabad and Griffiths (2006), adult individuals of a desert plant, *Panicum antidotale*, had the highest $^{15}N$ uptake under a continuous supply of water and

**(a)**



**(b)**
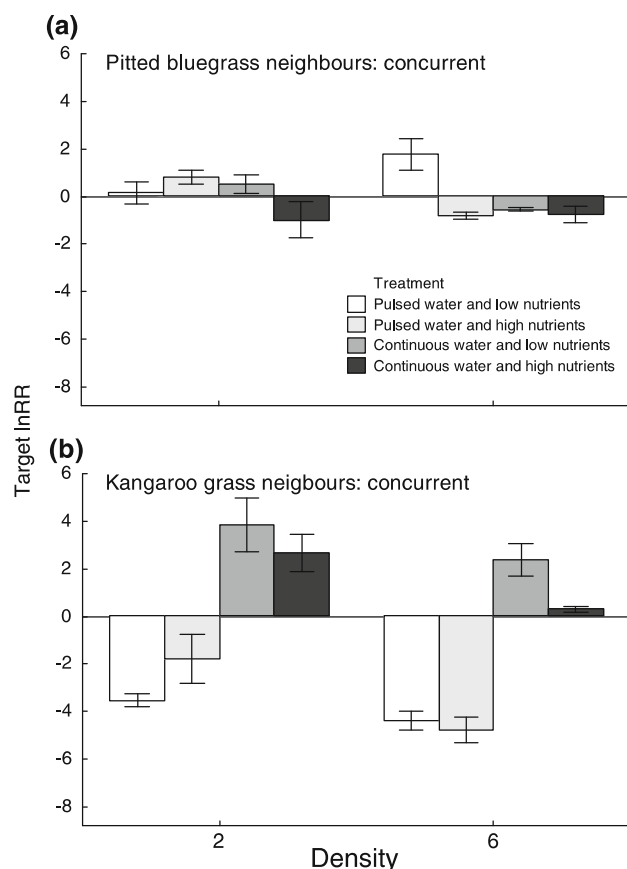


**Fig. 4** Intraspecific effects of **a** Pitted bluegrass on target individuals of the same species under all water and nutrient treatments when established concurrently and **b** Kangaroo grass. lnRR values mean ± SE, $n = 3$

nutrients, reflecting an ability to efficiently utilise resources when consistently available, e.g. accessing deep stores of water and nutrients within the soil profile. Juveniles had the highest $^{15}$N uptake when water and nutrients were pulsed, reflecting an ability to use recharge resources efficiently (Jankju-Borzelabad and Griffiths 2006). These findings suggest that size asymmetries may also affect the response of individuals to resource timing and competition.

The competitive responses shown by the native grasses to Lovegrass may reflect adaptations by the different species to temporal rainfall patterns when competing for resources. Sher et al. (2004) found evidence for local adaptations to intra-seasonal temporal variations in resources when comparing the growth and survival of Mediterranean and desert congeneric pairs. Kangaroo grass is one of the most widespread grasses within Australia (Sharp and Simon 2002). It is also a widespread species across Africa. On both continents, its natural distribution ranges from high to low rainfall, summer to winter rainfall regions and sand to clay edaphic conditions (Bayer 1955; Sharp and Simon 2002). Its widespread distribution and our findings suggest a generalist approach to

resource use in that this species thrives when moisture is readily available but is not as effective at foraging when water availability is limited and subjected to interspecific competition (Bazzaz 1996; Grime 2001). Pitted bluegrass has a narrower distribution in the summer rainfall regions of New Eastern Australia and some parts of Asia (Sharp and Simon 2002; Tothill and Hacker 1993). The narrower range of Pitted bluegrass, its more conservative growth characteristics after emergence, and its ability to tolerate competition under pulsed water availability may favour a competitive advantage in areas prone to periodic drought.

**Do the native grasses suppress the growth of the functionally similar invader?**

The performance of Lovegrass was not suppressed by native grass neighbours when sown concurrently. The concurrent establishment time mimicked situations where a species is able to colonise earlier or at the same time as another, because of post-disturbance conditions and niche differences. In this case, the native grass neighbours had little or no effect on the growth of Lovegrass, regardless of the water and nutrient treatments and the density of the neighbours. However, when the establishment of Lovegrass was delayed even for a short period (21 days), its growth was significantly inhibited by the native grass neighbours, suggesting asymmetrical competition for light (Hautier et al. 2009). This result indicates that Lovegrass was competitively affected by previously emerged neighbours and suggests mechanisms that allow its seed to colonise early are critical for its persistence.

These results provide insight into how invasion by Lovegrass occurs in native grasslands. Competition appears to play a mechanistic role in the dominance of Lovegrass, but is likely not the sole driver given its reduced performance when competing with more advanced neighbours. Although we did not measure the impacts of disturbance on coexistence, or how it affects their interactions, we found evidence that the native grasses were capable of suppressing Lovegrass under all resource conditions with as little as a 3-week head-start. This appears to be supported empirically, as the distribution of Lovegrass within Australia and in its native range is associated with repeated disturbance from roadside and railway verges, as well as multi-trophic interactions, i.e. selective grazing by ungulates (ungulates are a relatively recent introduction into Australian landscapes where previously only macropods existed) (Campbell 1983; Firn 2009; Parsons and Cuthbertson 1992).

**Conclusion, can native grasses win?**

Generalisations on how to alter the competitive hierarchy of species in natural systems based on results from a controlled

glasshouse study are difficult (Freckleton and Watkinson 2000; Gibson et al. 1999). Accordingly, the results of pairwise competition experiments have been criticised when used to predict community assembly because only the effects and responses of individual species can be measured not the resultant species composition and abundance, which may be explained by the interaction of other mechanisms (Aarssen and Epp 1990; Gibson et al. 1999).

In invasion ecology in general, and in our study specifically, the final result of community assembly is known—the invader is dominant. In this case, the aim is not to predict community composition but to unravel the possible mechanisms that explain this outcome. For this reason, pairwise competition experiments can provide invaluable insight concerning the general competitive ability of an invader when designed and analysed in consideration of the abiotic and biotic conditions that are realistically possible in the field (Aarssen and Epp 1990; Cousens 2000; Freckleton and Watkinson 2000).

Based on our results, protecting native grasslands from frequent disturbance could aid in resisting the spread of this invasive grass species. With only a 3-week head-start the native grasses suppressed the growth of Lovegrass, regardless of the treatment combinations. A similar finding and recommendation was made from a pairwise competition glasshouse study comparing the competitive ability of another invasive grass species, *Nassella trichotoma*, to native Australian grass species (Badgery et al. 2005). We also found evidence that certain nutrient and water conditions enhance the performance of the natives when grown with neighbours. The performance of Pitted bluegrass was facilitated by Lovegrass neighbours under low nutrients and pulsed water supply, while the performance of Kangaroo grass was facilitated by Lovegrass neighbours under continuous water supply. During restoration, attempting to create these resource conditions or timing activities when these resource conditions exist may increase the performance of native grasses.

Restoration efforts in areas dominated by Lovegrass should avoid control measures that create large-scale disturbances that may favour the invader (e.g. Buckley et al. 2003; Firn et al. 2008). The intolerance of Lovegrass to intraspecific competition suggests that its growth and fitness could be reduced as its density increases. This reduction has been observed for some pernicious invaders, where wide differences in performance exist between the invasion front and the longer-established populations behind the front (Dwyer and Morris 2006; Hansen and Wilson 2006). What is unclear, however, is whether the strength of this density-dependent suppression of Lovegrass is sufficient to allow subordinate species to recover from rarity, as predicted by some facets of niche theory (e.g. Chesson 2000). In its native range in South Africa,

this has been observed to occur, where Lovegrass dominates following disturbance, but in the absence of disturbance is eventually (in this study 10 years) displaced (Snyman 2003). Whether this can occur in the invaded range of Australia has yet to be observed.

Overall, our results show that choosing functionally similar native species to resist the establishment of an invader or to decrease the invasibility of a community is more challenging than matching the individual characteristics of species. Instead, what is also needed is a test of the competitive interactions between species under different abiotic and biotic conditions. Coupling information on the individual characteristics of species with information on their competitive abilities will provide more detailed information for restoration efforts.

## References

Aarssen LW, Epp GA (1990) Neighbour manipulations in natural vegetation: a review. J Veg Sci 1:13–20
Abrams P (1983) The theory of limiting similarity. Annu Rev Ecol Syst 14:359–376
Anderson E (2003) Plants of Central Queensland, their identification and uses. Queensland Department of Primary Industries, Brisbane
Badgery W, Kemp D, Michalk D, King W (2005) Competition for nitrogen between Australian native grass and the introduced weed *Nassella trichotoma*. Ann Bot 96:799–809
Bayer AW (1955) The Ecology of grasslands. In: Meredith D (ed) The grasses and pastures of South Africa. Cape Times Press, Capetown, pp 539–571
Bazzaz FA (1996) Plants in changing environments: linking physiological, population, and community ecology. Cambridge University Press, Cambridge
Biggs A, Coutts A, Harris PS (eds) (1999) Central Darling Downs land management manual. Queensland Department of Primary Industries, Brisbane
Buckley YM, Briese DT, Rees M (2003) Demography and management of the invasive plant species *Hypericum perforatum*. I. Using multi-level mixed-effects models for characterizing growth, survival and fecundity in a long-term data set. J Appl Ecol 40:481–493

Campbell MH (1983) Area, distribution and weed potential of *Eragrostis curvula* (Schrad.) Nees in New South Wales. Aust Weeds 2:107–112

Chapin FS III, Torn MS, Tateno M (1996) Principles of ecosystem sustainability. Am Nat 148:1016–1037

Chesson P (2000) Mechanisms of maintenance of species diversity. Annu Rev Ecol Syst 31:343–366

Chesson P, Kuang JJ (2008) The interaction between predation and competition. Nature 456:235–238

Cousens R (2000) Greenhouse studies of interactions between plants: the flaws are in interpretation rather than design. J Ecol 88:352–353

Crawley MJ (2002) Statistical computing, an introduction to data analysis using S-Plus. Wiley, West Sussex

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. J Ecol 88:528–534

Dukes JS (2001) Biodiversity and invasibility in grassland microcosms. J Ecol 126:563–568

Dwyer G, Morris W (2006) Resource-dependent dispersal and the speed of biological invasions. Am Nat 167:165–176

Emery SM (2007) Limiting similarity between invaders and dominant species in herbaceous plant communities. J Ecol 95:1027–1035

Fargione J, Brown C, Tilman D (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. Proc Natl Acad Sci USA 100:8916–8920

Firn J (2009) African lovegrass in Australia: a valuable pasture species or embarrassing invader. Trop Grassland 43:86–97

Firn J, Rout T, Possingham HP, Buckley YM (2008) Managing beyond the invader: manipulating disturbance of natives simplifies control efforts. J Appl Ecol 45:1143–1151

Firn J, House APN, Buckley YM (2010) Alternative states models provide an effective framework for invasive species control and restoration of native communities. J Appl Ecol 47:96–105

Freckleton RP, Watkinson AR (2000) Designs for greenhouse studies of interactions between plants: an analytical perspective. J Ecol 88:386–391

Funk JL, Cleland EE, Suding KN, Zavaleta ES (2008) Restoration through reassembly: plant traits and invasion resistance. Trends Ecol Evol 23:695–703

Gibson DJ, Connolly J, Hartnett DC, Weidenhamer JD (1999) Designs for greenhouse studies of interactions between plants. J Ecol 87:1–16

Goldberg DE (1996) Competitive ability: definitions, contingency and correlated Traits. Philos Trans R Soc Lond B 351:1377–1385

Goldberg D, Landa K (1991) Competitive effect and response: hierarchies and correlated traits in the early stages of competition. J Ecol 79:1013–1030

Goldberg DE, Novoplansky A (1997) On the relative importance of competition in unproductive environments. J Ecol 85:409–418

Goldberg DE, Rajaniemi T, Gurevitch J, Stewart-Oaten A (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. Ecology 80:1118–1131

Grime JP (2001) Plant strategies, vegetation processes, and ecosystem properties, 2nd edn. Wiley, New York

Hansen MJ, Wilson SD (2006) Is management of an invasive grass *Agropyron cristatum* contingent on environmental variation? J Appl Ecol 43:269–280

Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. Science 324:636–638

Henry DR, Hall TJ, Jordan DJ, Milson JA, Schefe CM, Silcock RG (1995) Pasture plants of southern inland Queensland. Queensland Department of Primary Industries, Brisbane

Ives AR, Zhu J (2006) Statistics for correlated data: phylogenies, space, and time. Ecol Appl 16:20–32

Jankju-Borzelabad M, Griffiths H (2006) Competition for pulsed resources: an experimental study of establishment and coexistance for an arid-land grass. Oecologia 148:555–563

Keddy PA (2001) Competition, 2nd edn. Kluwer, Dordrecht

Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. Proc R Soc Lond B 270:775–781

MacArthur RH, Levins R (1967) The limiting similarity, convergence and divergence of coexisting species. Am Nat 101:377–385

MacDougall A, Turkington R (2004) Relative importance of suppression based and tolerance based competition in an invaded oak savanna. J Ecol 92:422–434

MacDougall AS, Gilbert B, Levine JM (2009) Plant invasions and the niche. J Ecol. doi:10.1111/j.1365-2745.2009.01514.x

McMahon SM, Diez JM (2007) Scales of association: hierarchical linear models and the measurement of ecological systems. Ecol Lett 10:437–452

McNaughton SJ, Wolf LL (1970) Dominance and the niche in ecological systems. Science 9:131–139

Mitchell M (2002) Native grasses: an identification handbook for temperate Australia. Landlinks, Collingwood

Novoplansky A, Goldberg DE (2001) Effects of water pulsing on individual performance and competitive hierarchies in plants. J Veg Sci 12:199–208

Parsons WT, Cuthbertson EG (1992) African Lovegrass. In: Noxious weeds of Australia. CSIRO Publishing, Melbourne, pp 106–109

Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-plus. Springer, New York

Rout ME, Callaway RM (2009) An invasive plant paradox. Science 324:734–735

Sharp D, Simon BK (2002) AusGrass: Grasses of Australia. Australian Biological Resources Study, Canberra and Environmental Protection Agency, Queensland

Sher AA, Goldberg DE, Novoplansky A (2004) The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. Oecologia 141:353–362

Snyman HA (2003) Revegetation of bare patches in a semi-arid rangeland of South Africa: an evaluation of various techniques. J Arid Environ 55:417–432

Strauss SY, Webb CO, Salamin N (2006) Exotic taxa less related to native species are more invasive. Proc Natl Acad Sci USA 103:5841–5845

Tilman D (1988) Plant Strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Tothill JC, Hacker JB (1993) The grasses of southern Queensland. University of Queensland Press, St-Lucia

Turnbull LA, Rahm S, Baudois O, Eichenberger-Glinz S, Wacker L, Schmid B (2005) Experimental invasion by legumes reveals non-random assembly rules in grassland communities. J Ecol 93:1062–1070

Vila M, Weiner J (2004) Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. Oikos 105:229–238

Voight PW, Kneebone WR, McIlvain EH, Shoop MC, Webster JE (1970) Palatability, chemical composition, and animal gains from selection of Weeping Lovegrass, *Eragrostis curvula* (Schrad.) Nees. Agron J 62:673–676

Weigelt A, Jolliffe P (2003) Indices of plant competition. J Ecol 91:707–720