

Competition for Nitrogen between Australian Native Grasses and the Introduced Weed *Nassella trichotoma*

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- **Background and Aims** *Nassella trichotoma* is an unpalatable perennial grass weed that invades disturbed native grasslands in temperate regions of south-eastern Australia. This experiment investigated whether elevated N levels, often associated with disturbance, increases the competitiveness of *N. trichotoma* relative to C3 and C4 native Australian grasses.
- **Methods** A pot experiment investigated competitive interactions between four native grasses, two C3 species (*Microlaena stipoides* and *Austroanthonia racemosa*) and two C4 species (*Themeda australis* and *Bothriochloa macra*), and *N. trichotoma* at three different N levels (equivalent to 0, 60 and 120 kg ha⁻¹) and three competing densities (zero, one and eight neighbouring plants), using an additive design.
- **Key Results** All native grasses were competitive with *N. trichotoma* at low N levels, but only *M. stipoides* was competitive at high N. High densities of native grasses (8:1) had a major competitive effect on *N. trichotoma* at all N levels. The competitive ranking of native grasses, across all N levels, on *N. trichotoma* was: *M. stipoides* > *A. racemosa* > *B. macra* > *T. australis*. The C3 species were generally more competitive than the C4 species and C4 grasses were not inherently more productive at low N levels, in contrast to the results of other studies.
- **Conclusion** To resist invasion from *N. trichotoma*, these native grasses need to be maintained at a high density and/or biomass. The results do not support the theory that species such as *N. trichotoma*, with high tissues density, are always less competitive than those of low tissue density; in this case competitiveness depended on N levels. The ability of *N. trichotoma* to accumulate biomass at a higher rate than these native grasses, helps to explain why it is a major weed in disturbed Australian native grasslands.

Key words: Australia, C3 and C4 competition, invasive species, *Nassella trichotoma*, native grasses, perennial grass weed, pot experiment, unpalatable grass.

INTRODUCTION

Nassella trichotoma is a C3 perennial grass native to temperate South America. It is unpalatable to livestock because of its high leaf fibre content (Campbell and Irvine, 1966), low tissue nutrient content (Campbell, 1965) and because of its growth habit—a moderate-sized tussock usually containing much senesced material (Campbell, 1998).

Over the past century *N. trichotoma* has invaded grasslands in south-eastern Australia (Jones and Vere, 1998; McLaren *et al.*, 1998), South Africa (Wells, 1974) and New Zealand (Healy, 1945), and has been recorded in the northern hemisphere (Ridley, 1930; Westbrooks and Cross, 1993). In Australia, *N. trichotoma* now occurs over more than a million hectares (Jones and Vere, 1998; McLaren *et al.*, 1998) and in some situations completely dominates grasslands (Campbell and Vere, 1995). The presence of *N. trichotoma* reduces grassland plant species diversity, and livestock production declines in proportion to *N. trichotoma* abundance (Auld and Coote, 1981). The management of *N. trichomata* is complicated because much

of the area invaded by *N. trichotoma* is steep and inaccessible, or site productivity is low (Jones *et al.*, 2000).

The invasion of pastures by *N. trichotoma* is commonly associated with heavy grazing (Healy, 1945; Campbell, 1977). Continuous grazing combined with other disturbances has changed the composition of most native grasslands (Moore, 1970; Garden and Bolger, 2001); species that are less grazing-tolerant, e.g. *Themeda australis*, have been reduced in abundance or eliminated (Mott *et al.*, 1992). The reduced native perennial grass biomass offers little competition to invading *N. trichotoma* plants (Campbell and Vere, 1995; Badgery, 2004).

Pasture composition is shaped by a complex of mechanisms including competition for more than one resource. In the generally nutrient-poor soils where *N. trichotoma* commonly invades, competition for nutrients is one of the more important mechanisms. Australian native grasses have evolved generally under lower soil fertility (especially N) than has *N. trichotoma* (Badgery, 2004). Moreover, the Australian flora contains a significant number of C4 perennial grasses and it has been postulated that these have the ability to grow at lower soil N concentrations than C3 grasses (Wedin and Tilman, 1996). In the absence of defoliation, and at low soil N concentrations, it might

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be expected that *N. trichotoma* would be less competitive than Australian native perennial grasses, especially C4 species, in the absence of grazing. If true this would be important for weed management.

The relationship between *N. trichotoma* and other perennial grass species and the interaction with grazing has been described from field studies (Badgery *et al.*, 2002). However, little research has examined the mechanisms that underpin the responses between these species. Understanding these competitive relationships is considered central to the development of integrated weed management systems for *N. trichotoma* (Michalk *et al.*, 1999).

In the study reported here (part of a wider programme investigating the ecology and management of *N. trichotoma*) competitive relationships between *N. trichotoma* and the Australian native perennial grass species (*Austrodanthonia racemosa* and *Microlaena stipoides*, C3 species; *Bothriochloa macra* and *T. australis*, C4 species) were investigated in a glasshouse experiment. The effects of soil N status, stage of plant growth and density were investigated in the absence of defoliation, to determine the competitive potential of native grasses with *N. trichotoma* for the development of integrated weed management systems for non-arable landscapes.

MATERIALS AND METHODS

This experiment was done in a temperature-controlled glasshouse at the Orange Agricultural Institute (33.39°S 149.02°E), Orange, New South Wales, Australia. The experiment had two different starting times: June 2000 (winter) for the two C3 native grasses (*A. racemosa* and *M. stipoides*) and January 2001 (summer) for the C4 native grasses (*B. macra* and *T. australis*). The different starting times ensured appropriate conditions for the growth of C3 and C4 grasses as glasshouse conditions did vary with seasons. Seed was obtained for each species from local grasslands. The temperature in the glasshouse was controlled using evaporative air-conditioning and heaters: the mean daily temperature was 18 °C, ranging from 11 to 24 °C from winter to summer.

Experimental design

The experiment was a factorial additive design where neighbouring species (*A. racemosa*, *M. stipoides*, *B. macra* or *T. australis*) were planted at three densities (zero, one and eight neighbouring plants) around a single *N. trichotoma* plant and fertilized with three N levels (equivalent to 0, 60 and 120 kg N ha⁻¹). Pots were harvested at either 12 or 36 weeks to estimate seedling and mature plant competition separately. The experiment was replicated four times (72 pots per species per harvest).

The experiment used a variation of an additive series design in which *N. trichotoma* was always at the centre of the pot (150 mm diameter, 1.6-L pots) with the neighbouring plants at an equal distance from the target plant (~37 mm) and from each other (~30 mm for eight native plants per pot). Each of the neighbouring species was also grown as a monoculture (i.e. without any target plants), at

both densities (one and eight), to enable separate assessment of the competitive effect of the target plant and intraspecific competition. The experimental layout was a completely randomized design and pot positions were re-randomized every 2 weeks to minimize the effects of variations in watering, temperature and light across the benches.

The pots were filled with a Ferrosol soil (Isbell, 1996), in which *N. trichotoma* commonly occurs. It was first passed through a 5-mm sieve and mixed (1 : 1) with sand to reduce the N level. Superphosphate (9 % P applied at rate equivalent to 250 kg ha⁻¹) and lime (2.5 t ha⁻¹) were added to each pot to ensure adequate pH and P supply to isolate N as the sole limiting nutrient from these other common deficiencies.

Nitrogen was applied in the form of NH₄NO₃ (Nitram[®]) fertilizer. The fertilizer was applied at 4-week intervals for plants harvested at 12 weeks and at 8-week intervals for plants harvested at 36 weeks. The first application was 1 week after the experiment began. The equivalent of 0, 20 or 40 kg of N ha⁻¹ was applied three times to give a total N application of 0, 60 or 120 kg ha⁻¹ for each treatment.

Seeds were germinated on pads in Petri dishes and transplanted to the pots after 1 week when they were approx. 5–10 mm high. Any seedlings that died after planting were replaced during the first 2 weeks. After this time they were not replaced.

Both root and shoot masses were measured at each harvest to assess the impacts of competition. Soil was washed from the roots first and then each plant was oven dried (60 °C for 48 h), cut to separate the roots from the shoots, and weighed. The root samples were retained and representative samples of different plant species, harvest dates and plant sizes were ashed to estimate the amount of residual soil that could not be washed from the roots. Analyses showed that only plant size appeared to affect the amount of residual soil retained on the roots. Linear regressions between root weight plus residual soil versus residual soil were used to correct root weights, which were then combined with shoot weights to give corrected weights for whole plants. The corrected total biomass (shoot + root) data for all plants was natural-log transformed prior to analysis.

As *N. trichotoma* was the only target plant and at times there was only one competing neighbour, pots were excluded when mortality occurred in one of these plants. Mortality may have been due to competition, but since plant death may have been caused by other factors these pots were excluded. In part of this experiment (not reported in this paper) *Nassella trichotoma* seedlings were transplanted into pots of four mature neighbouring native grasses, with very low success rates from several attempts. In this case, mortality was probably due to competition as the losses were greater than in other treatments. However, the large numbers of plant deaths meant that valid statistical analyses could not be done reliably.

Analyses

Differences between the biomass of plants of each species grown without competition were tested using ANOVA (Genstat[®] for Windows, 7th edition; Payne *et al.*, 2003). For *N. trichotoma*, the two different start times, winter

TABLE 1. Competitive effects (a values with standard error) and R^2 values of the yield-loss function at different N levels for each neighbouring species (the function was fitted to both biomass and density data)

Regression	Neighbour species	N (kg ha ⁻¹)	a	s.e.	R^2
Density	<i>A. racemosa</i>	0	0.87	0.81	0.72
		60	0.44	0.20	0.66
		120	0.71	0.25	0.79
	<i>M. stipoides</i>	0	2.48	1.52	0.78
		60	0.41	0.28	0.43
		120	3.38	2.40	0.80
	<i>T. australis</i>	0	0.26	0.11	0.80
		60	0.24	0.14	0.63
		120	0.11	0.14	0.26
	<i>B. macra</i>	0	1.82	1.30	0.66
		60	0.35	0.21	0.71
		120	0.14	0.04	0.79
Biomass	<i>A. racemosa</i>	0	4.54	7.85	0.72
		60	0.24	0.10	0.59
		120	0.32	0.13	0.69
	<i>M. stipoides</i>	0	3.38	2.21	0.79
		60	0.38	0.18	0.70
		120	0.53	0.33	0.82
	<i>T. australis</i>	0	0.53	0.21	0.85
		60	0.13	0.07	0.49
		120	0.04	0.06	0.18
	<i>B. macra</i>	0	1.59	0.65	0.92
		60	0.31	0.15	0.75
		120	0.12	0.04	0.64

and summer, were analysed separately. N level and harvest time were used as factors in this analysis. The competitive response of *N. trichotoma* to neighbouring plant species and density was analysed at different harvests at each N level, using ANOVA. The competitive effect of *N. trichotoma* on each neighbouring species was then analysed at each harvest time by comparing its growth in the presence and absence of *N. trichotoma*. The interactions between *N. trichotoma* and neighbours were analysed for each individual species.

The competitive effects of the different neighbouring species on *N. trichotoma* was assessed using the yield-loss function:

$$P_x = P_{C0}(1 + aY)^{-1} \quad (1)$$

where P_{C0} is the biomass of the *N. trichotoma* plant in the absence of competition, a is the co-efficient that describes the strength of the competitive interactions, Y is the density or biomass (g) of competing plants of species y and P_x is the yield (g) of the *N. trichotoma* plant competing with species y (Freckleton and Watkinson, 1997).

Yield-loss equations were calculated for plants harvested at 36 weeks (Table 1 and Figs 6 and 7) and were calculated using density and biomass separately.

RESULTS

Comparison of species without competition

Harvest time had the largest influence on plant biomass (Fig. 1). At 12 weeks there was no significant difference

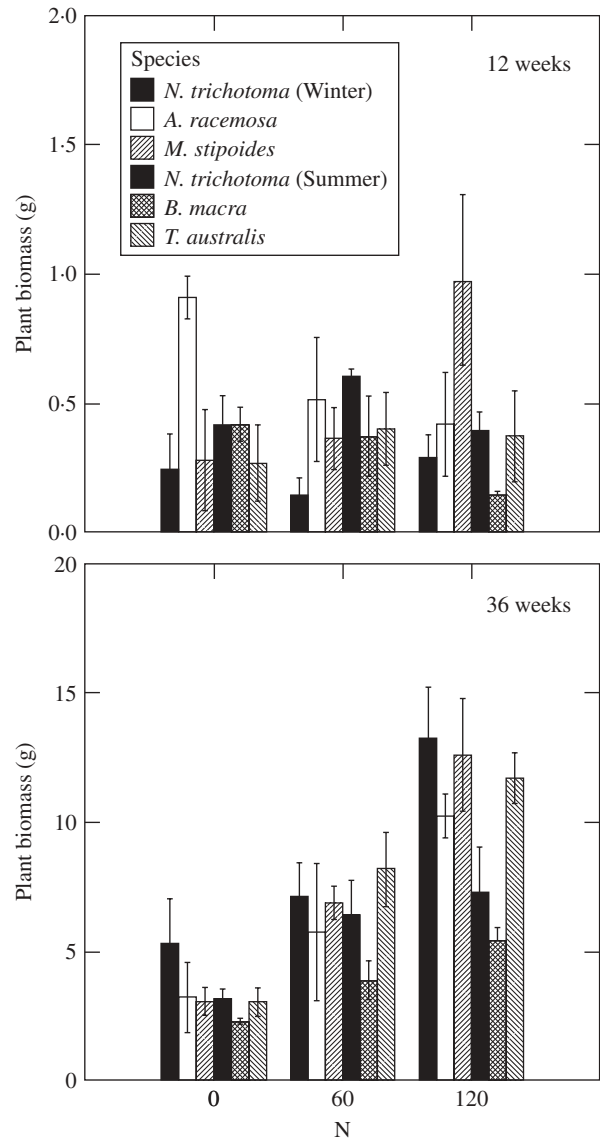


FIG. 1. Biomass (mean \pm standard error) of single plants of each species grown without competition at different N levels (0, 60 or 120 kg ha⁻¹) for each harvest (12 or 36 weeks). *Nassella trichotoma*, *A. racemosa* and *M. stipoides* were sown in winter and *N. trichotoma*, *B. macra* and *T. australis* were grown in summer.

in biomass between species at any N level. For plants harvested at 36 weeks, however, there was a significant difference in biomass among species ($P < 0.001$, d.f. = 5, $F = 9.20$) and biomass also increased with increasing N level ($P < 0.001$, d.f. = 2, $F = 85.65$). When averaged over the three nitrogen treatments, the rank order was (species sharing a superscript are not significantly different): *N. trichotoma*^a (planted in winter) > *M. stipoides*^{ab} > *T. australis*^{ab} > *A. racemosa*^b > *N. trichotoma*^b (planted in summer) > *B. macra*^c.

The competitive response of *N. trichotoma* to neighbours

When harvested at 12 weeks, the biomass of *N. trichotoma* was always reduced ($P < 0.05$, d.f. = 2,

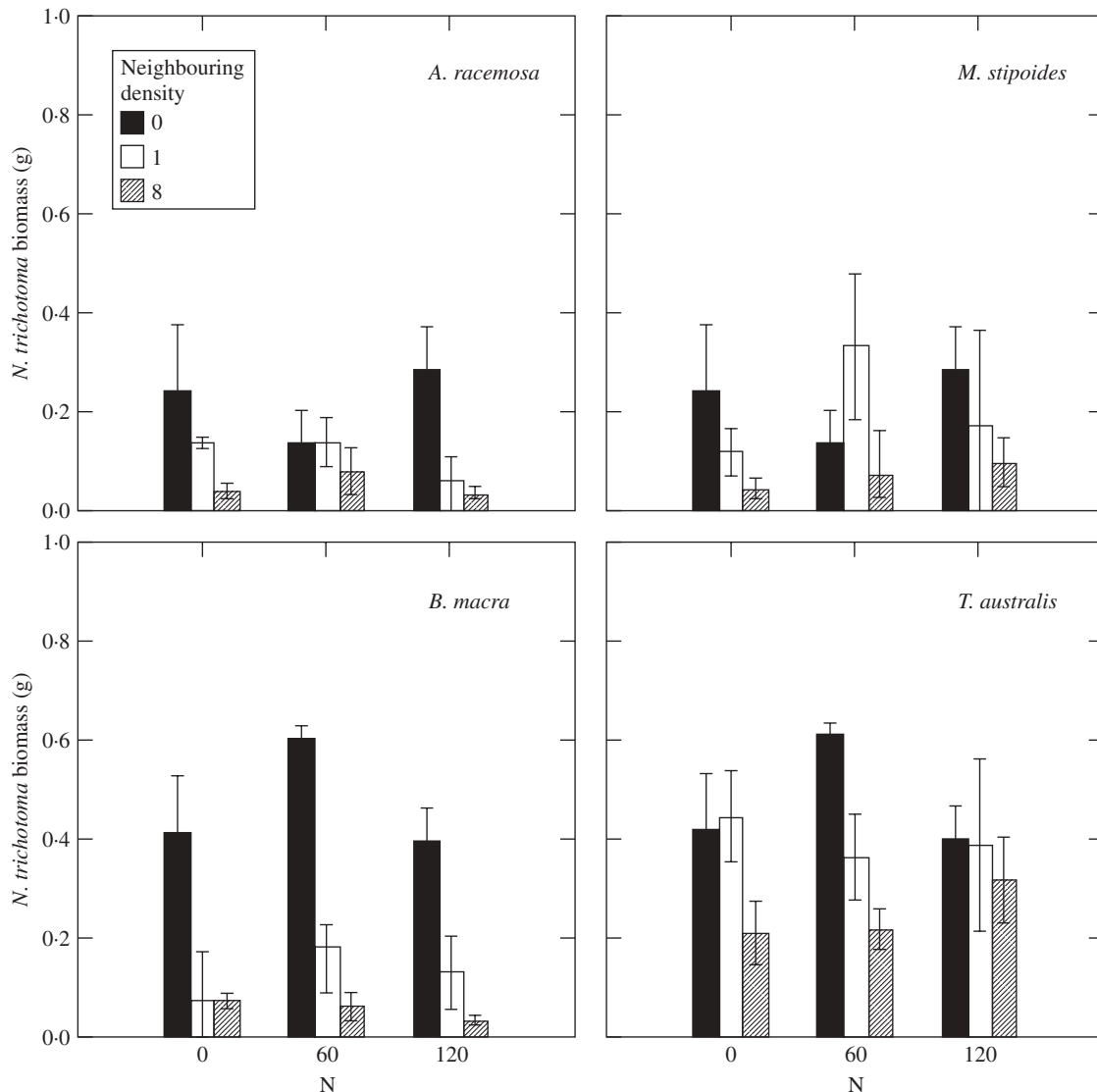


FIG. 2. Biomass (mean \pm standard error) of *N. trichotoma* grown in the presence of each neighbouring species at different densities (zero, one or eight plants per pot) and N levels (0, 60 or 120 kg ha⁻¹) when harvested at 12 weeks.

$F = 6.07$ *A. racemosa*; 4.71 *M. stipoides*; 7.87 *T. australis*; 36.22 *B. macra*) in the presence of eight neighbouring plants irrespective of species (Fig. 2). Further, *A. racemosa* also significantly reduced the biomass of *N. trichotoma* with only 1 neighbouring plant ($P < 0.01$). On average, N level did not affect *N. trichotoma* biomass in the presence of neighbouring plants when harvested at 12 weeks.

When harvested at 36 weeks, all four species caused a significant reduction ($P < 0.01$, d.f. = 2, $F = 49.12$ *A. racemosa*; 44.92 *M. stipoides*; 57.92 *T. australis*; 15.18 *B. macra*) in *N. trichotoma* biomass at a density of eight neighbouring plants (Fig. 3). *Microlaena stipoides* and *B. macra* also reduced ($P < 0.001$) the biomass of *N. trichotoma* at a neighbouring density of one plant. On average *N. trichotoma* biomass increased ($P < 0.01$, d.f. = 2, $F = 11.83$ *A. racemosa*; 10.14 *M. stipoides*; 10.26 *T. australis*; 27.96 *B. macra*) with increasing N application (Fig. 3).

The competitive effect of *N. trichotoma* on neighbours

The single 'target' *N. trichotoma* plant had, on some occasions, a competitive effect on neighbouring plants. At the 12-week harvest, *N. trichotoma* had no effect on any species at any N level (Fig. 4). The only significant effect observed was the decreased per plant biomass of *A. racemosa* and *M. stipoides* at densities of eight plants per pot.

For single-neighbour plants harvested at 36 weeks, the presence of *N. trichotoma* reduced ($P < 0.01$, d.f. = 1, $F = 65.60$ *A. racemosa*; 10.37 *M. stipoides*; 127.31 *T. australis*; 59.10 *B. macra*) plant biomass for neighbouring species (Fig. 5). The average per plant biomass for neighbouring species was always lower ($P < 0.05$, d.f. = 1, $F = 59.37$ *A. racemosa*; 4.84 *M. stipoides*; 125.75 *T. australis*; 59.10 *B. macra*) at a density of eight plants compared with one.

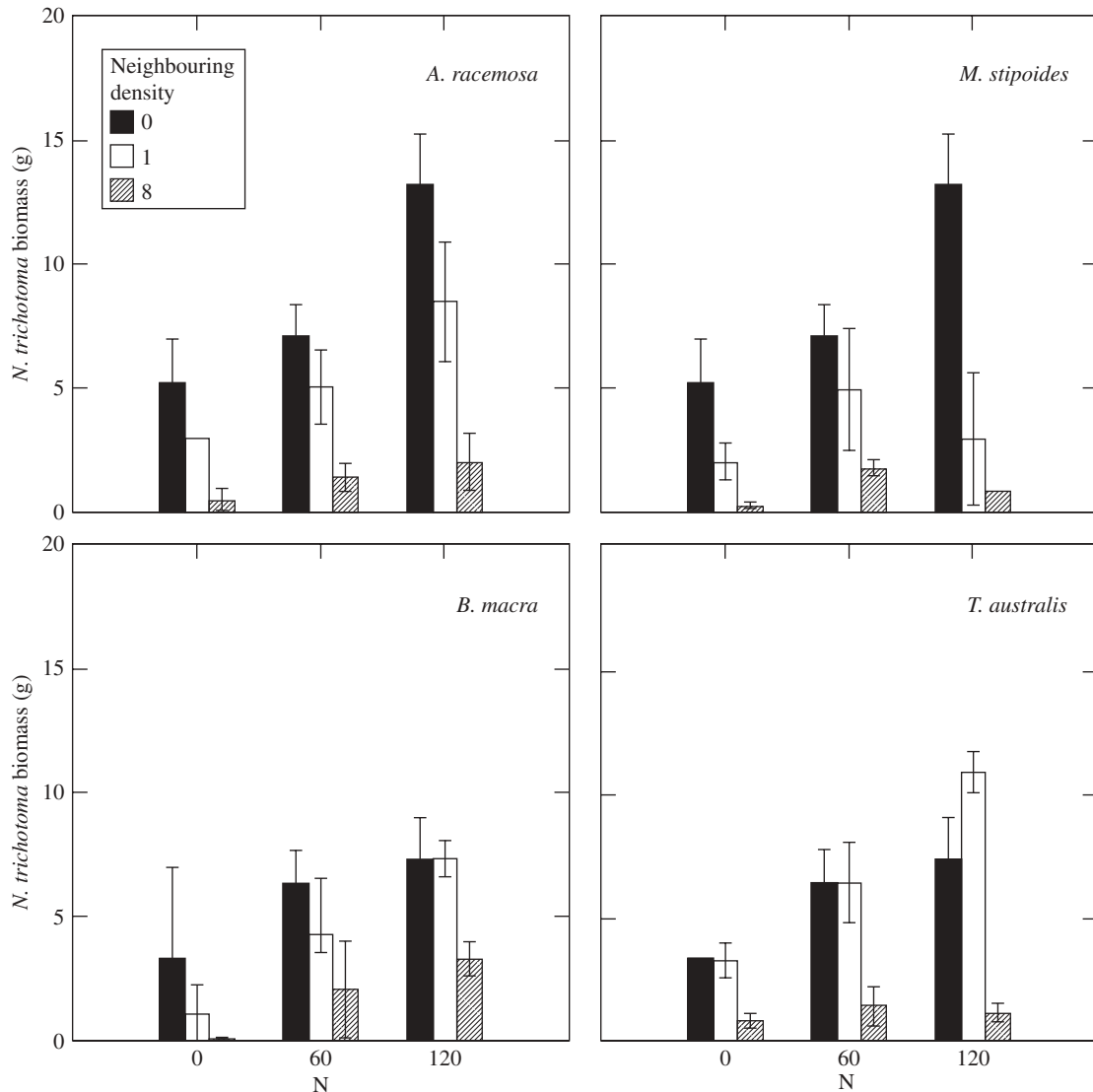


FIG. 3. Biomass (mean \pm standard error) of *N. trichotoma* grown in the presence of each neighbouring species at different neighbouring plant densities (zero, one or eight plants per pot) and N levels (0, 60 or 120 kg ha⁻¹) when harvested at 36 weeks.

The biomass of individual neighbouring plants increased ($P < 0.001$, d.f. = 2, $F = 103.95$ *A. racemosa*; 7.65 *M. stipoides*; 129.13 *T. australis*; 10.69 *B. macra*) with increasing N application. However, two species showed an interaction between N application and the presence of *N. trichotoma*. While in the absence of *N. trichotoma* the average biomass of *A. racemosa* and *T. australis* plants increased with increasing N application rate, in the presence of *N. trichotoma* the application of 120 kg N ha⁻¹ did not have a significantly greater effect on biomass of those species than application of 60 kg ha⁻¹.

measured by the mean a value (eqn 1) with no added N was 1.36, with 60 kg N ha⁻¹ was 0.36 and with 120 kg N ha⁻¹ was 1.09. At each level of soil N, similar rankings of species competitive effects were observed for either density or biomass-derived data: Pearson's rank correlation coefficients determined for pairwise comparisons of the rankings from each of the three N treatments averaged 0.60 for density-derived data and 0.67 for biomass-derived data. Averaged over the three N treatments, the rank order was the same using either density or biomass: *M. stipoides* > *A. racemosa* > *B. macra* > *T. australis* (Figs 6 and 7).

Yield-loss functions

Using density-derived data, the competitive effect of the neighbouring species was greater at low soil N levels (Table 1). The strength of the competitive interactions,

DISCUSSION

In its native range, *N. trichotoma* is widely distributed throughout the temperate Pampa of Argentina in regions ranging from semi-arid to sub-humid (Connor, 1960). It is

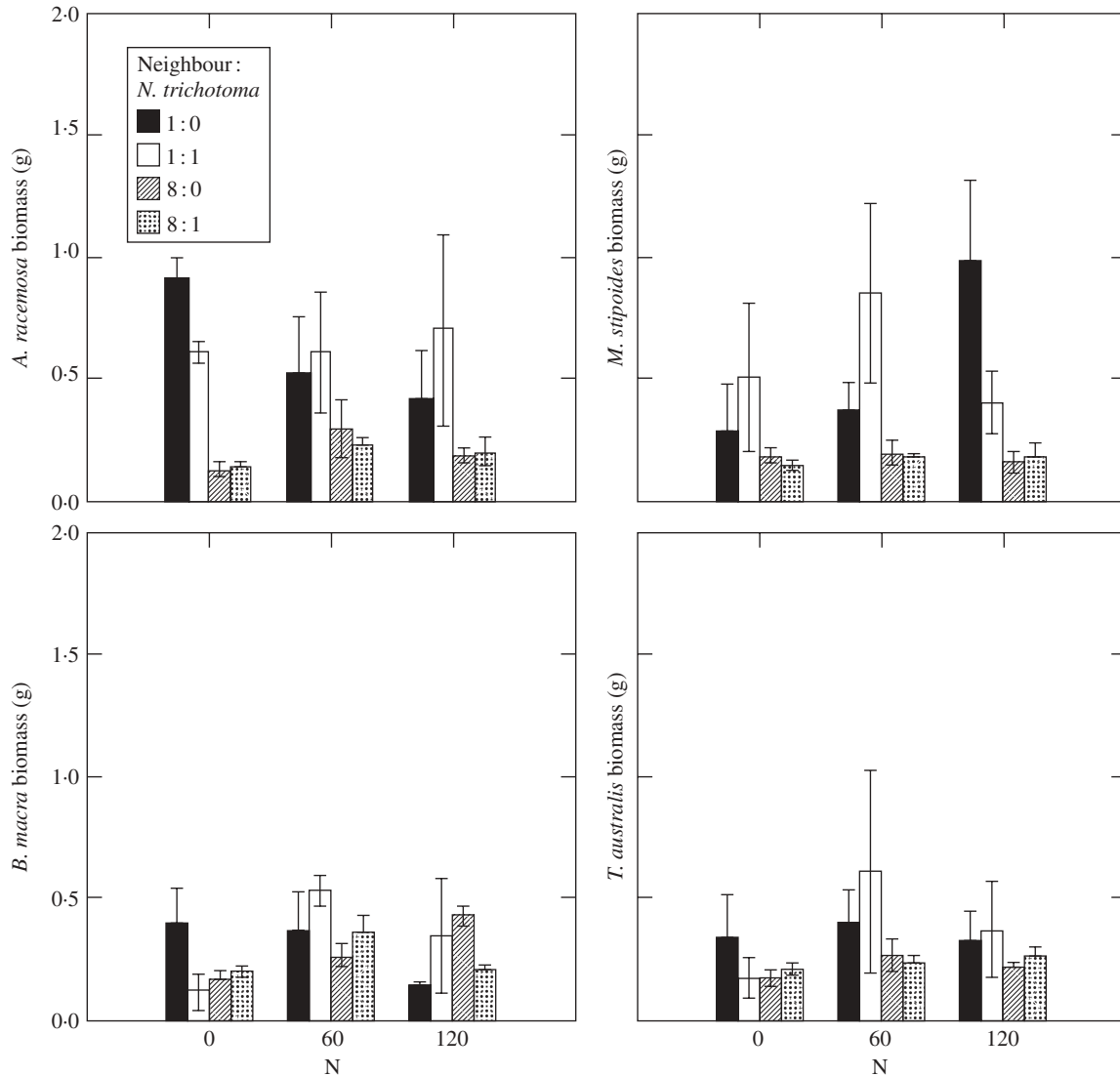


FIG. 4. Biomass (mean \pm standard error) of neighbouring plants grown at different densities, with or without *N. trichotoma*, at different N levels (0, 60 or 120 kg ha⁻¹), when harvested at 12 weeks.

not restricted by soil type, and soil fertility is generally high throughout its range. In Australia the distribution of *N. trichotoma* is likewise not strongly associated with any single environmental factor (Campbell and Vere, 1995). Rather, the invasion of *N. trichotoma* is often associated with soil disturbance (Healy, 1945; Wells, 1974). The rapid spread of *N. trichotoma* in Australian soils of low fertility (Jones and Vere, 1998) may be explained, in part, by increases in available soil nutrients as a consequence of soil disturbance (Vitousek and Walker, 1987). In addition, a reduction in native perennial grass density may provide increased opportunities for *N. trichotoma* to invade. This study provides support for those mechanisms.

Native Australian perennial grasses from the temperate region do not, in general, respond to increased soil fertility to the same extent as many introduced perennial grasses. This has been documented for *T. australis* (Fisher, 1974; Groves *et al.*, 2003), *Austrodanthonia* spp. (Navas *et al.*,

2002; Groves *et al.*, 2003) and *B. macra* (Cook *et al.*, 1976). However, in this experiment, at the highest fertility level, *M. stipoides* exceeded the biomass of *N. trichotoma* when grown in a 1:1 ratio. Thus, while the findings of previous work were supported for three native grass species, those studies had not included the rhizomatous *M. stipoides*. The biomass of *N. trichotoma* was significantly reduced by the presence of *M. stipoides* under these conditions. When the native grass to *N. trichotoma* density ratio was increased to 8:1, the total biomass of the native grasses exceeded that of *N. trichotoma* and severe effects on growth of *N. trichotoma* were recorded. This occurred at all fertility levels.

Yield-loss function analysis showed that the competitiveness of native grass species was least at the highest soil N level, with the exception of *M. stipoides*. At each fertility level, the rankings of competitiveness were consistent, with *M. stipoides* almost always the best competitor followed

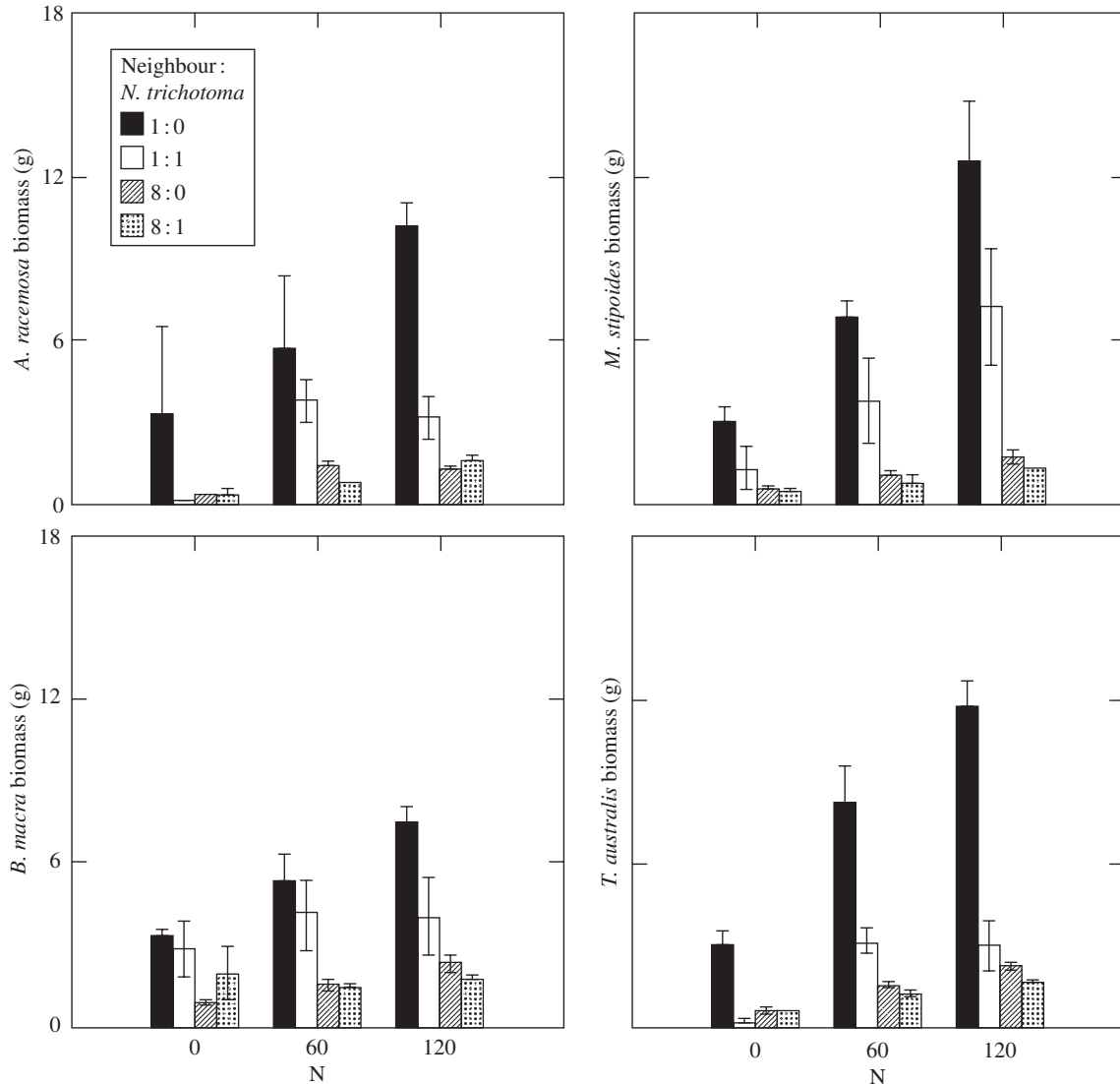


FIG. 5. Biomass (mean \pm standard error) of neighbouring plants grown at different densities, with or without *N. trichotoma*, at different N levels (0, 60 and 120 kg ha⁻¹), when harvested at 36 weeks.

by *A. racemosa* then *B. macra*, with *T. australis* being the weakest competitor. The suggestion that C4 grasses are likely to be more competitive due to a greater ability to use and reduce soil N to a lower level of availability than C3 perennial grasses (Wedin and Tilman, 1996; Wedin, 1999) was not supported in this study. In fact, C4 grasses were almost always the weakest competitor irrespective of soil fertility. This finding contradicts suggestions from field observations (e.g. Hocking, 1998; Michalk *et al.*, 1999) that *T. australis* competes strongly with *N. trichotoma*.

There could be a number of reasons why *T. australis* was a poorer competitor compared with field observations. Several mechanisms other than competition for N can affect species composition in the field. The population dynamics that enable *T. australis* to limit *N. trichotoma* invasion may not have applied in this experiment, since adult *T. australis* plants may compete well for N with *N. trichotoma*

seedlings. Field observations may also have come from areas of established *T. australis* that had resisted invasion from *N. trichotoma* rather than been the outcome of competition between the species. The hypothesis that grasslands with a high density of established native grasses can resist invasion from *N. trichotoma* was supported in a section of this experiment that was not reported here. Where *N. trichotoma* seedlings were sown amongst adult native grass plants, survival was so low that the results could not be analysed.

Nassella trichotoma is an unpalatable species due to a high density of indigestible tissue in the leaves (Campbell, 1965). It has been proposed that species with high tissue density grow at a slower rate than those with lower tissue density (Grime, 1979; Craine *et al.*, 2001; Craine, 2003), and they appear to be better adapted to low N soils. Species with high tissue density may compete successfully at low soil fertility because they accumulate biomass over a

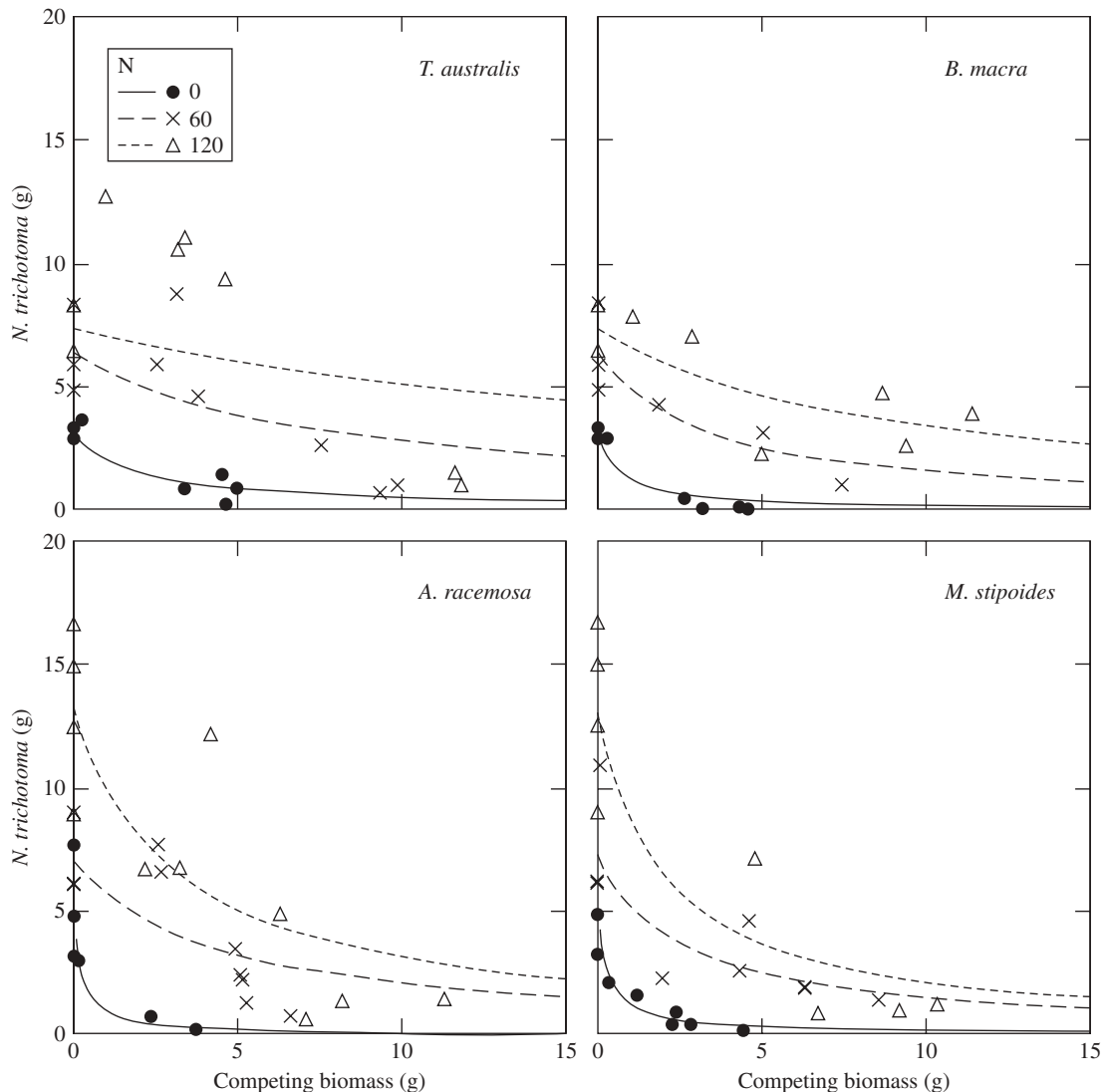


FIG. 6. Fitted curves for the yield-loss equation using biomass as the independent variable, at different N levels (0, 60 or 120 kg ha⁻¹). *Nassella trichotoma* was the target species grown with a single neighbouring species: *T. australis*, *B. macra*, *A. racemosa* or *M. stipoides*. The *a* values in Table 1 describe the curvature of the lines.

number of years, retaining limiting nutrients that species with low tissue density recycle back into the soil (Aerts and van der Peijl, 1993), as plant material takes longer to break down. *Nassella trichotoma* has relatively high tissue densities (digestibility 17–25%; McManus *et al.*, 1972), whereas the four native species have somewhat lower tissue densities (digestibility *T. australis* 54–75%, *B. macra* 48–59%, *Austroanthonia* spp. 45–75% and *M. stipoides* 55–80%; Lodge and Whalley, 1983; Robinson and Archer, 1988). In this experiment, however, *N. trichotoma* was able to grow as quickly as or faster than the native grasses when there were no, or low density of, competing plants. The ability to grow quickly through the early stages of growth even at low soil fertility and be able to monopolize nutrients over a much longer period, perhaps explains partly why it is such a successful weed in temperate Australian native grasslands. This study has not supported the view that species of high tissue density are inherently less competitive.

During this experiment, plants harvested at 12 weeks showed very little inter- or intra-specific competition. The absence of a response to N indicates that it was probably not a limiting factor at that early stage of plant development, i.e. initial germination and seedling growth for these species was not dependent upon soil N level.

Competition for soil N will not be the only mechanism that influences *N. trichotoma* invasion into native grasslands in the field. Other factors such as competition for moisture and light, different seasonal growth patterns, or differential impacts of grazing events can play a role in regulating invasion by *N. trichotoma*. In this experiment, different starting times were used for each of the C3 and C4 competitor types. Under field conditions, however, it is unlikely that a single germination/recruitment event would occur unless there was severe disturbance. Examining the competitive effect of adult native perennial grasses on *N. trichotoma* seedlings in the field may provide further

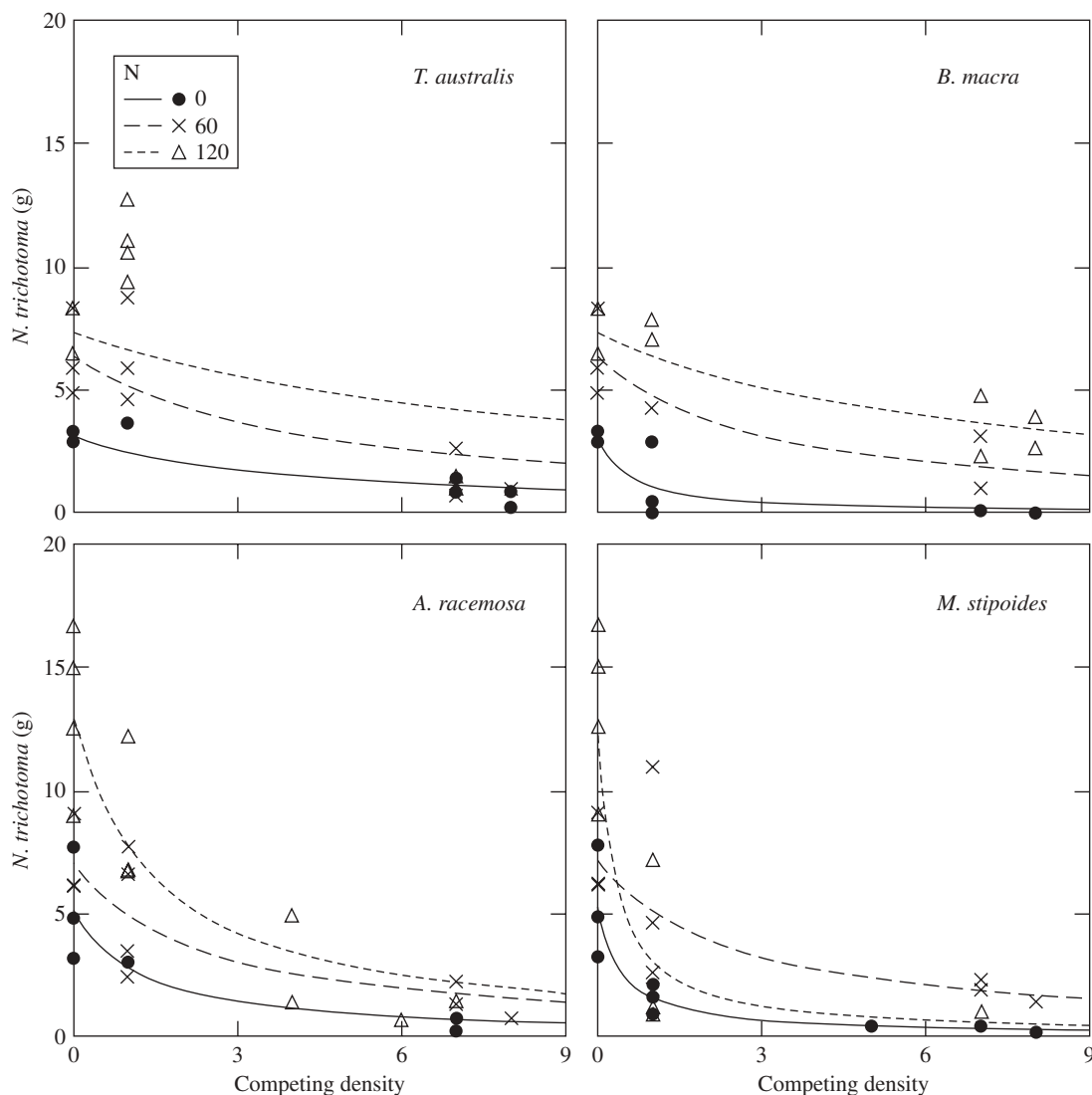


FIG. 7. Fitted curves for the yield-loss equation using density as the independent variable, at different N levels (0, 60 or 120 kg ha⁻¹). *Nassella trichotoma* was the target species grown with a single neighbouring species: *T. australis*, *B. macra*, *A. racemosa* or *M. stipoides*. The *a* values in Table 1 describe the curvature of the lines.

insight into competitive interactions. Once established, adult *N. trichotoma* plants have an extremely low natural mortality (Badgery, 2004), which indicates that mortality from the competitive effect of native grasses is probably minimal. Further experiments to determine the relative importance of these mechanisms in the field are certainly warranted.

Growing conditions

The experiment was done in a temperature-controlled glasshouse but there were different growing conditions for the two starting times (driven by temperatures varying with external conditions), highlighted by different growth patterns for individual *N. trichotoma* plants. Plants that were sown in winter grew slowly at first and had a lower biomass at 12 weeks compared with those that were sown in summer. Mean daily temperature across the experimental period fluctuated from 11 to 24 °C from winter to summer.

Between 12 and 36 weeks the temperature for growth increased in the winter-planted treatments and decreased for the summer-planted treatments, resulting in larger *N. trichotoma* plants when planted in winter than those planted in summer. This was observed in the field by Badgery (2004) who found that autumn-germinating *N. trichotoma* plants had a higher chance of surviving than spring germinating seedlings because the autumn seedlings were larger when the period of maximum stress occurred in summer.

Method of determining competition coefficients

In the analysis of this experiment both density and biomass of neighbouring plants were used as independent factors in the yield-loss function to assess the impact of competition on *N. trichotoma*. Neighbouring species biomass is nonlinearly related to the density and is not

generally used to predict competitive effects because of problems with independence (Freckleton and Watkinson, 2000). In this experiment, however, *M. stipoides*, a rhizomatous species, was found to show a different pattern of competition at high N levels. *Microlaena stipoides* had vegetative tiller recruitment from rhizomes within the experiment and one plant grew as much biomass as eight neighbouring plants when sown with *N. trichotoma*. This did not occur with any other species. As a consequence, consideration of biomass provided more insight than density for *M. stipoides*. It can be concluded that neighbouring species biomass may be better for calculating yield-loss competition coefficients for rhizomatous species than plant density, notwithstanding the assumptions about independence.

Practical outcomes

The more important outcome of this experiment is evidence that high native perennial grass density and/or biomass are essential for these native grasses to compete with *N. trichotoma*. This study has clarified that, as individual plants of three of these native grass species are not very competitive with *N. trichotoma*, a high density of perennial grass will be critical to provide sufficient competition against, and prevent invasion by, *N. trichotoma*, especially on more fertile soils. Higher soil fertility and low density of perennial grass are likely to favour *N. trichotoma*. One exception to this pattern found in this study was *M. stipoides*. It was competitive at low densities and higher fertility, in part because of its rhizomatous growth habit.

Current recommendations to farmers for *N. trichotoma* control commonly include the advice to apply fertilizer in the belief that this will make native perennial grass species more competitive. Such recommendations need to be qualified. To maximize competition of native grasses with *N. trichotoma*, management should focus on promoting a high density of actively growing native perennial grasses, which may be achieved by carefully managing grazing intensity and duration (e.g. Garden *et al.*, 2000, 2003).

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