

Resource pre-emption, rather than extending the growing season of native grass assemblages, reduces invasion by exotic species

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Abstract

Questions: In Mediterranean-type systems, invasive C3 annual grasses appear early in the season and can pre-empt resources and attain a competitive dominance over native perennial grasses. Here, we investigated whether planting C3 and C4 native grasses (a) combined, so that resources are extracted over a longer period, or (b) at higher density would make planted communities more competitive against invasive species.

Location: Para Woodlands Reserve, near Adelaide, South Australia.

Methods: In 72 experimental plots, native grasses were planted in combinations of seasonal patterns (three levels; single-season assemblages with either C3 or C4 and extended season with both C3 and C4) and planting density (two levels; high = 44 plants/m² and low = 20 plants/m²). Data were collected on native plant survival and biomass, invasive biomass and soil properties.

Results: Overall, C3 native grasses were superior competitors against both invasive C3 grasses and native C4 grasses. We found no interaction between the combination of C3 and C4 grasses planted together and density of planting. Assemblages with higher densities were successful at reducing exotic plant biomass; however, there was a trade-off with reduced individual performance among the native plants. Even though individual plants were larger in the low-density treatment, total biomass was lower in these plots suggesting that density limits the growth of native communities as a whole. The C3 native plants were planted earlier than the C4 native plants because of differences in phenology and therefore likely pre-empted resources and gained a size advantage, making them the superior competitor.

Conclusion: Native perennial grasses can outcompete exotic plants for resources if planted earlier in the season. This resource pre-emption appears to be more important than resource use over a longer period with C3 and C4 plants together and could be an effective restoration strategy.

KEYWORDS

annual grasses, competition, invasibility, life-history, Mediterranean-type climates, niche partitioning, perennial grasses, priority effects, resource pre-emption

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1 | INTRODUCTION

Invasive species can impact ecosystems profoundly (D'Antonio & Meyerson, 2002; Kulmatiski, 2006), and often hinder restoration of natural systems. Davis et al. (2000) suggested that a biotic community is more susceptible to invasive species when resource availability is greater than resource use for a significant period. Therefore, high plant density could increase resistance to invasive species if density increases resource use intensity. However, this strategy can also cause strong competition, which could exclude less-competitive reintroduced species (Antonovics & Levin, 1980; Čuda et al., 2015). Niche complementarity has also been suggested to reduce the performance of invasive species because species that use resources in a variety of ways can deplete a broad spectrum of resources, increasing the chance of niche overlap with potential invaders (Elton, 1958; Gooden & French, 2015). Given that the ability of a species to capture resources is strongly influenced by the seasonal timing of life-history events (germination, growth and reproduction), incorporating phenological differences into a system may be a way to reduce invasibility (Maron & Marler, 2007). In addition, density-dependent effects are often stronger in intraspecific competition than with interspecific competition (niche complementarity; Abrams, 1983; Tilman, 1982), therefore, a higher density of target plants may result in less intraspecific competition in phenologically diverse plantings. Interestingly, how the interaction between phenologically different plants and density affects the resistance to invaders has been seldom explored experimentally (but see Connolly et al., 1990) and few studies consider the performance of the native plants in the mix, with the focus of most studies on invasibility (but see Maron & Marler, 2008).

Species that start growth early in a season can pre-empt resources and thus influence the establishment and growth of later-emerging species, a process known as priority effects (Facelli & Facelli, 1993b; Grman & Suding, 2010). In Mediterranean-type grasslands where water is a limiting resource, such as those found in southern Australia and California, the highest productivity occurs over the winter and spring months because summers are dry. Priority effects from winter-growing (C3) invasive annual grasses are common in these areas because these species appear earlier in the season—i.e. when autumn rain breaks the summer drought—than C3 native perennial grasses, and thus the invasive plants attain competitive dominance via a seasonal-priority advantage and fast growth (Wainwright et al., 2012). Once established, they seem to be able to inhibit establishment of native grasses (Lenz et al., 2003). Therefore, overcoming this seasonal-priority advantage is critical to ensure successful re-establishment of native communities.

C3 plants can be superior competitors against annual invaders if they can overcome recruitment limitations, establish earlier and gain a size advantage (Grman & Suding, 2010; Perry et al., 2003; Seabloom et al., 2003). Suppression of early-emerging species by inter-seasonal effects from late-emerging species is uncommon, but not unheard of (Facelli & Facelli, 1993a; Lenz et al., 2003). Therefore, a suitable strategy against invasive species could be to incorporate

species with phenological differences, i.e. early- and late-growing species, resulting in resource use across a greater period (late autumn to mid-summer; Figure 1). In Mediterranean-type climates, C4 plants are active late in the growing season because their re-initiation of growth occurs after that of the C3 plants and they are the last to set seed before the soil dries out mid-summer. However, further investigations are needed to determine whether C4 plants can be competitive across seasons in Mediterranean-type climates where they are an important component of grassland communities (Cole et al., 2017).

We tested the hypothesis that C3 and C4 grasses, with peak growth at different times, would be more effective at suppressing invasive species when planted together than when planted separately (i.e. assemblages actively growing over a narrower period). We also hypothesised that higher densities would have stronger effects on invasive species. To achieve this, we planted different densities of C4 and C3 perennial grasses on their own (single-season assemblages) and together (extended-season assemblage). We measured the biomass of invasive species as the main response to determine the effectiveness of the various combinations of native grasses to suppress invasive annual grasses. We also investigated whether there was a trade-off between reduced invasion of exotics and the performance of planted species because this could have direct implications for restoration. We used two levels of plant density for each seasonal pattern assemblage and predicted that exotic biomass would be lowest in the extended-season high-density assemblages. We measured the performance of the planted assemblages by incorporating a weeded treatment to act as a baseline without the added impact of exotics. We predict that the reintroduced plants will be larger when planted at low density (more resources) and in extended-season assemblages (niche complementarity). We also measured levels of available resources (soil water and soil nutrients) to test whether the

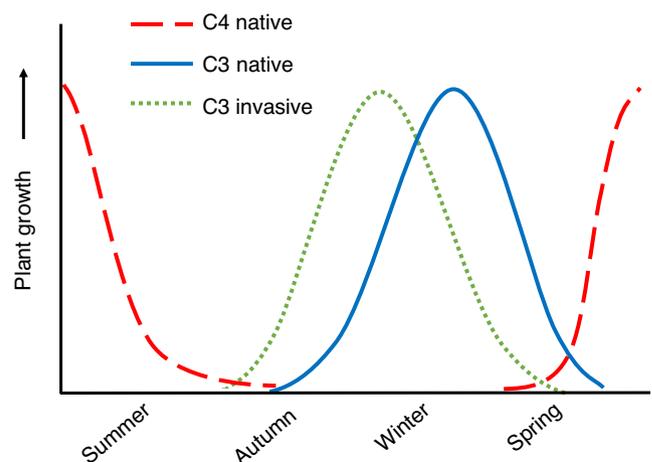


FIGURE 1 Schematic diagram of the active growing times (thus resource use) for native perennial grasses that are summer growing (C4 native) or winter growing (C3 native) and invasive annual grasses (C3 invasive) throughout the four seasons in a Mediterranean-type climate

responses of exotic species correspond to patterns of resource availability created by the resident community.

2 | METHODS

2.1 | Study site and species

The study was undertaken at Para Woodlands Reserve, South Australia, (34.628°S, 138.785°E) in an abandoned field that was a continuously cultivated cereal crop until 2004. The region has a Mediterranean-type climate with a mean annual air temperature of 23.6°C and an annual average rainfall of 450 mm (winter-dominated; Bureau of Meteorology, 2017). All plants present at the site before the experiment were invasive species, dominated by winter-growing annual grasses (mainly *Avena barbata*, but see Appendix S1 for methods and results of a pilot study and see Smith et al., 2020 for more site information on the system).

Four native grass species were chosen as test species based on their presence locally in grasslands and open grassy woodlands, and because they are commonly used in restoration practices in the area. They represent two patterns of seasonal growth: C3 grasses, *Rytidosperma caespitosum* and *Austrostipa flavescens*; or C4 grasses, *Enneapogon nigricans* and *Themeda triandra*. All species are perennial grasses; however, their tussocks vary in size and therefore are likely to vary in response to intraspecific and interspecific competition (Table 1; Jessop et al., 2006).

2.2 | Experimental design and implementation

The experiment included three combinations of seasonal growth patterns: two single-season growth treatments, C3 species planted together (single-C3 treatment hereafter) and C4 species planted together (single-C4 treatment hereafter); and an extended growth season treatment (all C3 and C4 species planted together, extended treatment hereafter). Two planting densities, high (44 plants/m²) and low (20 plants/m²), were chosen based on Greening Australia's revegetation guide for temperate grasslands (www.greeningaustralia.org.au). Planting density was used in combination with the seasonal growth patterns (planting assemblages hereafter) and each species in the planting assemblages was represented in equal numbers. To measure the performance of all species in each planting

assemblage combination, we included both C3 species in the single-C3 and extended assemblages and the same for the two C4 species. Each planting assemblage was repeated in 12 plots, half of which were weeded by hand regularly while the other half remained unweeded. Six replicates for each treatment combination resulted in 72 experimental plots (3 seasonal growth patterns × 2 densities × 2 weeding × 6 replicates).

Plots (1 m × 1 m) were established 3 m apart in May 2015 in a randomised block design to account for the differences in soil characteristics and topography (see Appendix S2 for details). The native grasses were grown from locally sourced seed during winter/spring 2014 at South Para Nursery (Kersbrook, South Australia). Seedlings were kept outside under shade, weeded regularly, watered using an automatic watering system and then planted as tubestock plants approximately 1 year after germination. Owing to the different phenology of the C3 and C4 species, planting was timed to suit the environmental conditions required by each group, i.e. C3 species were planted in May following the first substantial rains and C4 species were planted the following August. Plants were evenly spaced and randomly located within a template. During the establishment period (May to September 2015) all plots were weeded regularly. Afterwards only the plots in the weeded treatment continued to have any volunteering plant removed.

2.3 | Data collection

Survival of planted grasses was recorded every 3 weeks and dead plants were replaced in June (winter) and October (spring) 2015 and again in May 2016 using the same cohort of tubestock plants. The summer (December–February) was too dry to justify replanting. Supplement watering—20 L per plot—was required on two occasions to maintain the young experimental plants alive, once on 21 January and again on 19 February. Above-ground biomass was harvested between 5 and 25 October (spring) 2016 and all samples were dried for 48 h at 60°C and weighed. Replants from 2016 were not used in biomass analysis to account for differences between field and glasshouse conditions. Native plants were weighed individually, whereas exotic biomass was considered as all standing material, after the native plants were removed, in the unweeded plots.

Soil samples (10 cm diameter × 10 cm deep) were collected at the time of harvest, to measure differences in soil conditions that could reflect differences of resource use in each treatment

TABLE 1 Phenology of the test species

Functional group	Species	Max. height (cm)	Max. width (cm)	Leaf blade description	Flowering time
C4	<i>Themeda triandra</i>	150	50	Flat, 10–30 cm long, 1–8 mm wide	Summer
	<i>Enneapogon nigricans</i>	55	20	30 cm long, 1–5 mm wide	Summer
C3	<i>Rytidosperma caespitosum</i>	90	40	15–35 cm long, 1–4 mm wide	Spring
	<i>Austrostipa flavescens</i>	140	40	9–54 cm long, 2–7 mm wide	Spring

combination. The samples were collected from two random locations within the central section of each plot and combined as a single sample. Physiochemical analyses were carried out at CSBP laboratories (Bibra Lake, WA, USA) to measure nitrate nitrogen, ammonium nitrogen, plant-available (Colwell) phosphorus, potassium (Colwell), organic carbon (Walkley-Black), conductivity and pH (CaCl_2).

Long-term (1885–2016) daily precipitation and temperature data were collected from the Roseworthy Bureau Station (Bureau of Meteorology, 2017) and summarised to compare with conditions during the study. In three randomly selected experimental blocks (one, five and six; Appendix S2), soil volumetric water content (VWC) at 10–15 cm (%) was collected every 2 hr using Decagon 5TM soil moisture sensors (Decagon Devices Inc., Pullman, WA, USA) from 7 May to 5 October 2016.

2.4 | Data analysis

All analyses were conducted in R (version 3.3.3, R Core Team, 2017, R Foundation for Statistical Computing, Vienna, AT) and are described in detail in Appendix S3. Briefly, linear mixed models were used to analyse all plant biomass data. Exotic biomass was tested against seasonal pattern (extended, single-C3 and single-C4) and density as fixed effects and block as a random effect. The biomass of native plants, based on individual plant biomass without the 2016 replacements, was tested using the same factors as the exotic biomass model plus two additional fixed factors of weeding treatment and species, and there were only two levels of seasonal patterns (extended and the relevant single treatment for the species being tested). The total biomass of all plants per plot (including 2016 replacements and exotic plants) at the time of harvest (assemblage biomass hereafter) was analysed using linear models with the same fixed factors as individual native biomass. To analyse survival data, we fitted parametric survival models with seasonal pattern, density, weeding and species as fixed effects and block as a random effect, and a Weibull distribution.

Similarly, soil physiochemical properties were analysed separately as a function of seasonal pattern, density and weeding with block as a random factor. To determine differences in soil VWC between planting assemblages, the daily precipitation data collected at Roseworthy bureau station was used to determine drying-off periods (DPs). Six DPs were chosen as a single day during the 2016 growing season (winter, May–October) that followed five consecutive days of low rainfall, i.e. < 2 mm in 5 days for DP1–DP4 or < 6 mm for DP5 and DP6 (Figure 2). Soil VWC was then analysed as a function of seasonal pattern, density and weeding using linear models. However, owing to technical difficulties, there was never a time when all probes were working, therefore at each DP at least one treatment only had two replicate measurements. Multiple testing was accounted for by applying a Bonferroni correction to all p -values, whereby the adjusted alpha is set to 0.05/number of tests.

3 | RESULTS

3.1 | Exotic biomass

Exotic biomass was lowest when native plants were planted in high density (ANOVA, $p < 0.01$) and in the single-C3 treatment, and highest in the single-C4 treatment (Figure 3; ANOVA, $p < 0.01$). There was no interaction between density and seasonal pattern of native plants (ANOVA, $p = 0.82$).

3.2 | Native plant survival

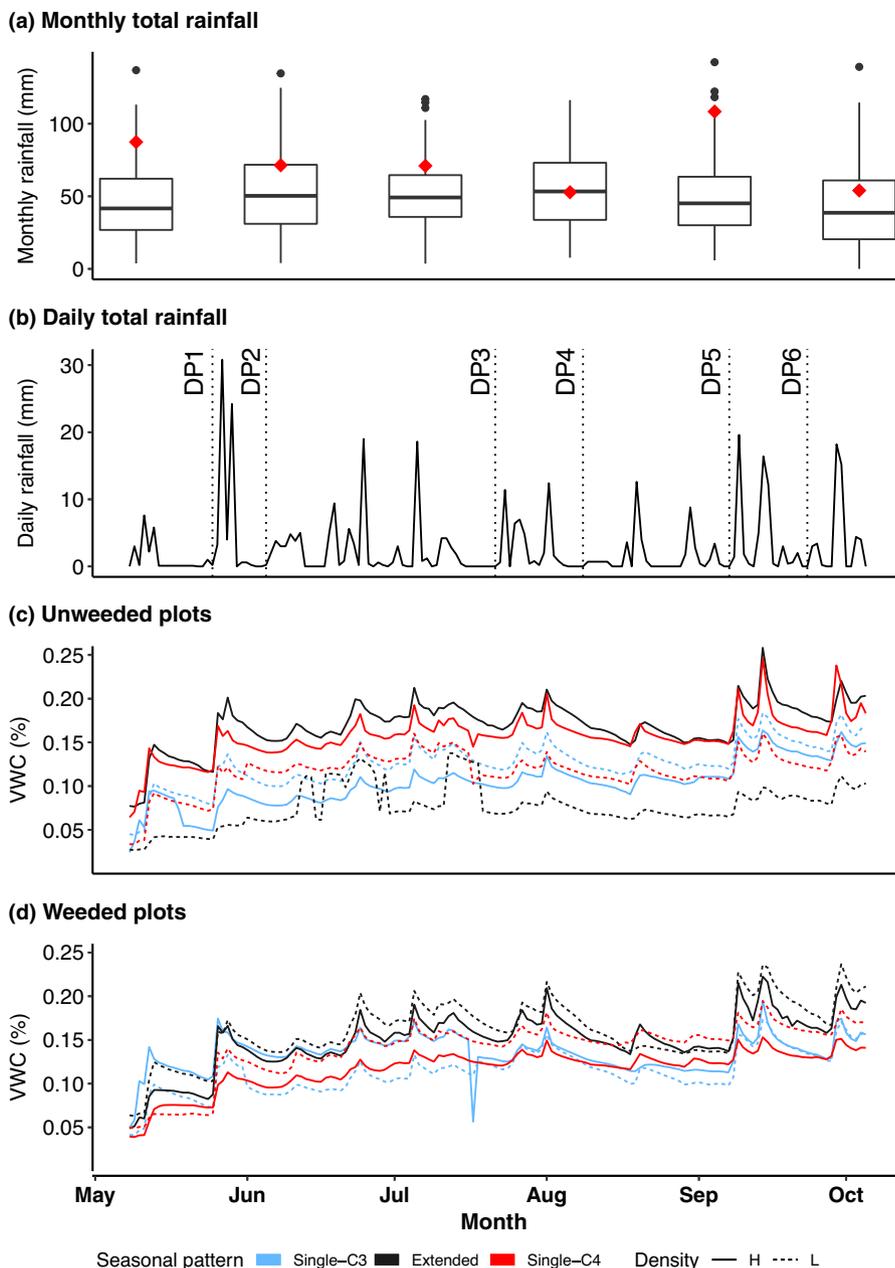
Of 3,004 native plants originally planted 5 were unaccounted for, and thus removed from analysis, and 304 died: 1 *R. caespitosum*, 134 *A. flavescens*, 69 *E. nigricans* and 100 *T. triandra*. For both C4 species, survival was reduced when planted in the extended treatment (Table 2a; Figure 4). Post hoc comparisons found that only *T. triandra* had lower survival in high-density plots (Tukey, $p = 0.04$) and only *E. nigricans* had higher survival when weeded (Tukey, $p < 0.01$; Figure 4). The two C4 species differed in their survival over time, but only in weeded plots (Tukey, $p < 0.01$) and high-density plots (Tukey, $p < 0.01$) where survival of *E. nigricans* was higher in both cases (Figure 4). For the C3 species, survival was higher for *R. caespitosum* than *A. flavescens*, and in low-density plots compared with high-density plots, and when planted in the extended treatment compared with the single treatment (Figure 4). There was no effect of weeding. See Table 2a for ANOVA results.

3.3 | Native plant biomass

Individual biomass was always higher for both C3 and C4 species when planted at low density (Table 2b; Figure 5). The differences in biomass between species within seasonal patterns were also significant, with *R. caespitosum* > *A. flavescens* (C3) and *T. triandra* > *E. nigricans* (C4) (Table 2b; Figure 5). For the C4 species, the individual biomass was always larger in the single treatment than in the extended treatment (Table 2b) and weeding only resulted in higher biomass in the single treatment (Tukey, $p < 0.01$) and not in the extended treatment (Tukey, $p = 0.38$; Figure 4). For the C3 species, we considered the three-way interaction between seasonal pattern, density and weeding as marginally significant and worth investigating via post hoc comparisons ($p = 0.054$). Also, there were three significant two-way interactions involving these factors suggesting that they are impacting on each other in complex ways (Table 2b). Overall, the individual biomass of C3 species was larger in the weeded plots, except when planted on their own (single treatment) at low density (Tukey, $p = 0.65$; Figure 5). Similarly, C3 species grew larger in the extended treatment except when grown in low-density unweeded plots (Tukey, $p = 0.06$; Figure 4).

For the total above-ground biomass per plot of each native species, we found that the total biomass of C3 native plants was always

FIGURE 2 Rainfall and mean soil volumetric water content (VWC) from May to October (winter months). Monthly total rainfall (a) from 1885 to 2016 is characterized by box and whisker plots, where the boxes show the 25th and 75th percentiles and the whiskers show 1.5x interquartile range. Red diamonds represent the total monthly rainfall during the sampling year (2016). Daily rainfall data during 2016 (b) was used to select drying-off periods (DP) throughout the season to use for comparisons in soil moisture in unweeded (c) and weeded (d) plots. The colour of the lines represents the seasonal pattern and line type represents the density of native grass planting. Monthly and daily data are from Roseworthy weather station (Bureau of Meteorology, 2017)



higher in weeded plots (Table 2c; Figure 6). As with the individual biomass, the total biomass of *R. caespitosum* was always larger than *A. flavescens* (Figure 6). Further comparisons found that total biomass was lower in extended treatments and low-density planting for *R. caespitosum* (Tukey, $p < 0.01$ for both), but not for *A. flavescens* (Tukey, $p = 0.61$ and $p = 0.28$ respectively, Figure 6). For the total biomass of C4 plants, most post hoc comparisons were highly significant (Tukey, $p < 0.01$) indicating that total biomass was always higher for *T. triandra* than for *E. nigricans* (reflecting individual biomass results), in high-density compared with low-density plots and in the single treatment compared with the extended treatment (Figure 6). Weeding resulted in higher total biomass in the single treatment (Tukey, $p < 0.01$), but not the extended treatment (Tukey, $p = 0.84$; Figure 6).

3.4 | Community biomass

Planned comparisons found that the community biomass (total above-ground biomass of all plant material per plot) was higher in the unweeded plots (Tukey, $p < 0.01$) except in the single-C3 plots where there was no difference (Tukey, $p = 0.21$; Figure 6). Over both levels of weeding treatment, total biomass was lower in the single-C4 plots than in the extended and single-C3 plots (Tukey, $p < 0.01$ for all; Figure 6). Community biomass was always lower in the weeded plots for both high- and low-density communities (Tukey, $p < 0.01$). Community biomass was lower in low-density plantings in weeded plots (Tukey, $p < 0.01$), but not in the unweeded plots (Tukey, $p = 0.81$; Figure 6). See Table 3 for ANOVA results.

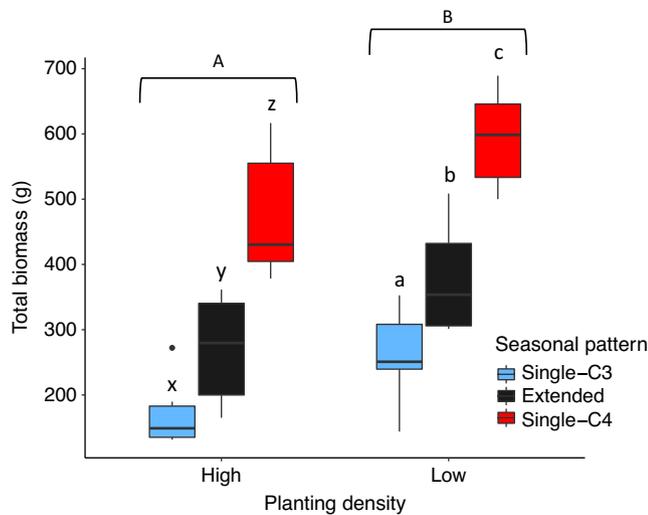


FIGURE 3 Total above-ground biomass of all exotic plants in experimental plots where native grasses were planted at high or low density or in different seasonal patterns. Significant differences in biomass, using Tukey's honest significant difference tests, are indicated by different letters, upper case for density and lower case for seasonal pattern ($N = 36$). The median is represented by the line inside the boxes; boxes show the 25th and 75th percentiles and whiskers show 1.5 \times interquartile range

3.5 | Soil properties

Of the seven soil physiochemical properties measured at the time of harvest, three were not affected by the treatment combinations, namely ammonium nitrogen, potassium and conductivity (Table 4; ANOVA results in Appendix S3). Nitrate nitrogen and organic carbon were higher in high-density plots (ANOVA, $p = 0.01$ and $p < 0.01$ respectively), whereas available phosphorus was higher in weeded plots (ANOVA, $p < 0.01$) and in the extended treatment compared with the single-C3 treatment (ANOVA, $p < 0.01$; Table 4). There was a statistically significant three-way interaction for pH ($p = 0.04$) and post hoc comparisons found that pH was lower in unweeded plots but only in high-density single treatments (Tukey, $p < 0.01$ and $p = 0.04$ respectively). In addition, there was lower pH in the high-density, single-C3, unweeded plots (Tukey, $p < 0.01$; Table 4).

In general, there was less variation in soil VWC in the weeded plots; however, there was no significant difference between weeded and unweeded plots after p -adjustments at any of the DPs. There was a significant difference between seasonal pattern treatments on three occasions mid-season, DP2 (4 June), DP3 (21 July) and DP4 (8 August), and the single-C3 treatment was lowest on each occasion (p -adjusted < 0.01 at each DP; Figure 2). Density of planting was also important in determining VWC on three occasions mid-season, DP3 (21 July), DP4 (8 August) and DP5 (7 September), where generally values were higher in high-density plantings, particularly in the unweeded plots (p -adjusted < 0.01 at each DP; Figure 2). There were no significant interactions after p -adjustments.

4 | DISCUSSION

It has been proposed that planting species with different seasonality of growth can be a potentially effective strategy to limit exotic invasion (Connolly et al., 1990; Maron & Marler, 2008). However, we found little evidence to suggest that planting perennial C3 and C4 grasses together is an effective method to reduce the performance of exotic annual C3 species. Although this planting strategy was more effective at reducing exotic biomass than planting C4 grasses on their own, C3 native grasses, particularly *R. caespitosum*, were the superior competitors and resulted in the greatest reduction in exotic plant biomass when planted on their own. It has also been proposed that higher density plantings can reduce weed invasion by reducing resources available for invading plants (Davis et al., 2000). We did find evidence in support of this hypothesis, because higher density plantings had lower exotic plant biomass. However, there was a trade-off with reduced individual growth among the native plants in higher density plots, a result that was consistent across all combinations of seasonal patterns. Interestingly, in low-density communities, the total biomass of the whole community was always lower in these treatments than in the high-density treatments when weeds were not present, despite higher individual biomass. Therefore, the number of individuals planted seemingly limits growth of the native community. Further, native C3 species were strong competitors against the C4 species, probably because of a priority effect, as shown by reduced survival and biomass of C4 plants in the extended treatments compared with the single treatments.

4.1 | C3 native plants are effective against invasive plants

There are a few possible explanations why the native C3 species were the most effective competitors against the exotic C3 species. First, the C3 natives had a well-established root system by the time the seedlings of the invasive species started to establish and therefore were able to pre-empt resources and outcompete the invading exotic plants (size-asymmetric competition, Perry et al., 2003; Weiner, 1985). This was emphasised by a reduction in two key soil resources, phosphorus and water content, to the lowest levels in the single-C3 treatment indicating that the native C3 species are strong below-ground competitors.

Second, many studies have found that resident species inhibit invaders from their own functional group more strongly than other functional groups (Dukes, 2001; Emery, 2007; Fargione et al., 2003; Gooden & French, 2015; Maron & Marler, 2007). The mechanisms for this competitive dominance can vary but most relate to niche overlap between similar species (limiting similarity, Abrams, 1983). Given that the C3 invasive species actively grow at the same time as the C3 natives it is likely that they were inhibited by an overlap in resource use. One example of resource overlap in our results was with phosphorus, which decreased both in the single-C3 plots (compared

TABLE 2 Results from the (a) parametric survival models, (b) linear mixed model and (c) linear models for the response variables of the planted native grass communities as a function of seasonal pattern (extended or single), density (high and low), weeding treatment (weeded and unweeded) and species (C3 = *Rytidosperma caespitosum* and *Aurolispa flavescens*; C4 = *Themeda triandra* and *Enneapogon nigricans*)

Fixed factors	df	(a) Survival (N = 2,999)				(b) Individual biomass (N = 2,695)				(c) Total biomass (N = 72)			
		C3		C4		C3		C4		C3		C4	
		χ^2	p-value	χ^2	p-value	χ^2	p-value	χ^2	p-value	SS	p-value	SS	p-value
Seasonal pattern (SP)	1	13.67	<0.01	98.54	<0.01	141.81	<0.01	260.79	<0.01	6.62	<0.01	778.35	<0.01
Density (D)	1	24.51	<0.01	0.65	0.42	3138.89	<0.01	218.79	<0.01	416.7	<0.01	137.44	<0.01
Weeding (W)	1	0.32	0.57	10.38	<0.01	303.66	<0.01	15.39	<0.01	1.92	0.02	71.18	<0.01
Species (S)	1	198.85	<0.01	9.51	<0.01	33.99	<0.01	56.85	<0.01	4.38	<0.01	49.73	<0.01
SP × D	1	0.53	0.47	0.08	0.77	7.47	0.01	3.21	0.07	2.75	<0.01	49.86	<0.01
SP × W	1	0.66	0.42	0.17	0.68	0.18	0.67	0.01	0.93	0.46	0.24	24.78	<0.01
D × W	1	2.05	0.15	0.31	0.58	0.69	0.41	3.00	0.08	8.14	<0.01	2.12	0.38
SP × S	1	2.90	0.09	2.78	0.10	4.92	0.03	13.13	<0.01	0.69	0.15	17.16	0.01
D × S	1	0.24	0.63	14.76	<0.01	4.12	0.04	3.04	0.08	0.33	0.32	1.85	0.42
W × S	1	1.09	0.30	10.89	<0.01	0.23	0.63	2.47	0.12	0	0.99	0.01	0.97
SP × D × W	1	0.09	0.77	0.13	0.72	0.57	0.45	1.07	0.30	0.01	0.84	10.48	0.05
SP × D × S	1	0.00	1.00	2.34	0.13	1.71	0.19	0.08	0.78	0.32	0.33	0.03	0.91
SP × W × S	1	0.00	1.00	1.69	0.19	3.73	0.05	0.00	0.96	0.18	0.46	0	0.99
D × W × S	1	0.00	1.00	0.08	0.78	0.18	0.67	1.91	0.17	0.07	0.63	1.2	0.51
SP × D × W × S	1	-2.90	1.00	0.77	0.38	0.05	0.82	0.59	0.44	0	0.94	0.31	0.74

Note: Analysis was carried out separately for C3 and C4 plants. Significant ($p < 0.05$) factors are shown in bold. Abbreviation: SS, Sum of Squares.

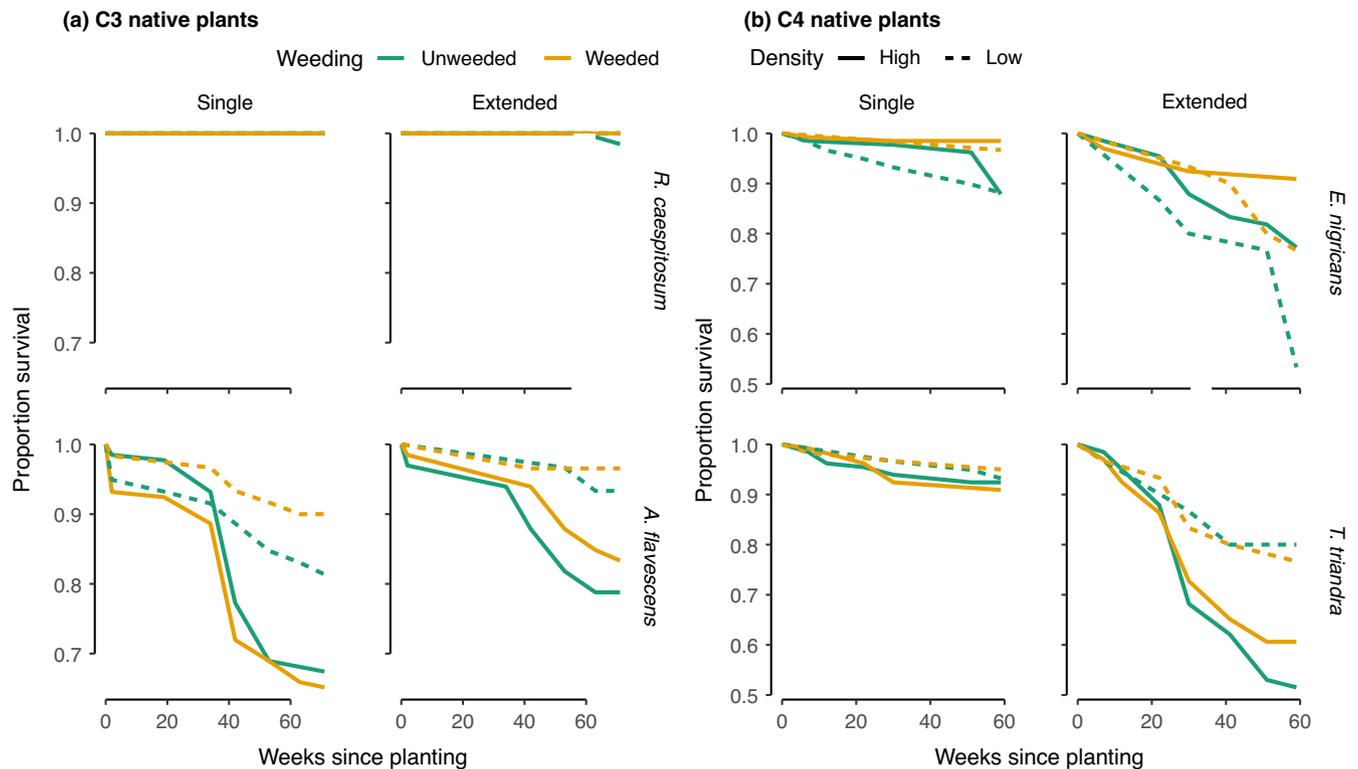


FIGURE 4 The proportion of survival for (a) C3 (*Rytidosperma caespitosum* and *Austrostipa flavescens*) and (b) C4 (*Enneapogon nigricans* and *Themeda triandra*) native plants over the course of the experiment (in weeks since planting from 28 May 2015 [C3 plants] or 19 August 2015 [C4 plants]; $N = 2,999$ individual plants). The left-hand panels show survival when the plants were grown in single-season assemblages and the right-hand panels show survival in extended-season assemblages. Planting density is represented by line type, and line colour represents weeding treatment

with when C4 plants were present) and when weeds were present (compared with the weeded plot).

Although our previous work has shown that *A. barbata* may prevent native perennial grass establishment via establishing through residual effects (i.e. positive feedback from the microbial communities or litter accumulation; Lenz et al., 2003; Smith et al., 2018a), perennial grasses have been shown to be superior competitors against this annual invader in the USA (Corbin & D'Antonio, 2004; Lulow, 2006). These studies demonstrated that the perennial grasses become more competitive over time as they grew larger in each successive year after planting. One explanation for this advantage is that annual species tend to allocate fewer resources to roots and more resources to leaf and seed production (Grime & Hunt, 1975; Jackson & Roy, 1986), which results in faster growth above-ground but makes them weaker competitors for below-ground resources compared with perennials (Garnier, 1991; Tilman, 1982). An earlier start in growth, such as in our study, and a well-established root system would allow perennials to take advantage of this difference and, in particular, exploit deeper water resources (Dyer & Rice, 1999; Seabloom et al., 2003). In addition, this earlier start may have allowed beneficial microbes to establish and create positive feedback for the native C3 grasses (Klironomos, 2002; Smith et al., 2018a, 2018b).

4.2 | C4 native plants were not strong competitors

The establishment time for the C4 species in our study may not have been sufficient to make them successful competitors. Another southern Australian study (but with higher average rainfall, particularly in summer), found that *T. triandra*, the dominant C4 species in our study, took longer than other species to become established (Gibson-Roy et al., 2009). We attempted to overcome this delay by planting mature tubestock plants rather than using direct seeding. Therefore, our native grasses would have been more developed than those in the study by Cole et al. (2017) who found that *Austrostipa* (C3 species) swards with successful recruitment of C4 grasses, including *T. triandra*, suppressed exotic annuals more than the *Austrostipa*-only. Alternatively, the climatic conditions may not have favoured the C4 species and thus have made them less competitive. For example, these species may depend on summer rains to become established or build up their individual tussock sizes (Cole et al., 2017; Lodge, 1981), whereas our site had below average rainfall over the summer (we watered to the average rainfall to aid establishment). In addition, the very wet spring of 2016 (200 mm above average; Figure 2) may have provided ideal conditions for the C3 plants (native and exotic) and given them a competitive edge over the C4 species. This may have been particularly important if

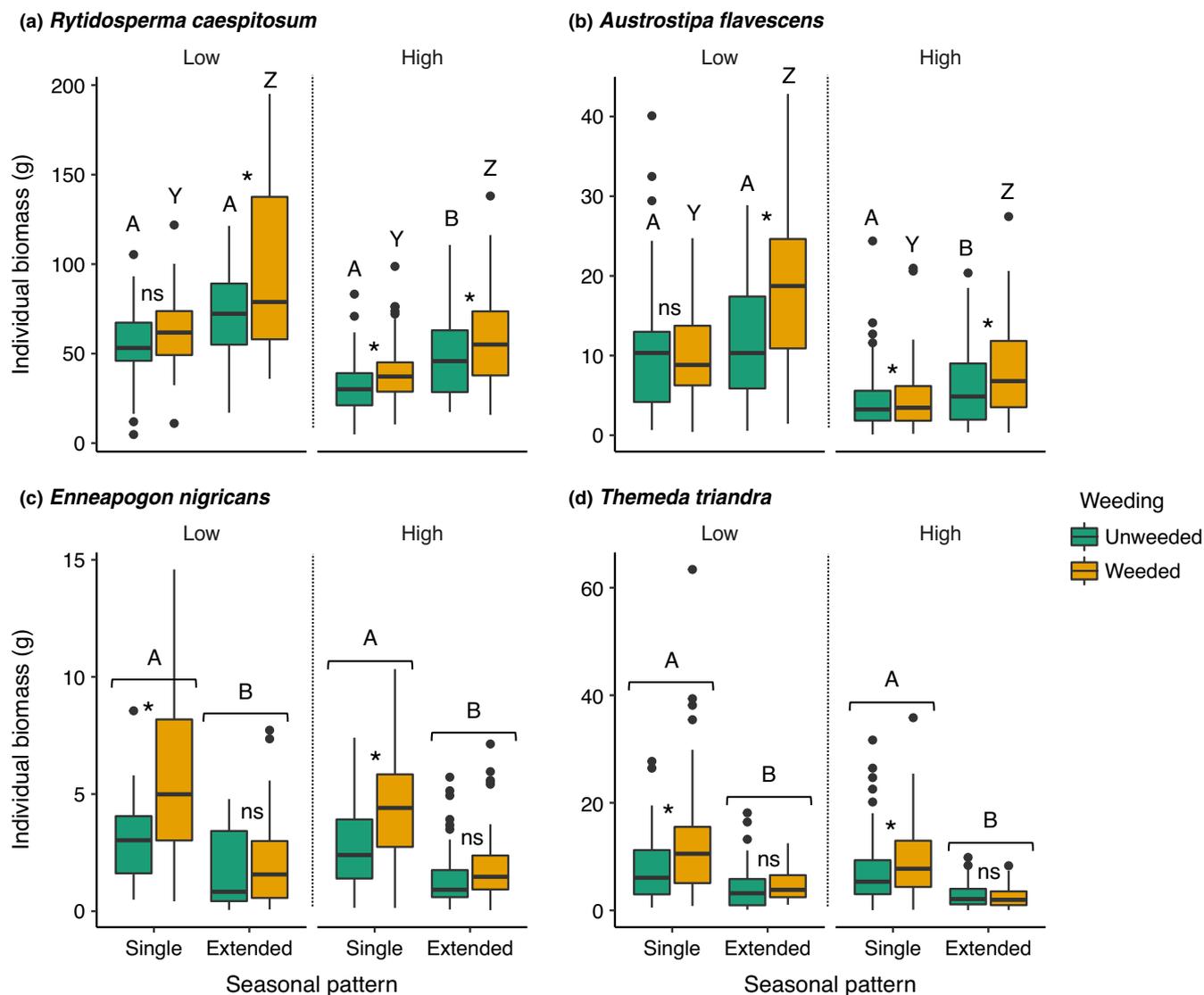


FIGURE 5 Individual above-ground biomass of C3 (upper) and C4 (lower) native plants ($N = 2,695$) when grown in either single-season assemblages or extended-season assemblages, at different densities (low = left of dotted line; high = right of dotted line) and weeding treatments (colours). The median is represented by the line inside the boxes; boxes show the 25th and 75th percentiles and whiskers show 1.5 \times interquartile range. Asterisks indicate significant differences between weeded and unweeded plots after Tukey's honest significant difference tests. ns: non-significant. Differences in biomass between seasonal pattern is indicated by different letters. In panels a and b letters indicate differences in biomass between seasonal pattern treatments within weeding treatments (AB for unweeded; YZ for weeded). Panels c and d show differences in biomass between seasonal pattern regardless of weeding treatment. These are based on planned comparisons following the ANOVA results in Table 2

the rains extended the growth of the C3 species to later in the season, increasing their biomass and creating resource pre-emption in the other direction we predicted. This is supported by Young et al. (2017) who found that priority effects were stronger in years with higher rainfall. In addition, the C4 species have a higher water use efficiency and therefore might not be as competitive in these wetter conditions (Ehleringer & Monson, 1993).

Reduced overlap in seasonality could also explain why the treatments that included native C4 species (single-C4 or extended season treatments) were less effective than the single-C3 treatment at reducing invasive species biomass. Because competition

between species with overlapping niche requirements, in space and time, is more intense than between those with different requirements, C4 grasses were likely not competing for the same resources (time separation) with the C3 invasive species, making them less-effective competitors. Given that the C4 grasses were actively growing later in the season, they were using limiting resources, such as water, at a different time to the invasive species which appeared earlier in the season (Figure 1). Thus, we did not detect any evidence of the pre-emptive effects we hypothesised that C4 grasses could have on invasive grasses starting their cycles in early autumn.

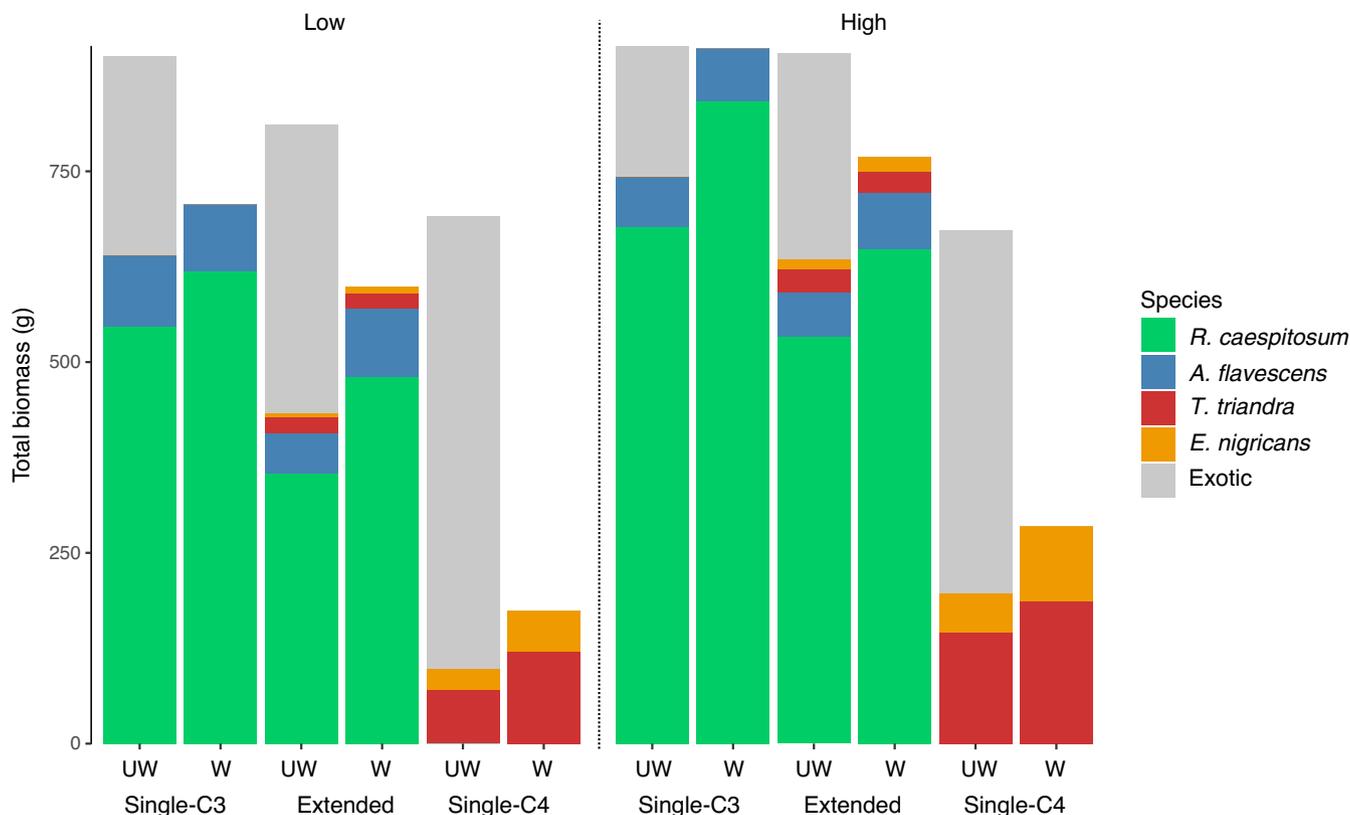


FIGURE 6 Mean total biomass of all standing plant material at the time of harvest in each community type; high and low density (low = left of dotted line; high = right of dotted line), weeded (W) and unweeded (UW) and single or extended seasonal patterns. Colours represent the mean total biomass of each native species and grey represents the total biomass of exotic plant material in the unweeded plots ($N = 72$)

TABLE 3 Results from the linear model for the community biomass as explained by seasonal pattern (extended, single-C3, single-C4), density (high and low) of the native plant community assemblages and weeding treatment (weeded and unweeded)

Factor	df	SS	p-value
Seasonal pattern (SP)	2	59.10	<0.01
Density (D)	1	4.26	<0.01
Weeding (W)	1	30.56	<0.01
SP × D	2	0.08	0.87
SP × W	2	19.87	<0.01
D × W	1	2.68	<0.01
SP × D × W	2	0.39	0.50

Note: Significant ($p < 0.05$) factors are shown in bold ($N = 72$).

Abbreviation: SS, Sum of Squares.

4.3 | Density effects

High-density planting reduced the biomass of both the exotic (total biomass) and native plants (individual biomass) and reduced the survival of *T. triandra* and *A. flavescens*, demonstrating a trade-off between a desirable effect on exotic species and an undesirable impact on native species. Indeed, this competitive effect could also be stronger on

minor components of the native community and lead to reduced diversity of restored communities and therefore be considered in restoration projects. Interestingly, there were no reductions in soil moisture or nutrients in high-density plantings suggesting other resources that were not measured, such as light availability, may have been more important (Dyer & Rice, 1999; Kardol et al., 2013). The increased growth of individual native plants in low-density communities did not result in the whole community biomass of native plants being the same between density treatments (in weeded plots). This suggests that the density of planting limits growth of the native community as a whole, at least within the time frame used here. There was no difference between total biomass of high- and low-density treatments in the unweeded plots, therefore the exotic species appear to be using up the remaining resources in the low-density communities, as evident by the increase in biomass of exotic species in these communities.

We predicted that competition in high-density plots would be more intense in the single-season treatment than the extended-season treatments due to resource partitioning in the later; however, there was no interaction between seasonal growth patterns and density for native plant biomass showing that these mechanisms acted independently. We planted the native species in higher densities than they are found naturally in Para Woodlands Reserve and nearby areas (Lenz & Facelli, 2005; Rosser, 2013); however, these species (or ecologically similar species from the same genus) have

TABLE 4 Mean (\pm SD) of soil physicochemical properties for the different community assemblages ($n = 6$) at the time of harvest

Functional complexity	Density	Weeding	NH ⁴⁺ -N (mg/kg)	NO ³⁻ -N (mg/kg)	P Cowell (mg/kg)	K (mg/kg)	Organic C (%)	Conductivity (dS/m)	pH (1:5 CaCl ₂)
Single-C3	High	UW	5.0 \pm 0.9	8.7 \pm 2.3 ^a	19.3 \pm 2.3 ^{ly}	822.3 \pm 28.8	2.8 \pm 0.5 ^a	0.09 \pm 0.03	6.6 \pm 0.6 ^{la}
Single-C3	High	W	5.2 \pm 1.5	9.8 \pm 4.2 ^a	20.2 \pm 4.1 ^{m,y}	814.0 \pm 78.3	3.0 \pm 0.4 ^a	0.12 \pm 0.02	7.1 \pm 0.4 ^m
Single-C3	Low	UW	5.0 \pm 2.2	8.2 \pm 1.5 ^b	16.7 \pm 3.4 ^{ly}	776.3 \pm 81.5	2.6 \pm 0.2 ^b	0.11 \pm 0.01	7.2 \pm 0.4 ^b
Single-C3	Low	W	5.0 \pm 1.8	7.5 \pm 2.1 ^b	17.0 \pm 4.5 ^{m,y}	769.2 \pm 47.8	2.4 \pm 0.3 ^b	0.10 \pm 0.03	7.0 \pm 0.5
Extended	High	UW	5.7 \pm 1.4	9.3 \pm 2.7 ^a	22.7 \pm 9.2 ^{lz}	795.8 \pm 82.3	2.7 \pm 0.4 ^a	0.11 \pm 0.03	7.0 \pm 0.7
Extended	High	W	4.2 \pm 0.4	7.8 \pm 1.2 ^a	26.3 \pm 6.6 ^{m,z}	822.0 \pm 80.4	2.9 \pm 0.4 ^a	0.11 \pm 0.04	7.2 \pm 0.5
Extended	Low	UW	4.7 \pm 1.9	7.2 \pm 1.5 ^b	22.2 \pm 6.8 ^{lz}	843.3 \pm 116.3	2.5 \pm 0.4 ^b	0.09 \pm 0.03	7.0 \pm 0.5
Extended	Low	W	4.5 \pm 1.2	7.8 \pm 1.3 ^b	26.3 \pm 9.5 ^{m,z}	822.0 \pm 59.5	2.5 \pm 0.3 ^b	0.10 \pm 0.03	7.2 \pm 0.5
Single-C4	High	UW	5.8 \pm 1.7	10.2 \pm 2.0 ^a	18.3 \pm 6.5 ^{lyz}	788.3 \pm 54.2	2.7 \pm 0.1 ^a	0.10 \pm 0.03	6.9 \pm 0.7 ^l
Single-C4	High	W	4.8 \pm 1.5	9.3 \pm 2.7 ^a	24.2 \pm 9.7 ^{m,yz}	756.5 \pm 51.6	2.6 \pm 0.3 ^a	0.11 \pm 0.03	7.3 \pm 0.5 ^m
Single-C4	Low	UW	4.2 \pm 1.0	8.2 \pm 1.0 ^b	16.2 \pm 3.4 ^{lyz}	749.2 \pm 85.5	2.4 \pm 0.2 ^b	0.11 \pm 0.04	7.3 \pm 0.4
Single-C4	Low	W	4.5 \pm 1.8	8.7 \pm 3.0 ^b	24.2 \pm 4.9 ^{m,yz}	820.3 \pm 62.1	2.3 \pm 0.1 ^b	0.10 \pm 0.03	7.2 \pm 0.6

Note: For the weeded treatment UW = unweeded and W = weeded. Differences between planting treatments using Tukey's honest significant difference tests are indicated by different letters (ab for density, yz for seasonal pattern, lm for weeding).

been recorded to occur at much higher densities, particularly after fire (Morgan, 1999). Perhaps we would see an interaction using higher densities than in this study.

4.4 | Competition within the native planted communities

Of the four native species planted, *R. caespitosum* grew the largest, had the lowest mortality (only one plant died) and had overall the strongest negative effect on the other species, making it the superior competitor. This suggests that, in this system, species identity is more important than their phenology (namely C3 and C4) in that plants that are intrinsically larger dominate and those weaker are more likely to be dominated, or suffer high mortality. This strong competitive effect is surprising given that these species, or at least species from the same genera, have been shown to co-exist in artificial communities of similar trials (Cole et al., 2017; Gibson-Roy et al., 2009) and in remnant areas of Para Woodlands Reserve (Rosser, 2013) and within the surrounding region (Hattersley, 1983; Hyde, 1995; Kirkpatrick et al., 1995). Therefore, it is likely that these species can co-exist because of the storage effect model (Chesson & Warner, 1981), whereby environmental variability promotes co-existence. For example, in the year we sampled, high spring rainfall would have favoured the C3 plants; however, years with a dry spring and wet summer may allow C4 plants to increase in abundance and this can buffer their populations against extinctions.

4.5 | Implications and future work

Here, we show that planting density and seasonal patterns in the assemblage can have profound effects on both the native and

invasive species and, interestingly, that these two factors did not interact. The extended season treatment was not as effective at reducing exotic biomass as we had predicted. Rather the evidence suggests that matching seasonal cycles to potential invaders and/or size asymmetric competition is more important for community resilience. Therefore, for successful restoration projects, it is important to consider the functional identity of potential invaders and ways to give the target community time to become established to attain a size advantage. Here, we used tubestock plants to achieve this advantage, which could be a method for small-scale projects, projects with strong volunteer participation or areas used as a seed source for surrounding areas. Larger scale projects that use direct seeding will need to find alternative ways to achieve this, such as thorough soil management and weed control prior to seeding and an investment in weed control for at least the first two years after seeding.

The somewhat unexpected result of the extended-season treatment being less effective at reducing exotic biomass also highlights the need to conduct these types of studies in different climates. Currently, most available literature comes from higher latitudes, where there is very little growth in winter, and shows that C4 grasses can be effective competitors in systems in which they actively grow in the middle of the growth season (Fargione et al., 2003) but perhaps suppression of early-emerging species by inter-seasonal effects from late-emerging species are less common. In addition, it appears that processes of pre-emption are important in the assembly of these communities as seen by the competitive dominance of the C3 native plants over those that arrived or were planted after, i.e. both the C4 native and C3 invasive species. Changing the planting time so that the native C4 are introduced first will help to decipher whether this is the case or if the climatic reasons mentioned above have more impact.

This study focused on the first season after establishment of a native community, which was shown to be important in determining

resistance to invasion of exotics (Gibson-Roy et al., 2009). The next stage would be to expand the time frame to determine how sustainable the community assemblages are and whether longer establishment times allow the C4 species to become more competitive. Future work could also benefit from incorporating higher diversity. We focused on grasses because during a pilot study, exotic grasses made up the majority of biomass with three exotic forbs only present in low abundances (<1% cover). However, at the time of harvest forbs made up 25% of the biomass regardless of treatment (data not shown). This increase could have been caused by a number of factors such as disturbance from planting or weeding or for climatic reasons, particularly higher rainfall in the winter months.

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AUTHOR CONTRIBUTIONS

MES, LMP and JMF conceived the study and designed the methodology. MES collected data, was the lead writer and performed the analysis. JMF assisted with the analysis and interpretation. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are openly available in FigShare at 10.6084/m9.figshare.16577705.v1.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1. Pilot vegetation study

Appendix S2. Soil sampling and design at the beginning of the experiment

Appendix S3. Detailed statistical analysis

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