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Invasive success of exotic wild oat depends on nutrient availability and competition in temperate grasslands of southern Australia

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Abstract

Aims Invasion by exotic species commonly influences the structure and diversity of natural grasslands particularly in fertile soils. This study examined the effect of resource availability on intra- and interspecific competition between a native and an exotic grass, and provides mechanistic explanations for the successful invasion of exotic species in temperate grasslands of southern Australia.

Methods Frequently co-occurring exotic *Avena barbata* (wild oat) and native *Rytidosperma caespitosum* (wallaby grass) of temperate grasslands in southern Australia were grown with and without competition across a soil nutrient and moisture gradient in a glasshouse experiment.

Results Wallaby grass and wild oat showed similar growth responses to soil nutrient levels: both performed better at lower levels. Intra- and interspecific competition significantly reduced plant biomass and relative growth rate, but their effects depended on resource availability. Higher soil nutrient availability promoted the performance of the exotic grass and strengthened its competitive advantage over the native grass because of their different responses to the interaction of competition, soil nutrient and moisture. Moreover, changes in relative competition intensity suggested wallaby grass experienced stronger suppression from interspecific competition than wild oat in mixture which led to its decreasing abundance.

Conclusions Nutrient accumulation due to management for grazing combined with high rainfall during the wet season can reduce the interspecific competitive ability of native grass and favors exotic invasion in temperate grasslands of southern Australia. The ongoing climate changes may dramatically increase wild oat's prevalence and pose a great challenge on the restoration of native temperate grasslands in Australia.

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Introduction

Temperate grasslands are one of the most endangered ecosystems worldwide. Their extension has

been greatly reduced by clearance while the increase in dominance of exotic plants in remnants caused a decline of native grasses and poses a challenge to the management of these natural grasslands (Lenz et al. 2003). Developing effective management and conservation strategies for resident species require better understanding of invasion mechanism by exotic species, which have great influence on plant community assemblage and biodiversity in natural grasslands (Tilman 1997; Vilà et al. 2011; Byun et al. 2013; Ransijn et al. 2015). It is well-documented that resource competition is an important mechanism that contributes to the successful invasion of exotic species (Vilà and Weiner 2004; Bottollier-Curtet et al. 2013; Craine and Dybzinski 2013; Gioria and Osborne 2014; Broadbent et al. 2018; Schultheis and MacGuigan 2018). Exotic plants usually have functional traits, including high growth rate and large leaf area, which confer them with superior competitive ability and fitness when competing for resources with native plants (Fogarty and Facelli 1999; Keser et al. 2014; Sheppard and Burns 2014; te Beest et al. 2015; Luo et al. 2019). In addition, it is suggested that the phenotypic plasticity in performance or traits can also provide the invaders with competitive advantage over the native plants across certain environmental gradients (Richards et al. 2006; Davidson et al. 2011). Greater phenotypic plasticity relative to resident species favors the population fitness of invaders and leads to competitive superiority (Funk 2008; Skálová et al. 2012, 2013). Evidence from natural experiments suggests that the consequence of resource competition and exotic invasion is strongly species-specific and condition-dependent (Daehler 2003; Vilà and Weiner 2004; Liu et al. 2018). Thus, better understanding of resource competition between native and invasive species will enhance our knowledge of the drivers of plant community assemblage and contribute to the development of conservation strategies for natural grasslands.

Changes in soil nutrient availability have great impact on resource competition between invasive and native plants (Littschwager et al. 2010; Liu and van Kleunen 2017; Delerue et al. 2018; Edwards et al. 2019). High availability of limiting soil nutrients, in particular nitrogen (N), could result in competitive superiority of invasive species in both nutrient-rich (Blank 2010; Bradley et al. 2010; Gioria and Osborne 2014) and nutrient-poor habitats (Brooks 2003; Funk

and Vitousek 2007; Vallano et al. 2012). However, increased soil nutrient does not consistently facilitate the invasion of exotic species. For example, the addition of limiting N improved the resistance of Serpentine grassland to invasion by *Bromus diandrus* Roth. (Going et al. 2009). Actually, the post-invasion outcome strongly depends on resource competition intensity between native and invasive species, and their relative magnitude of niche overlap and fitness difference to soil nutrient as proposed by classic niche theory (MacDougall et al. 2009; Skálová et al. 2013; Lai et al. 2015).

Strong competitors usually can rapidly acquire nutrients, or they can deplete resource to lower levels, thus suppressing or excluding other species (Grace and Tilman 1990; Suding et al. 2004). Thus the addition of limiting nutrients might be assumed to decrease the intensity of interspecific competition and allow species coexistence. However, several experiments found that the addition of soil nutrient accelerated the exclusion of native species by increasing the competitive ability of exotic plants (Huenneke et al. 1990; Grove et al. 2003; Blumenthal 2005; Rao and Allen 2010). Enhanced availability of limiting resource following episodic events and disturbance may increase the invasibility of the resident community, while the differentiation of resource niches allows the coexistence of invasive and native species as proposed by the environmental fluctuation hypothesis (Davis et al. 2000; Goldstein and Suding 2014). These theoretical considerations and empirical results clearly indicate that studies on the interactions between native and invasive plants along nutrient gradients are critical to understand how the impact of competition on the patterns and dynamics of plant community depends on resource availability.

In South Australia, the shift of native plant community to exotic grass dominated systems provides a dramatic example of habitat alteration (Lenz and Facelli 2006), yet little is known about the factors and mechanisms that drive the invasion process. The hills surrounding Burra in South Australia (33˚66′24.12″S, 138˚91′80.92″E), and indeed large areas of the Mid-North Region of South Australia, were once dominated by perennial grasses and forbs. The invasion by Mediterranean annual grasses coupled with intense grazing has converted the middle and lower slopes into areas dominated by exotic annuals (Eliason and Allen 1997; Lenz and Facelli 2006). A patchy

distribution of native grasses is often found in the crest of the hills as sub-dominant species (personal observation). This distribution pattern suggests the exotic species might directly outcompete most other native species, particularly in the lower sections of slopes because of higher resource availability (Lenz et al. 2003). The dominance of exotic annuals seems correlated to the distribution patterns of soil resources, since the rainfall run-off from the hills create dry conditions in the crests and upper slopes, while the water run-in increase water and nutrient availability in the lower slopes and swales. The lower slopes are often used for agriculture because of its deeper soil and higher nutrient availability.

We grew the frequently co-occurring common exotic wild oat (*Avena barbata* (Pott ex Link)) and native *Rytidosperma caespitosum* (Gaudich.) Connor & Edgar (formerly *Danthonia caespitosa* Gaudich., henceforth wallaby grass) of temperate grasslands in southern Australia in a glasshouse experiment and measured their performance to evaluate the intra- and interspecific competition across a gradient of soil nutrient and moisture. Comparative analysis allows us to assess the effects of resources on plant performance and competition ability of native and exotic grasses. Based on our observation and previous studies (Lodder et al. 1994; Lenz and Facelli 2006), we predict that the competitive advantage of wild oat in this region is related to soil nutrient availability and would be increased by higher soil resource availability (i.e. soil nutrient and water). At higher levels of soil resources wild oats would be competitively dominant (Fig. 1 S_E in dash area), but at lower levels of soil resources native perennial grasses would have competitive advantage over wild oat and be less affected by the interspecific competition with wild oat, and could then be the dominant species in the plant community (Fig. 1 S_N dark area). Higher nutrient availability caused by water supply will also favor the performance of exotic grass and lead to its competitive advantage over native grass (Fig. 1 S_E in dot area). Moreover, we also predict that soil resource availability would alter the relative importance of interspecific vs. intraspecific competition for native and exotic species. At higher soil nutrient availability, interspecific competition from invaders should be stronger than intraspecific competition for native species, while for the invader intraspecific competition is equal to or larger than interspecific competition.
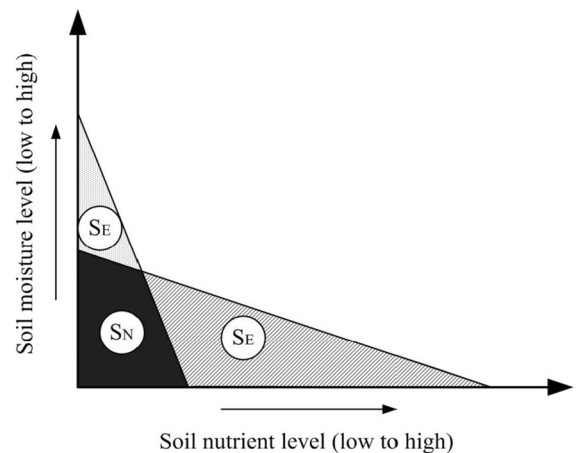

Fig. 1 Conceptual model illustrating the impacts of soil nutrient, moisture, and their interaction on competition relationship between native wallaby grass and exotic wild oat. At higher resource levels wild oat would be competitively dominant (S_E in dash area), but at lower resource levels native perennial grasses would be less affected by the interspecific competition with wild oat (S_N in dark area). Higher level of soil moisture would favor the performance of exotic grass through enhanced nutrient availability, and lead to its competitive advantage over native grass (S_E in dot area)

Testing these predictions allow us to identify and evaluate the importance of resource availability variation on intra- and interspecific competition and therefore explain their impacts on the patterns of plant community assemblage in the natural grassland.

Materials and methods

Plant species

In the Mid-North Region of South Australia the most abundant native and exotic plants are wallaby grass and wild oats respectively. Wallaby grass is a perennial tussock grass widely distributed throughout southern Australia. Its climate range extends from a hot arid environment at its northern limit (roughly 32°S) to a cool and moist temperature environment at its southern limit in Tasmania. Wallaby grass has high drought tolerance and grows well in shallow soil with low nutrient availability (Waters et al. 2008; Dear et al. 2008). This species is of considerable importance to the livestock industry, especially in the semiarid winter rainfall region. The annual

exotic grass wild oat was introduced to Australia from central Asia and the Mediterranean Basin. Previous field studies reported that the abundance of wild oats was closely associated with higher soil fertility and higher cool-season rainfall in temperate grasslands of southern Australia (Lenz and Facelli 2005, 2006). The growth season of both species broadly overlaps since the arrival of autumn–winter rains triggers the breaking of summer dormancy of wallaby grass and the germination of wild oat. They both continue to grow through the winter till the onset of the dry season in late spring in a range of abundances depending largely on soil moisture or the amount of winter rainfall (Lenz and Facelli 2006).

Experimental design

A completely random design was used in the glasshouse experiment, with five nutrient treatments and two water availability levels combined with five plant competition treatments. Fertilizer levels were manipulated by adding 0 (A), 1.5 (B), 3.0 (C), 4.5 (D), and 6.0 g (E) slow-release Osmocote fertilizer (the Scotts Company, Marysville, OH; 18% total N, 4.5% total P) per pot to obtain a soil nutrient gradient. Water availability levels were simultaneously controlled to 10% and 20% soil water content respectively by weighting pots weekly. The competition series consisted of single plant of each species per pot, monoculture (three individuals of one species per pot) and mixture (three individuals of each species per pot).

Similar sized seedlings (approximately 8 cm tall) of wallaby grass and wild oat were selected and prepared for planting to minimize the prior effect of seedling size. To reduce the dormancy, seeds of wallaby grass and wild oats, which had been collected from the natural grassland in Burra (33°39′48.7692″S, 138°55′50.2536″E; 500 m above sea level), were stored at 5 °C for ten days and then germinated in premium vermiculite for three weeks with sufficient water. Then they were supplied with sufficient Hoagland solution for another three weeks before the competition experiment was carried out. Fewer seeds of wild oats germinated and the number were not sufficient for the requirement of our experiment. To solve this, seedlings of wild oat were collected directly in a former paddock in the Waite campus, the University of Adelaide. Before transplanting, seedlings of similar size (approximately 8 cm tall) were selected and

soils around roots were washed carefully to obtain the intact root systems without damage. On 10 July the seedlings of both species were transplanted to plastic pots (10 cm in diameter and 15 cm in height) filled with 1 kg of sandy clay loam with low nutrient content and similar to soils in the Burra area. All treatment combinations were replicated five times, making the total number of pots 250. All pots were arranged randomly on benches and re-randomized weekly to minimize bench location effects.

This experiment was carried out from July to September (winter to spring in the southern hemisphere) 2009 over 12 weeks in the glasshouse in Department of Ecology and Evolutionary Biology, the University of Adelaide, Australia (34°55′10.0776″S, 138°36′2.8764″E). At most times, the temperature and humidity in the glasshouse were similar to the temperature outside, but air conditioners would keep daytime temperatures below 35 °C.

Harvesting and measurements

After 12 weeks, data were collected from each pot on tiller number and tiller height for vegetative and reproductive tillers. Plant material in each pot was divided into above and below ground parts by species. Plant roots in mixture could be separated carefully without strong entanglement. Shoot were divided into stem, dead and live leaves; and the latter was used for leaf area measurements using a leaf area scanner. All plant parts were oven-dried at 65 °C for 48 h and weighed. The whole plant material was then grounded completely and stored for N measurement. The total N content was determined by using the Kjeltec 2333 Nitrogen Analyzer (Foss Analytical, HillerØd, Denmark).

The relative growth rate of each plant species was calculated as

$$RGR = \ln(M_2/M_1)/(t_2 - t_1)$$

for each treatment, where M_1 is the initial biomass of transplanting seedlings (which was calculated by measuring biomass of five sets of thirty seedlings with similar size), M_2 is the final plant biomass at harvest, and t_2-t_1 is the growth period of 84 days (Harper 1977). The biomass and RGR were used to evaluate the response of plant species to soil nutrient and water availability, and calculate the intensity

of intra- and interspecific competition. Leaf area and specific leaf area (SLA, leaf area/total leaf mass) was estimated using image analysis software based on leaf image, which was scanned using a printer against a plain background. The relative competition intensity, calculated as

$$RCI = (RGR_{NC} - RGR_C)/RGR_{NC}$$

was used to evaluate the strength of competition by comparing the plant performance in absence and presence of plant neighbor (Grace 1995). RGR_{NC} is the average RGR of plants grown individually, and RGR_C is the average RGR of plant grown in monoculture or in mixture. RCI in monoculture (RCImono) represents the relative effect of intraspecific competition on plant performance, while RCI in mixture (RCImix) represents the joint effect of intra- and interspecific competition. In addition, RCImix minus RCImono (RCI(mix-mono)) was calculated to indirectly estimate the effect of interspecific competition in mixture. RCI > 0 means that plant interaction has negative effects on plant performance. Moreover, relative importance of competition in mixture and in monoculture was represented using relative yield (RY),

$$RY = Y_{mix}/Y_{mono}$$

where Ymix and Ymono is the averaged individual biomass of one species grown in mixture and in monoculture respectively (Silvertown and Charlesworth 2001). RY = 1 means competition in mixture is equal to that in monoculture; RY > 1 means competition in monoculture is greater than that in mixture and RY < 1 means the reverse (Weigelt and Jolliffe 2003).

Statistical analysis

The fixed effects of soil nutrient, moisture and competition were analyzed using a full factorial, three-way multivariate analysis of variance (MANOVA) for the plant biomass, RGR, SLA, root to shoot ratio (R/S) and N content per plant by using a permutation multivariate analysis of variance (PerMANOVA; Anderson 2005) for wallaby grass and wild oat respectively. MANOVA followed by Tukey's HSD test was used to determine the significant difference of effects of soil nutrient, moisture and competition on plant biomass,

RGR, SLA and R/S after testing normality and homogeneity of variances. Normality and homogeneity were tested by using Kolmogorov–Smirnov test and Levene's test respectively performed with SPSS 15.0 software. SLA and R/S were transformed to meet the assumptions of MANOVA. Moreover, linear models were used for fitting the relationship between RGR and N content per plant for both wallaby grass and wild oat across nutrient and moisture levels respectively. T-test was used to statistically compare the performance of wallaby grass and wild oat when they were grown within the same nutrient and competition condition. T-test was also used to compare the performance of plants (wallaby grass or wild oat) grown in monoculture and mixture under the same nutrient condition. All figures are finished using Prism 5.

Results

Plant performance in response to soil nutrient and moisture

Soil nutrient, moisture, competition, and the two-way interactions including nutrient × moisture and nutrient × competition had significant effects on the plant biomass of wallaby grass (Table 1). When grown individually and in monoculture, wallaby grass had a maximum biomass at nutrient level B and decreased rapidly at the higher nutrient level from C to E, while wallaby grass grown in mixture showed less response to nutrient level (Fig. 2a and b). To some extent, soil water moisture improved the plant biomass of wallaby grass by about 3.1–50.5% across all nutrient levels, and this effect was not influenced by plant competition as indicated by the non-significant effect of soil moisture × competition interaction (Fig. 2a and b; Table 1).

Soil nutrient, moisture, competition, and their two-way and three-way interactions had significant effects on the plant biomass of wild oat (Table 1). In general, the average biomass of wild oats grown under wet soil condition was 45.4–83.7% larger than those under dry soil condition across all nutrient levels. When grown singly, plant biomass decreased with increased nutrient level under dry soil conditions, but showed its greatest biomass at nutrient level B under wet soil condition (Fig. 2c and d). Moreover, biomass of wild oat was reduced by 43.6% and 29.7%

Table 1 Analysis of variance test for the plant biomass, relative growth rate (RGR), specific leaf area (SLA) and root to shoot ratio (R/S) of wallaby grass and wild oat as affected by soil nutrient (five levels), moisture (two levels) and competition (absence, intraspecific competition, intra- plus interspecific competition). Absence of competition refers to the situation where wallaby grass and wild oat were grown individually. Intraspecific competition and intra- plus interspecific competition refer to plants grown in monoculture and mixture respectively

Fators	d.f	Plant biomass		RGR		§SLA		§R/S	
		F-value	P	F-value	P	F-value	P	F-value	P
Wallaby grass									
Soil nutrient (N)	4	23.757	0.0001*	4.095	0.0013*	15.7525	0.0001*	8.9722	0.0001*
Soil moisture (M)	1	6.213	0.0059*	-0.281	0.7536	3.4702	0.0575	4.8797	0.0188*
Competition (C)	2	39.712	0.0001*	11.244	0.0001*	24.9437	0.0001*	57.7557	0.0001*
N×M	4	2.948	0.0103*	0.115	0.8538	5.0509	0.0002*	1.1265	0.3395
N×C	8	5.942	0.0001*	2.134	0.0490*	3.9326	0.0004*	3.1942	0.0007*
M×C	2	1.125	0.3182	0.924	0.4664	3.7380	0.0185*	8.2161	0.0002*
N×M×C	8	1.107	0.3506	0.687	0.6916	1.9861	0.0382*	2.3129	0.0125*
Wild oat									
Soil nutrient (N)	4	8.721	0.0001*	6.974	0.0001*	8.5272	0.0002	4.4382	0.0013*
Soil moisture (M)	1	33.849	0.0001*	18.419	0.0001*	53.9409	0.0001*	0.2246	0.6967
Competition (C)	2	22.118	0.0001*	12.678	0.0001*	0.7170	0.4945	7.9150	0.0002*
N×M	4	2.853	0.0119*	1.113	0.3436	2.5461	0.0390*	0.9444	0.4440*
N×C	8	4.247	0.0001*	2.431	0.0052*	2.3523	0.0166*	5.2053	0.0001*
M×C	2	3.547	0.0137*	0.860	0.4566	3.1741	0.0411*	1.4583	0.2310
N×M×C	8	2.243	0.0111*	1.180	0.2860	1.1954	0.3021	1.5032	0.1469

§ means SLA and R/S were log-transformed to meet the assumptions of MANOVA. * means $P < 0.05$

in monoculture and mixture (Fig. 2c and d) without consistent responses to nutrient levels.

Functional traits in response to soil nutrient and moisture

Soil nutrient, competition and their interaction had significant effects on the RGR for both wallaby grass and wild oat (Table 1). Wallaby grass generally showed highest RGR at nutrient level B, and then decreased from level C to E. When grown individually, plants grew faster than those in monoculture, and plants in mixture had the lowest growth rate (Fig. S1a and b). When wild oat was grown individually, it showed strong response to nutrient level, having greatest RGR at nutrient level B as wallaby grass did. However, wild oat showed weaker responses to nutrient levels in monoculture and mixture, indicating that competition weakened plant responses to increasing nutrient availability. In addition, wild oat had higher RGR under wet than dry condition (Fig. S1a and d).

Generally, wild oat showed greater R/S and SLA than wallaby grass (paired t-test, $P < 0.01$). When grown individually, wallaby grass had lowest R/S than those in monoculture and mixture under both dry and wet conditions (Fig. 3a and b). For wild oat, intra- and interspecific competition increased R/S by 30.6% and 21.6% under dry condition, but had no effect under wet condition (Fig. 3c and d). Compared to wallaby grass grown individually, SLA was reduced by about 22.3% in monoculture and 22.5% in mixture respectively (Fig. S2a and b). But competition had no significant effect on SLA of wild oat (Table 1; Fig. S2c and d).

Relative competitive intensity in response to soil nutrient and moisture

RCI of wallaby grass and wild oat showed complex responses to the combination of soil nutrient and moisture. RCImix generally was higher than RCImono because plant performance was influenced by intra- plus interspecific competition when in mixture (paired t-test for RCImono and RCImix, $P < 0.001$, Fig. 4). Wallaby grass grown in mixture experienced highest competition (i.e. there was a higher RCI) at
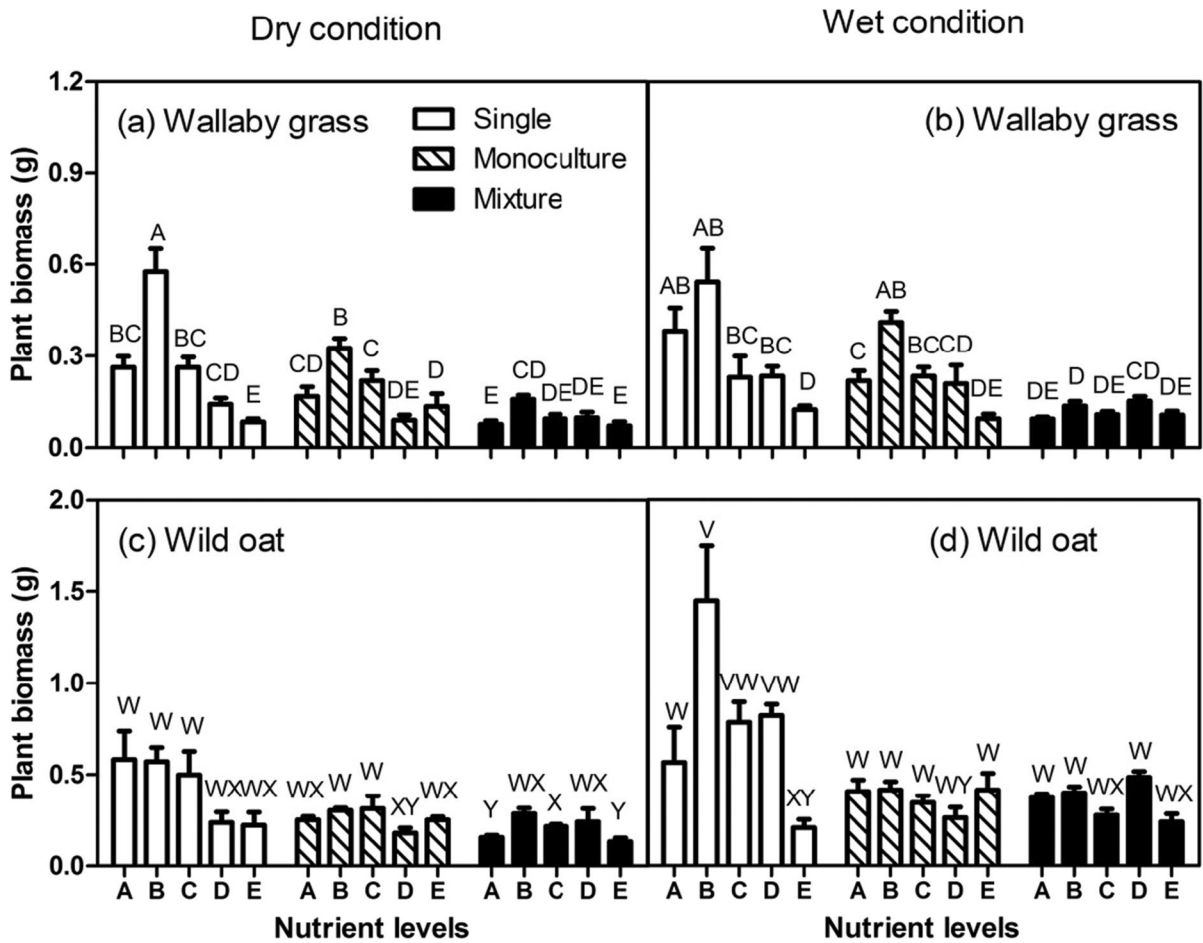
Fig. 2 Plant biomass (per individual) of wallaby grass and wild oat responded to the soil nutrient (A to E nutrient levels) and moisture (wet and dry conditions) when plants were grown individually, in monoculture and mixture. Different let-ters (A-E) or (V–Y) above bars indicate means are significantly different for wallaby grass (a and b together) or for wild oat (c and d together) at $P \leq 0.05$ level

lowest nutrient level (A) than at any other nutrient levels (Fig. 4a and b). Compared to dry condition, wallaby grass grown under wet condition was more influenced by interspecific competition than intraspecific competition as indicated by the larger value of RCI(mix-mono) at lower nutrient levels (A to C).

For wild oat, RCImix decreased gradually across nutrient levels in dry soil (Fig. 4c), but RCImix in wet soil increased at lower nutrient levels and then declined at higher nutrient levels (Fig. 4d). RCImono of wild oat was positive in most cases, and increased from low to medium nutrient levels, but declined at highest nutrient level (E). By contrast, RCI(mix-mono) of wild oat usually was lower than RCImono at lower nutrient levels with the exception of wild oat

grown at lowest nutrient level under dry condition (Fig. 4c and d).

In most cases, the influences of competition (intra-plus interspecific competition) on wallaby grass and wild oat in mixture were greater than intraspecific competition in monoculture indicated by RY<1, especially at lower nutrient levels (Fig. 5). The exceptions to this was wallaby grass grown in dry soil and wild oat grown in wet soil at nutrient level D, which experienced relative higher intraspecific competition as indicated by RYs>1. Moreover, the larger difference of RY between wallaby grass and wild oat under wet condition indicated that the impact of competition on wallaby grass was greater than that on wild oat (Fig. 5b).
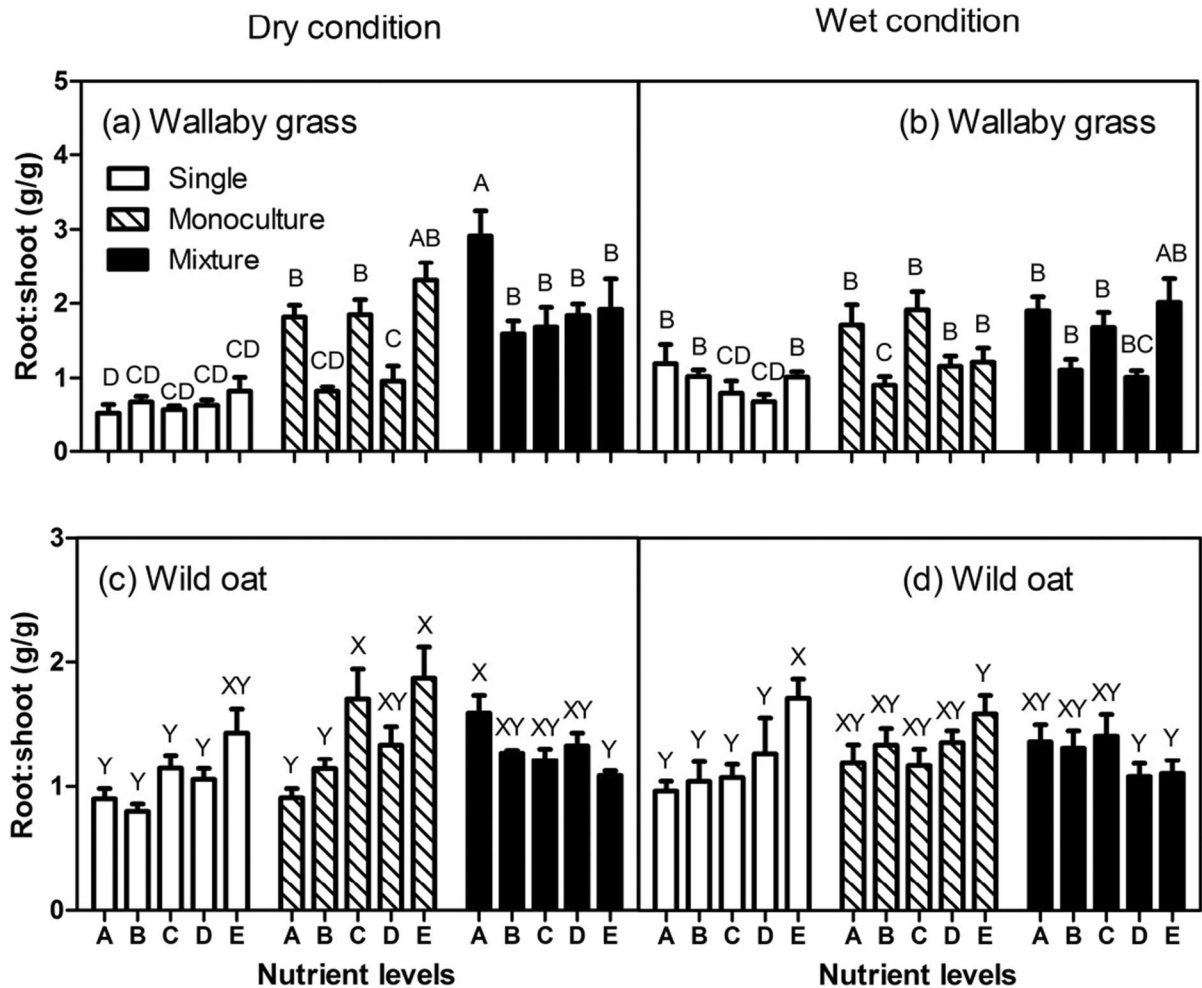
Fig. 3 Root to shoot ratio (R/S) of wallaby grass and wild oat responded to the soil nutrient (A to E nutrient levels) and moisture (wet and dry conditions) when plants were grown individually, in monoculture and mixture. Different letters

(A-D) or (X–Y) above bars indicate means are significantly different for wallaby grass (a and b together) or for wild oat (c and d together) at $P \leq 0.05$ level

Relationship between plant performance and N content

Plants grown individually usually had higher N content, RGR and biomass than those grown in monoculture and mixture. Moreover, there were significant positive correlations between RGR and N content for wallaby grass and wild oat across all nutrient and moisture levels (Fig. 6), indicating strong competition for soil nutrient. The N content of wallaby grass accounted for 68.8% variation in RGR (Fig. 6a), while the N content of wild oat explained 67.5% variation in RGR (Fig. 6b).

Discussion

Effects of soil nutrient and water availability on plant growth

We found evidence that the growth of wallaby grass is limited by soil resources, especially by N, as reflected by the effect of nutrient addition on N concentration in plant tissues. Meanwhile the growth of wild oat is co-limited by both soil N and water availability. The biomass and RGR of both species showed similar bell-shaped curve patterns across soil nutrient levels. Response of wallaby grass was consistent with a
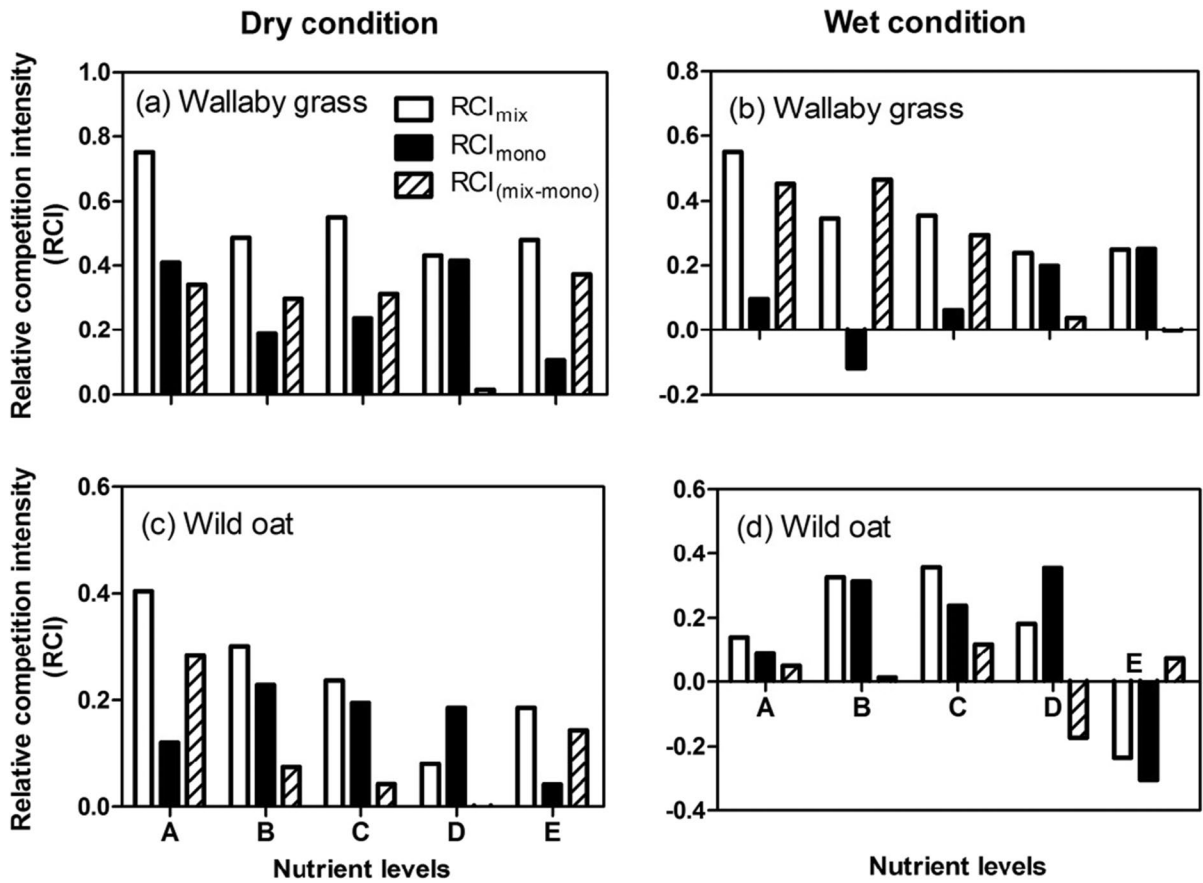
Fig. 4 Relative competition intensity (RCI), as indicated of the strength of competition, responded to the soil nutrient (A to E nutrient levels) and moisture (wet and dry conditions) for wallaby grass (a and b) and wild oat (c and d), respectively
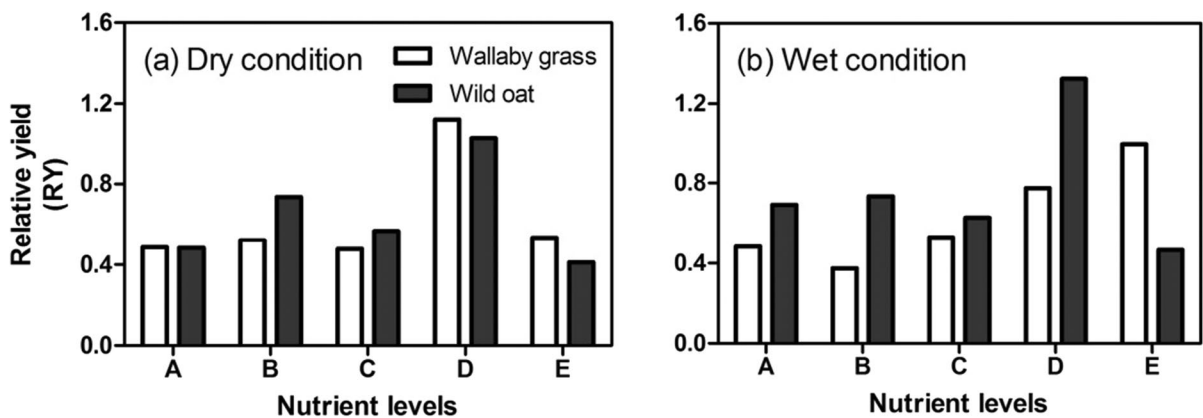

Fig. 5 Relative yield (RY), as an indicator of the importance of competition in monoculture and mixture, responded to the soil nutrient (A to E nutrient levels) when wallaby grass and wild oat were grown under dry (a) and wet (b) conditions
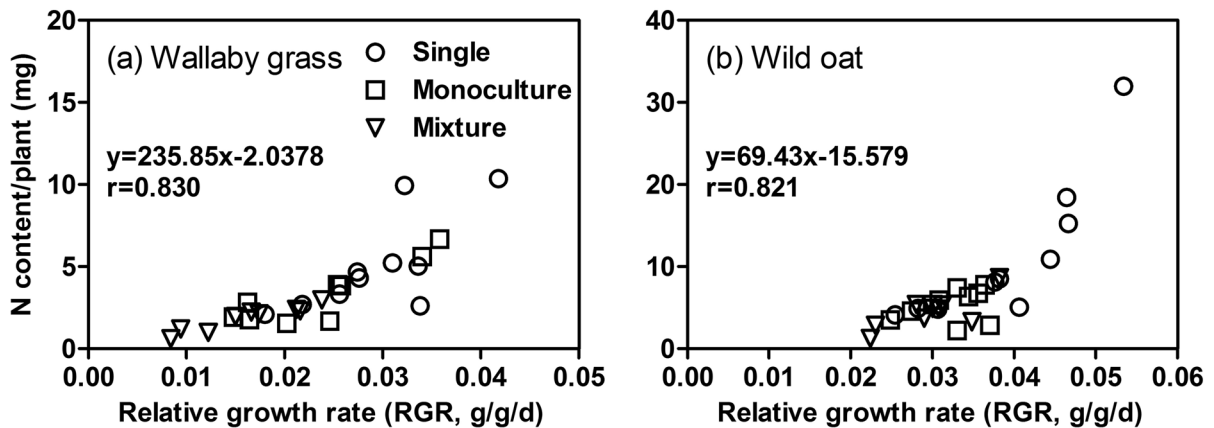
Fig. 6 Relationships between relative growth rate (RGR) with N content for wallaby grass (a) and wild oat (b), respectively

previous study (Lodder et al. 1994), but wild oat, contrary to our expectation, did not show linear response to the soil nutrient gradient. Wallaby grass and wild oat have seemingly similar ecological soil resource requirement and could well adapt to low nutrient soils, which helps to explain their wide and overlapping distribution in the temperate grasslands of southern Australia, where shallow and rocky soils are common. In contrast, wallaby grass and wild oat showed very different responses to soil water availability, which is a critical factor influencing the performance of exotic species in arid and semi-arid region (Thebaud et al. 1996; Funk 2013). These results are consistent with the distribution of the two species at the continental level (where wallaby grass extend further north into drier areas) and with reported distribution patterns at the landscape level (wild oat less abundant on drier hill tops and more abundant in foothills in the Mid-North Region of South Australia (Lenz et al. 2003)). The divergent responses to soil water availability might partially confer exotic species an advantage over native grasses. Higher rainfall in the wet season (winter) in southern Australia might improve the competitive ability of wild oat by improving soil nutrient availability, thus reducing the abundance of co-occurring native species. Although the phenotypic plasticity in plant morphological traits was not qualified directly, wild oat exhibited higher plasticity in size traits than wallaby grass in response to various levels of soil nutrient and moisture, which might partially contribute its higher fitness and competitive ability in fluctuating environment (Skálová et al. 2013).

Effects of competition on plant performance

Competition can be a major biotic factor that influences plant abundance and community structure in nature (Tilman 1988). In this study, resource competition had different effects on the performance of wallaby grass and wild oat, and its effects were dependent on soil nutrient and water availability. The significant interactive effect of nutrient×water×competition on the performance of wild oat supports our first prediction that high nutrient and soil water availability together change the resource competition balance in favour of the exotic grass over the native grass.

In the high water availability treatment, watering may have enhanced the release of nutrients from the slow release fertilizer and strengthen the competitive advantage of wild oats thanks to its efficient nutrient uptake. Nutrient enrichment reduced the joint effect of intra- and interspecific competition on wallaby grass and wild oats grown under dry conditions. This finding is in line with other studies which suggest that the addition of limiting nutrients can reduce the competitive effect of native on exotic species (Barger et al. 2003) and therefore facilitate exotic invasion (Brooks 2003; Leishman and Thomson 2005; Vallano et al. 2012; Funk 2013). Further, wild oat grown under wet condition also experienced lower interspecific competition at highest nutrient level than those grown at moderate nutrient levels, indicating that enhanced soil moisture in the wet season could increase soil nutrient availability and decrease competition intensity (Davis et al. 1998).

Classical competition theory predicts that intraspecific competition should be greater than interspecific competition because individuals within one species share highly similar resource requirements (Adler et al. 2018). By contrast, interspecific competition had greater impacts on plant performance of native wallaby grass than intraspecific competition under low nutrient condition, especially under wet condition. Meanwhile, there was no significant difference between RCI values in mixture and monoculture for wild oat. These results partially supported our prediction that native species experienced stronger interspecific competition from invaders, and can lead to its reduction in natural grasslands (Mangla et al. 2011; Sheppard and Burns 2014). In addition, the non-significant difference between the RY value of wallaby grass and wild oat in dry soil indicated that the interspecific and intraspecific competition had similar effect on wallaby grass and wild oat. However, under wet condition the lower RY of wallaby grass indicated that the impact of competition on wallaby grass was greater than that on wild oat in mixture (Weigelt and Jolliffe 2003), while the importance of intraspecific competition for wild oat was greater than for wallaby grass.

The mechanisms of invasive success

This study provides insight into the mechanisms that allow the invasion of wild oat in native grasslands of southern Australia and can explain the documented changes of abundance and assemblage pattern of native wallaby grass and exotic wild oat along Mid-North Region of South Australia (Lenz and Facelli 2006). Competition from wild oat reduced the performance (in parameters such as plant biomass, RGR and N content) of wallaby grass, which was closely related to competitive ability. Meanwhile, wallaby grass showed higher R/S and lower SLA to reduce the effects of soil nutrient addition and light competition. The substantial suppression caused by interspecific competition on wallaby grass strongly suggests that resource competition is an important driver during its replacement by wild oat. However, it is unlikely to be the sole driver given that its performance when competing with native neighbors varied with soil nutrient and water availability.

Based on the above results, a conceptual model of the impacts of soil nutrient availability and moisture

on the abundance change of wallaby grass and wild oat is proposed. The model suggested that the joint effect of soil nutrient and moisture on resource competition is a potential mechanism that influences the assembly pattern of native and exotic species in the temperate grassland system (Fig. 7). Rainfall in wet seasons could enhance soil nutrient availability of the lower sections of hill slope and strengthen the dominate status of exotic species. Meanwhile, higher soil nutrient availability increases the competitive ability of exotic species, and this leads to the quick displacement of native plant by the exotics. Snow addition with summer rainfall or N deposition were also found to improve the invasion of exotic forb species at the southern end of the mixed grass prairie of North America, which is characterized by low precipitation and low soil nutrient availability (Blumenthal et al. 2008). On the contrary, the invasive ability of exotic species could also be restricted by drought condition coupled with low nutrient availability because wallaby grass is well adapted to drought and showed higher competitive ability under those conditions (and hence, we expect, biological resistance to exotic invasion). The degree of similarity and differentiation of resource requirement (resource niche) in native and invasive species determines their relative responses to nutrient addition and the outcome on resource competition (Daehler 2003; Suding et al. 2004). Species exclusion would occur when niches overlap broadly
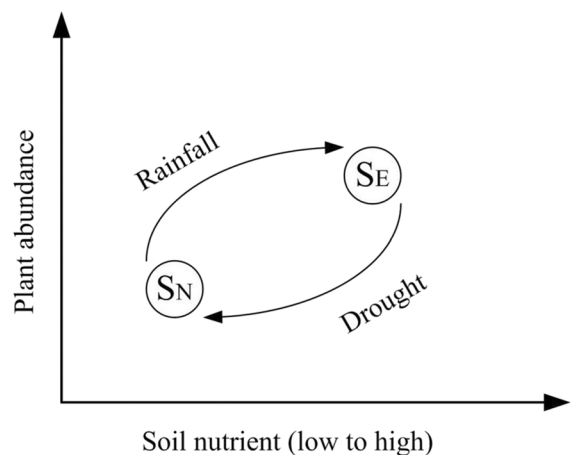

Fig. 7 A concept model for explaining the abundance change of native and exotic species (S_N and S_E respectively) in response to the variation of soil nutrient and rainfall in temperate grasslands of southern Australia

and the invaders have superior competitive ability or fitness than the natives (MacDougall et al. 2009; Goldstein and Suding 2014).

Our results also suggest that invasion success of exotic species is strongly associated with nutrient availability and their capacity to acquire resources (Tilman 1997; Daehler 2003; Seabloom et al. 2003). Compared to the native resident species, having higher biomass, RGR, SLA and R/S in wet soil is likely to assist wild oat with higher fitness and invasibility. Wild oat is not a good interspecific competitor when water is limited. By contrast, higher water supply will largely result in wild oat being a fast-growing competitor and favor its invasion into the native communities (Rao and Allen 2010). Meanwhile, native wallaby grass could be considered as a conservative grower with higher tolerance to soil nutrient and drought stress (Waters et al. 2008), thus it is less limited by resource competition (Craine and Dybzinski 2013; Gioria and Osborne 2014). This life history strategy also confers wallaby grass with higher resistance and competitive advantage over invader wild oat under dry condition.

Conclusion

In the present study we found evidence suggesting that increased nutrient availability associated to topography and local rainfall regime, and resource competition are the drivers that shape the observed abundance of native and exotic grasses in native grasslands of southern Australia. Based on our results, we propose that the ability of resident vegetation to resist invasion may be increased by a slight increase in precipitation. However, the soils and rainfall regime of the southern Australia are conducive to the exclusion of the native wallaby grass by the exotic wild oat. Overall, our study provides key insights into potential conservation strategies in hill grasslands of temperate Australia by informing on some important factors. Future studies including several species pairs should be developed to better understand the invasive success of exotic species by examining their phenotypic plasticity to soil conditions and competition.

Author contributions JM Facelli original conceived the idea. L Ba and JM Facelli designed this experiment and wrote the manuscript. L Ba performed the pot experiment and analyzed the data.

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