

# Studies of competition between *Nassella trichotoma* (Nees) Hack. ex Arechav. (serrated tussock) and native pastures. 1. Adult plants

W. B. Badgery<sup>A,B,D</sup>, D. R. Kemp<sup>B</sup>, D. L. Michalk<sup>A</sup>, and W. McG. King<sup>C</sup>

<sup>A</sup>NSW Department of Primary Industries, Orange Agricultural Institute, Forest Rd, Orange, NSW 2800, Australia.

<sup>B</sup>The University of Sydney/Charles Sturt University, Faculty of Rural Management, Leeds Pde, Orange, NSW 2800, Australia.

<sup>C</sup>AgResearch, Raukura Research Centre, Private Bag 3123, Hamilton 3240, New Zealand.

<sup>D</sup>Corresponding author. Email: warwick.badgery@dpi.nsw.gov.au

**Abstract.** *Nassella trichotoma* (serrated tussock) is a hardy perennial grass weed that rapidly invades disturbed areas. Pasture competition is an important component of an integrated weed-management system for native pastures. This paper reports on a field experiment to ascertain the level of competition from native grasses for adult *N. trichotoma* plants. Native grasses prevented *N. trichotoma* plants from increasing in biomass and basal area when rotationally grazed or when grazing was removed and fertiliser was withheld. Smaller *N. trichotoma* plants (<500 mm<sup>2</sup>) were more likely to vary in size with very little change in larger plants. Flupropanate efficiently killed all *N. trichotoma* plants but caused considerable damage to perennial native species, resulting in an uncompetitive pasture dominated by broadleaf weeds.

**Additional keywords:** pasture competition, integrated weed management, flupropanate, grazing management, soil fertility.

## Introduction

*Nassella trichotoma* (Nees) Hack. ex Arechav. (serrated tussock) is a hardy perennial grass weed that currently infests up to 1 million ha of temperate south-eastern Australia (Jones and Vere 1998; McLaren *et al.* 1998). It is unpalatable to livestock due to a high leaf fibre content (Campbell and Irvine 1966), low nutrient concentrations (Campbell 1965), and tussocky growth habit where green leaves are dispersed among senesced material (Campbell 1998). *N. trichotoma* readily invades disturbed pasture areas that have been degraded by over grazing (Campbell and Vere 1995; Campbell 1998).

Evidence suggests that a strong perennial grass component is imperative to limit the invasion of many weeds in pastures (Dellow *et al.* 2002). Sowing introduced perennial grasses (especially *Phalaris aquatica* L.) to compete with *N. trichotoma* is commonly used in accessible areas where rainfall and soil fertility are adequate, but when either is deficient, or the area is inaccessible, then pasture sowing becomes unreliable (Johnston 1996) and uneconomic (Jones *et al.* 2000).

Little is known about how *N. trichotoma* interacts with native perennial grasses, which are common in areas invaded by *N. trichotoma*. It is not understood whether competition from these grasses is a significant factor affecting *N. trichotoma* invasion. Native grasses may not be inherently competitive (Groves *et al.* 2003), but there are few field experimental data to confirm this. Competition from native perennial grasses could become an important part of an integrated weed-management (IWM) program for unproductive or inaccessible landscapes.

*Nassella trichotoma* is rarely found growing among dense swards of C<sub>4</sub> (summer-growing) native grasses such as *Themeda australis* (R.Br) Stapf and *Bothriochloa macra* (Steud.) S.T. Blake (Hocking 1998; Michalk *et al.* 1999; Badgery *et al.* 2001). However, it is not clear if this is due to competition preventing *N. trichotoma* from establishing from seed or whether competition also extends to adult plants. One proposed mechanism is that C<sub>4</sub> species may reduce available soil nitrogen (N) to a level lower than that required by C<sub>3</sub> species (including *N. trichotoma*) (Wedin and Tilman 1996; Wedin 1999). However, *N. trichotoma* is a stress-tolerant species (Grime 1979) and adult plants have a capacity to withstand long periods of nutrient stress, which may make them less susceptible to competition.

Grazing influences plant competitive interactions directly through consumption of plant tissue and indirectly by affecting nutrient cycling and creating soil disturbance (Crawley 1983; Hulme 1996). Grazing increases the rate of nutrient cycling, releasing more nutrients to plants (Wedin 1999), whereas removal of grazing has the opposite effect and can tie up nutrients (Moretto and Distel 2002). Selective grazing disadvantages desirable palatable species and promotes unpalatable species such as *N. trichotoma*. By removing grazing altogether or reducing selective grazing using deferred rotational grazing (i.e. large numbers of animals confined to small areas for short periods of time, followed by long rest periods), palatable species may become more competitive (Kemp *et al.* 1996) and may be able to compete with larger *N. trichotoma* plants.

Spraying with flupropanate is one of the most effective means to control *N. trichotoma* (Campbell 1979; Viljoen and Erasmus 1996; Viljoen 1999), but most native grasses are also susceptible to this residual herbicide (Keys and Simpson 1993; Campbell and Van de Ven 1996). It is unknown whether the herbicide causes long-term damage to native grasses, or whether the native grasses can be managed to effectively recolonise and prevent reinvasion of *N. trichotoma*. It is likely, however, that the disturbance to community structure created by the herbicide will provide ideal conditions for *N. trichotoma* seedlings to re-establish, after the residual action of the herbicide has dissipated.

Competition from native perennial grasses resulted in the death of most *N. trichotoma* seedlings (Badgery *et al.* 2008), but established *N. trichotoma* plants are extremely hardy, long-lived, and it is not known whether native grasses could have any competitive effect. Native grass competition may reduce reproductive rates, plant size, and plant growth rates, but complete mortality would be unlikely. This paper reports on a study that investigated the mechanisms of competition between native grasses and adult *N. trichotoma* plants and the relative effect of different grazing methods, fertility levels, and herbicide treatments.

## Methods

### Site

The experiment was located at Trunkey Creek on the Central Tablelands of New South Wales (33.83°S, 149.35°E). The site has an elevation of 860 m and a mean annual rainfall of 795 mm. Temperature and rainfall for the experimental period and the 30-year averages are outlined in Table 1. The 30-year averages were estimated using the Datadrill<sup>®</sup> program that predicts climatic data for given coordinates from surrounding weather stations (Jeffrey *et al.* 2001). Native and naturalised species dominated the grassland composition; both *C<sub>4</sub>* (*T. australis* and *B. macra*) and *C<sub>3</sub>* (*Microlaena stipoides* (Labill.) R.Br and *Austrodanthonia* spp. H.P. Linder) perennial native grasses were present and *N. trichotoma* accounted for >50% of the pasture biomass within the paddock. Prior to establishment

the experimental site had been moderately to heavily grazed, mostly by sheep. The site had a gently sloping easterly aspect and the soil was a Chromosol (Isbell 1996).

### Experimental design

The experiment was a factorial split-plot design of 3 grazing treatments × 3 fertility treatments × 2 herbicide treatments, replicated in 3 blocks. Grazing treatments were main plots (20 by 10 m), fertility treatments subplots (20 by 3.3 m), and herbicide treatments sub-subplots (2 by 2 m). An open communal grazing design was used for this experiment (Kemp and Dowling 2000). Within each treatment combination an area of 0.9 by 0.9 m was permanently marked for measurements. The measurement area was located where a suitable combination of species was present, i.e. *N. trichotoma* plus *C<sub>3</sub>* and *C<sub>4</sub>* native grasses. Areas of rocks or where a single species dominated were avoided.

### Grazing

The 3 grazing treatments were nil ( $G_{\text{nil}}$ ), active ( $G_{\text{act}}$ ), and continuous ( $G_{\text{con}}$ ) grazing. The  $G_{\text{nil}}$  treatment was not grazed for the duration of the experiment, whereas the  $G_{\text{con}}$  treatment was continually grazed at 3–4 DSE (dry sheep equivalent)/ha throughout the experiment. The  $G_{\text{act}}$  treatment was a rotational grazing treatment that was grazed at 200 DSE/ha twice a year for 3 days on each occasion (i.e. equivalent to ~3 DSE/ha annually and only marginally less than the continuous grazing treatment). Grazing occurred when edible biomass (above-ground standing plant herbage excluding *N. trichotoma*) reached ~2 t/ha and stock were removed when it was grazed down to ~1 t/ha. To benefit *C<sub>4</sub>* native species no grazing was imposed to the  $G_{\text{act}}$  in the summer.

### Fertility

The 3 fertility (subplot) treatments were fertility addition ( $N_{\text{add}}$ ), nil ( $N_{\text{nil}}$ ), and fertility minus ( $N_{\text{min}}$ ). The  $N_{\text{add}}$  treatment received 120 kg nitrogen (N)/ha, 30 kg phosphorus (P)/ha, and 18 kg sulfur (S)/ha applied each year in the form of 250 kg/ha of Granulock<sup>®</sup> 15 (N: 15, P: 12, S: 7) plus 170 kg/ha of urea (N: 48),

**Table 1.** Monthly and 30-year average (SILO Datadrill, Jeffrey *et al.* 2001) rainfall (mm), and maximum ( $T_{\text{max}}$ ) and minimum ( $T_{\text{min}}$ ) temperatures (°C) at Trunkey Creek

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
<i>Rainfall</i>													
2001				53	30	62	58	83	70	90	61	13	
2002	39	250	30	35	57	50	45	21	56	1	10	52	646
Average	85	61	50	50	55	59	73	77	77	77	65	64	794
<i>Temperature</i>													
$T_{\text{max}}$													
2001				18.3	13.3	11.7	10.4	10.6	15.6	16.1	19.6	24.6	
2002	26.7	23.2	22.8	20.3	13.4	10.8	10.2	12.7	15.6	19.8	25.8	26.2	19.0
Average	27.5	26.9	24.2	19.8	15.5	11.8	10.8	12.4	15.5	18.9	22.2	26.0	19.3
$T_{\text{min}}$													
2001				5.1	1.6	0.6	1.0	0.4	4.3	3.8	6.4	7.7	
2002	10.7	11.4	8.8	6.9	2.1	0.0	-2.6	-0.5	2.0	3.2	9.0	10.5	5.1
Average	13.2	13.3	10.8	7.0	4.4	1.9	0.9	1.7	3.9	6.3	8.6	11.2	6.9

in 4 seasonal applications. The  $N_{\text{nil}}$  treatment had no fertiliser added. The  $N_{\text{min}}$  treatment had sucrose applied to stimulate uptake of available nutrients by microorganisms, thereby reducing their availability to plants (Vitousek 1982; Hunt *et al.* 1988; McLendon and Redente 1992; Freeman *et al.* 1998; Reeve Morghan and Seastedt 1999). The sucrose was applied at a rate of 1.25 kg/m<sup>2</sup> annually in equal amounts every 5 weeks. As large quantities of sucrose were required, it was applied only to a 4 m<sup>2</sup> area with the permanent measurement quadrats at the centre. Fertiliser and sucrose were first applied in March 2001.

### Herbicide

The herbicide treatment (HE) had 1.49 kg a.i./ha of flupropanate applied with a hand-held pneumatic sprayer on 17 April 2001. The HE treatment was designed to remove adult and seedling *N. trichotoma* plants and control seedling recruitment for 12–18 months through the residual effect of the herbicide.

### Measurements

A 0.9 by 0.9 cm permanent quadrat was established for each sub-subplot treatment. The quadrat was divided up into a grid of 81, 100-mm<sup>2</sup> squares that were assessed every spring, before grazing in the  $G_{\text{act}}$  treatment. Dry weight ranks of the 3 most abundant species and the total dry weight of all species were estimated for each 100-mm<sup>2</sup> square using BOTANAL procedures (Tothill *et al.* 1992). Estimates were corrected using 10 calibration cuts per site (average  $R^2 = 0.96$ ).

The 81 squares in the quadrats were averaged to give a detailed estimate of species composition per plot on a biomass basis and also provided presence/absence and frequency data for analyses of the spatial dynamics of adult *N. trichotoma* with other functional plant types.

The growth and development of *N. trichotoma* were monitored in the  $N_{\text{add}}$  and  $N_{\text{nil}}$  fertility treatments, in all grazing treatments, where herbicide was not applied. Depending on the number of plants present in the quadrat, 1–4 adult *N. trichotoma* plants were tagged and measured for basal circumference and seed production every 3 months. The total number of seedheads was counted and 10 seedheads were collected and seeds counted to estimate the amount of seed per seedhead and total seed production per plant.

Soil samples were collected from the fertility subplot treatments in spring 2001 and 2002. In spring 2000, soil samples were taken for each grazing treatment and pooled for the 3 fertility treatments. Ten soil cores (each 25 mm diameter by 75 mm deep) were randomly collected on each occasion from within each treatment combination plot, with the exception of the  $N_{\text{min}}$  treatment where soil cores were only taken where the sugar was added. Herbicide sub-subplot treatments were not sampled. Soil samples were collected at the end of the day, frozen within 2 h of sampling, and stored. Soil samples taken in 2000 and 2002 were all analysed within 1 month of sampling, but soil samples taken in 2001 were stored for 12 months.

Prior to analysis, soil samples were thoroughly air-dried at 40°C and ground to pass through a 2-mm sieve. The analyses are listed in Table 2.

**Table 2. Soil analysis methods**

Analysis	Details	Test no. <sup>A</sup>
pH	1 : 5 soil : water	4A1
	1 : 5 soil : 0.01 M CaCl <sub>2</sub>	4B2
NO <sub>3</sub> <sup>-</sup> and NH <sub>4</sub> <sup>+</sup>	2 M KCL	7C2
Total N	LECO <sup>B</sup>	
P	Bray	9E1
Exch. cations	Ca, Mg, Na, K, Al	15E1 and 2

<sup>A</sup>Test numbers refer to Rayment and Higginson (1992).

<sup>B</sup>Anon. (2003).

### Data analyses

GENSTAT (version 6, Payne *et al.* 2006) was used for all analyses. ANOVA was used for analysis of balanced designs and a mixed model restricted maximum likelihood (REML) for repeat measurements and unbalanced designs.

### Soil nutrients

An ANOVA was performed on each nutrient measured; the factors in the analysis were fertility and grazing. Where nutrient concentrations were below detectable limits of the clinical test, the value of the detection limit was used in the data analysis. For example, NO<sub>3</sub><sup>-</sup> was often found at levels <0.3 mg/kg and was assigned a value of 0.3 mg/kg. A combined soil sample was taken across all fertility treatments within each grazing treatment in 2000 before the start of fertility treatments. Fertility was not included as a factor in the 2000 analysis.

### Plant species composition

All species were combined into *a-priori* functional types using a subjective process based on physiological, morphological, and life-span characteristics (Gitay and Noble 1997). The functional types were *N. trichotoma*, C<sub>4</sub> native perennial (C4NP) grasses, C<sub>3</sub> native perennial (C3NP) grasses, C<sub>3</sub> introduced perennial grasses (C3IP), annual grasses (AG), and other species (OTH).

An ANOVA on initial composition showed that there was statistically significant variation in *N. trichotoma* and C4NP biomass between treatments. To account for this variation the initial biomass was used as a covariate in an ANOVA for data from spring 2001 and 2002, with grazing ( $G_{\text{con}}$ ,  $G_{\text{act}}$ , and  $G_{\text{nil}}$ ), soil fertility ( $N_{\text{add}}$ ,  $N_{\text{nil}}$ , and  $N_{\text{min}}$ ), and herbicide treatments (+/-) as factors.

### Effects on individual plants

The basal circumference of *N. trichotoma* was measured and converted to basal area for analysis (assuming a circle) to determine whether it changed over the measurement period. Since a different number of plants was measured in every plot (i.e. 1–4), depending on the initial number of plants, a mixed-model restricted maximum likelihood (REML) was used to overcome the unbalanced experimental design. Mixed-model REML analyses were done initially on the basal area change over time in all treatments, then sequentially on treatment effects at the first harvest and on treatment effects of plants <500 mm<sup>2</sup> at the final harvest, which were standardised. Linear regression was

then done on standardised data. Basal area was standardised using log ratios, i.e. the basal area  $\ln(\text{final measurement}/\text{initial measurement})$ , an approach used by Wilson and Shay (1990) to determine the effect of treatments over time. Log ratios were used in preference to percentages of the initial basal area as the data were not normally distributed (Hedges *et al.* 1999).

Seed production was measured in 2 seasons, December 2001 and December 2002, and standardised to seeds/cm<sup>2</sup> of basal area for analysis, an approach used for *N. trichotoma* by Moretto and Distel (1999). A mixed-model REML was used to determine differences between treatments within and between years.

## Results

### Soil fertility manipulation

There were no significant effects on soil fertility due to grazing ( $P > 0.05$ ) or on grazing by fertility ( $P > 0.05$ ), but there were differences among fertility treatments (Table 3). Fertility treatments ( $N_{\text{add}}$ ,  $N_{\text{nil}}$ , and  $N_{\text{min}}$ ) were designed to create a gradient in soil fertility against which the competitive interactions between *N. trichotoma* and other functional plant types could be evaluated.  $N_{\text{min}}$  treatments significantly ( $P < 0.001$ ) reduced available soil N levels (measured as  $\text{NO}_3^-$  and  $\text{NH}_4^+$ ) by 2002 (Table 3) and all  $\text{NO}_3^-$  readings were below the detection limit ( $< 0.3$  mg/kg). The  $N_{\text{add}}$  treatment increased soil P levels by 2002: there was a significant gradient of P, with the lowest levels in the  $N_{\text{min}}$  treatment, increasing to the  $N_{\text{nil}}$  treatment, and higher again in the  $N_{\text{add}}$  treatment ( $P < 0.001$ ). The addition of fertiliser in the  $N_{\text{add}}$  treatment increased exchangeable Al ( $P < 0.05$ ) in 2001 compared with that in the  $N_{\text{min}}$  treatment (Table 3).

### Total biomass

Total pasture biomass changed in treatments as the experiment progressed (Table 4). Initially, there were no significant differences in total biomass among treatments, but by 2001, biomass was highest in the  $G_{\text{nil}}$  treatment compared with the other grazing treatments ( $P < 0.05$ ). Total biomass in the  $G_{\text{con}}$

treatment continued to decrease in 2002, although it was not significantly different from the other grazing treatments, but it was less in the  $G_{\text{con}} N_{\text{min}}$  treatment in 2001 than in the other treatments ( $P < 0.05$ ). In 2001, there was no difference in the total biomass of fertility treatments, but in 2002 the total biomass of the  $N_{\text{add}}$  fertility treatment was higher than of the  $N_{\text{min}}$  treatment ( $P < 0.05$ ). The HE treatment decreased total biomass in both 2001 and 2002 ( $P < 0.001$ , both years). In 2002, total biomass in the HE treatment was larger when combined with  $G_{\text{act}}$  or  $G_{\text{nil}}$  treatments than with the  $G_{\text{con}}$  treatment. In the plots where herbicide was not applied the  $G_{\text{nil}}$  treatment had a larger biomass than the  $G_{\text{act}}$  and  $G_{\text{con}}$  treatments ( $P < 0.01$ ).

### Botanical composition

#### Initial species abundance

Measurements of species biomass taken 1–2 months after grazing treatments began showed that composition was relatively consistent across all of the treatments (Table 4), although there were between-treatment differences in some functional plant types. There was less *N. trichotoma* in the  $G_{\text{act}}$  treatment than in the other grazing treatments ( $P < 0.05$ ), which was associated with a substantially lower amount in  $N_{\text{nil}} G_{\text{act}}$  plots ( $P < 0.01$ ). *N. trichotoma* also varied within the grazing  $\times$  herbicide ( $P < 0.05$ ) and fertility  $\times$  herbicide ( $P < 0.01$ ) treatments. C4NP grasses were lower in the  $N_{\text{nil}} G_{\text{act}}$  and  $N_{\text{nil}} G_{\text{con}}$  treatments ( $P < 0.01$ ), but all other functional types showed no variation within treatments in spring 2000. Although the initial differences in composition were relatively small, they were statistically significant and so initial composition was used as a covariate in the analysis of 2001 and 2002 data, i.e. 1 and 2 years, respectively, after treatments were first imposed.

#### Grazing

Grazing did not affect *N. trichotoma* biomass, but it had an effect on other plant functional types (Table 4). There were more C4NP grasses in  $G_{\text{nil}}$  than in the other grazing treatments in 2001 ( $P < 0.05$ ). In 2002, the amount of C4NP grasses decreased in

**Table 3. Average soil test results for each fertility treatment (except in 2000)**

\* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$

Soil test	2000		2001			P-value	2002			P-value
	Units	Mean <sup>A</sup>	$N_{\text{min}}$	$N_{\text{nil}}$	$N_{\text{add}}$		$N_{\text{min}}$	$N_{\text{nil}}$	$N_{\text{add}}$	
pH (water)		5.6	5.6	5.4	5.4		5.6	5.5	5.4	
pH (CaCl <sub>2</sub> )		4.6	4.7	4.6	4.6		4.7	4.6	4.6	
NH <sub>4</sub>	mg/kg	14.1	8.7	8.8	8.3		6.6	10	12	***
NO <sub>3</sub>	mg/kg	1	0.8	1.1	1		0.3	2.1	2.3	***
N (total)	%w/w	0.2	0.1	0.2	0.2		0.1	0.1	0.1	
P (Bray)	mg/kg	7	3.2	4.2	7.1	**	2.4	4.3	8.1	***
4 Cation exchange	meq/100 g	3.3	3.1	3.4	3.3		3	3.1	3.2	
Ca	%	79.2	75	78	77		78	78	78	
Mg	%	13.3	16	15	15		15	15	14	
Na	%	3.6	3.9	3.3	3.9		4.2	3.8	4.1	
K	%	5.6	6.8	5.1	6		5	4.7	4.8	
Exch. Al	mg/kg	22.3	23	26	31	*	24	25	29	

<sup>A</sup>In 2000 the mean was of 10 samples taken over the whole grazing treatment and was not the average of the 3 N levels ( $N_{\text{min}}$ ,  $N_{\text{nil}}$ , and  $N_{\text{add}}$ ).

Table 4. Total biomass (kg/ha) and biomass of each functional group for each treatment measured in spring from 2000 to 2002

Grazing	Fertility	Herbicide	<i>N. trichotoma</i>	C4NP	C3NP	C3PI	AG	OTH	Total	
2000										
G <sub>nil</sub>	N <sub>add</sub>	+	397	134	839	6	383	236	1995	
		-	1010	660	346	1	513	263	2794	
	N <sub>nil</sub>	+	716	418	564	117	811	400	3025	
		-	935	557	695	385	287	275	3135	
G <sub>act</sub>	N <sub>min</sub>	+	581	565	328	406	169	180	2229	
		-	1986	91	866	6	429	448	3825	
	N <sub>add</sub>	+	532	479	418	168	240	331	2168	
		-	351	614	385	1	194	178	1722	
G <sub>con</sub>	N <sub>nil</sub>	+	382	98	650	175	187	247	1740	
		-	85	259	586	0	268	105	1303	
	N <sub>min</sub>	+	326	175	552	109	170	244	1576	
		-	1311	480	533	329	148	271	3072	
G <sub>act</sub>	N <sub>add</sub>	+	2081	138	496	189	259	304	3466	
		-	602	234	595	145	210	259	2045	
	N <sub>nil</sub>	+	1982	110	703	140	232	177	3344	
		-	975	142	758	158	291	315	2640	
G <sub>con</sub>	N <sub>min</sub>	+	542	297	655	73	189	250	2007	
		-	571	322	463	32	501	212	2100	
	2001									
	G <sub>nil</sub>	N <sub>add</sub>	+	372	260	43	3	399	813	1891
-			693	639	345	0	779	221	2676	
N <sub>nil</sub>		+	669	550	70	9	113	971	2383	
		-	945	1129	683	81	140	316	3294	
G <sub>act</sub>	N <sub>min</sub>	+	754	1094	60	0	8	325	2241	
		-	1897	450	655	1	2	342	3349	
	N <sub>add</sub>	+	319	74	6	20	454	442	1314	
		-	576	282	614	82	422	234	2211	
G <sub>con</sub>	N <sub>nil</sub>	+	222	52	6	0	208	398	886	
		-	70	383	562	35	195	150	1396	
	N <sub>min</sub>	+	497	181	99	87	37	291	1193	
		-	810	409	381	15	7	126	1747	
G <sub>act</sub>	N <sub>add</sub>	+	1540	33	3	0	282	317	2174	
		-	570	90	412	0	461	134	1668	
	N <sub>nil</sub>	+	1304	44	16	0	194	327	1886	
		-	918	75	523	51	169	265	2001	
G <sub>con</sub>	N <sub>min</sub>	+	423	111	13	0	7	213	767	
		-	574	169	337	0	1	94	1175	
	2002									
	G <sub>nil</sub>	N <sub>add</sub>	+	2	60	0	185	386	329	961
-			1636	804	710	250	411	543	4355	
N <sub>nil</sub>		+	4	200	1	67	173	373	818	
		-	1399	1417	796	156	41	385	4193	
G <sub>act</sub>	N <sub>min</sub>	+	4	427	7	21	19	263	740	
		-	2522	394	564	4	0	211	3694	
	N <sub>add</sub>	+	6	42	8	295	415	540	1306	
		-	1508	558	647	136	344	222	3415	
G <sub>con</sub>	N <sub>nil</sub>	+	4	110	14	140	178	536	982	
		-	224	450	528	28	147	224	1601	
	N <sub>min</sub>	+	17	229	72	23	34	509	884	
		-	1251	378	470	12	1	131	2242	
G <sub>act</sub>	N <sub>add</sub>	+	26	1	4	16	182	264	493	
		-	1545	121	415	44	238	62	2424	
	N <sub>nil</sub>	+	3	5	0	23	257	213	502	
		-	1342	69	455	47	117	202	2233	
G <sub>con</sub>	N <sub>min</sub>	+	5	57	15	2	58	226	364	
		-	927	190	287	0	7	80	1492	

$G_{con}$  and was much lower than the other grazing treatments, but this difference was not significant. There were more C3NP grasses in  $G_{act}$  than in the other grazing treatments by 2002 ( $P < 0.05$ ). No other plant functional types were significantly affected by the grazing treatments.

#### Fertility

The addition of nutrients ( $N_{add}$ ) increased biomass from the initial measurement for *N. trichotoma* by 2002 ( $P < 0.05$ ), AG in 2001 and 2002 ( $P < 0.001$ ), and OTH in 2001 ( $P < 0.05$ ). Where the fertility was depressed ( $N_{min}$ ), biomass was less for *N. trichotoma* by 2002, particularly in the  $G_{act}$  treatment compared with the  $G_{con}$  ( $P < 0.05$ ), for AG in 2001 and 2002, and for C3IP grasses by 2002 ( $P < 0.01$ ). The biomass of C4NP grasses was higher ( $P < 0.05$ ) in the  $N_{min}$  treatment in 2001 and 2002, and higher for C3NP grasses by 2002 ( $P < 0.01$ ).

#### Herbicide

HE treatment reduced the amount of *N. trichotoma* in 2001 (by 28%,  $P < 0.01$ ) and 2002 (by 93%,  $P < 0.001$ ). In 2001, measurements taken 6 months after flupropanate application showed that while *N. trichotoma* biomass was significantly reduced, the plants had not been completely killed. However, by 2002, all adult plants in the herbicide treatments were dead and any *N. trichotoma* present at the end of the experiment was a result of germination of seedlings (Badgery *et al.* 2008).

Abundance of C4NP grasses was reduced by the HE treatment but not as severely as C3NP grasses. Biomass of C4NP was reduced significantly in 2001 (9%,  $P < 0.01$ ) with further reductions in 2002 (71%,  $P < 0.001$ ). Biomass of C3NP was severely reduced by herbicide in 2001 (98%,  $P < 0.001$ ) and in 2002 (97%,  $P < 0.001$ ). The amount of C3IP grasses was lower in 2001 ( $P < 0.05$ ), but recovered to pre-herbicide levels by 2002. Annual grasses were not initially affected by the HE treatment in 2001, but in 2002 they were at higher levels than in the other treatments, but were still at lower levels than in 2000 ( $P < 0.001$ ). The OTH functional type increased proportionally in the HE treatment in 2001 and 2002 ( $P < 0.001$ , 99% in 2001 and 16% in 2002), due to an increase in the forbs *Hypochaeris radicata* L. and *Acetosella vulgaris* (Koch) Fourr.

By 2002, plots treated with flupropanate had more C4NP ( $P < 0.01$ ) and more C3NP ( $P < 0.001$ ) grasses in the  $N_{min}$  treatment than at other fertility levels (Table 4). Biomass of C4NP grasses in these plots was not significantly different from any of the non-herbicide treatments. In plots that had herbicide applied, there were more C3NP species in the  $G_{act}$  treatment than in the other grazing treatments by 2002 ( $P < 0.001$ ).

#### Relationship between biomass and frequency

There was a strong positive correlation between functional type biomass and frequency, hence the plant frequency data are not presented. A linear regression showed a strong relationship for *N. trichotoma* ( $R^2 = 0.519$ ), C4NP ( $R^2 = 0.670$ ), and AG ( $R^2 = 0.772$ ), with weaker though still significant relationships for C3PN ( $R^2 = 0.254$ ) and OTH ( $R^2 = 0.366$ ). C3PI also had a strong relationship but this was unreliable due to the high number of zero values.

#### Individual plant effects

##### *N. trichotoma basal area*

Only small changes were measured in basal area for most *N. trichotoma* plants during the experiment. Initially there was no significant difference in basal area among treatments, although there was a large natural variability between plants and treatments (data not presented).

##### Treatment effects on basal area of *N. trichotoma*

Regressions of the log ratio of basal area and harvest times showed a differential plant response for treatments. Basal area increased in  $G_{con}$  compared with the  $G_{act}$  and  $G_{nil}$  treatments that did not change (Table 5). A regression analysis in groups showed that basal area increased in the  $G_{con}$  treatment compared with the  $G_{nil}$  treatment ( $P < 0.01$ ).

Basal area was affected by fertility treatments (Table 5). The slope of the regression showed that basal area in the  $N_{add}$  fertility treatment increased at a greater rate than in the  $N_{nil}$  fertility treatment ( $P < 0.05$ ). The regression slope of the  $N_{add}$  fertility treatment was significantly greater than 0 where the  $N_{nil}$  treatment was not ( $P < 0.05$ ).

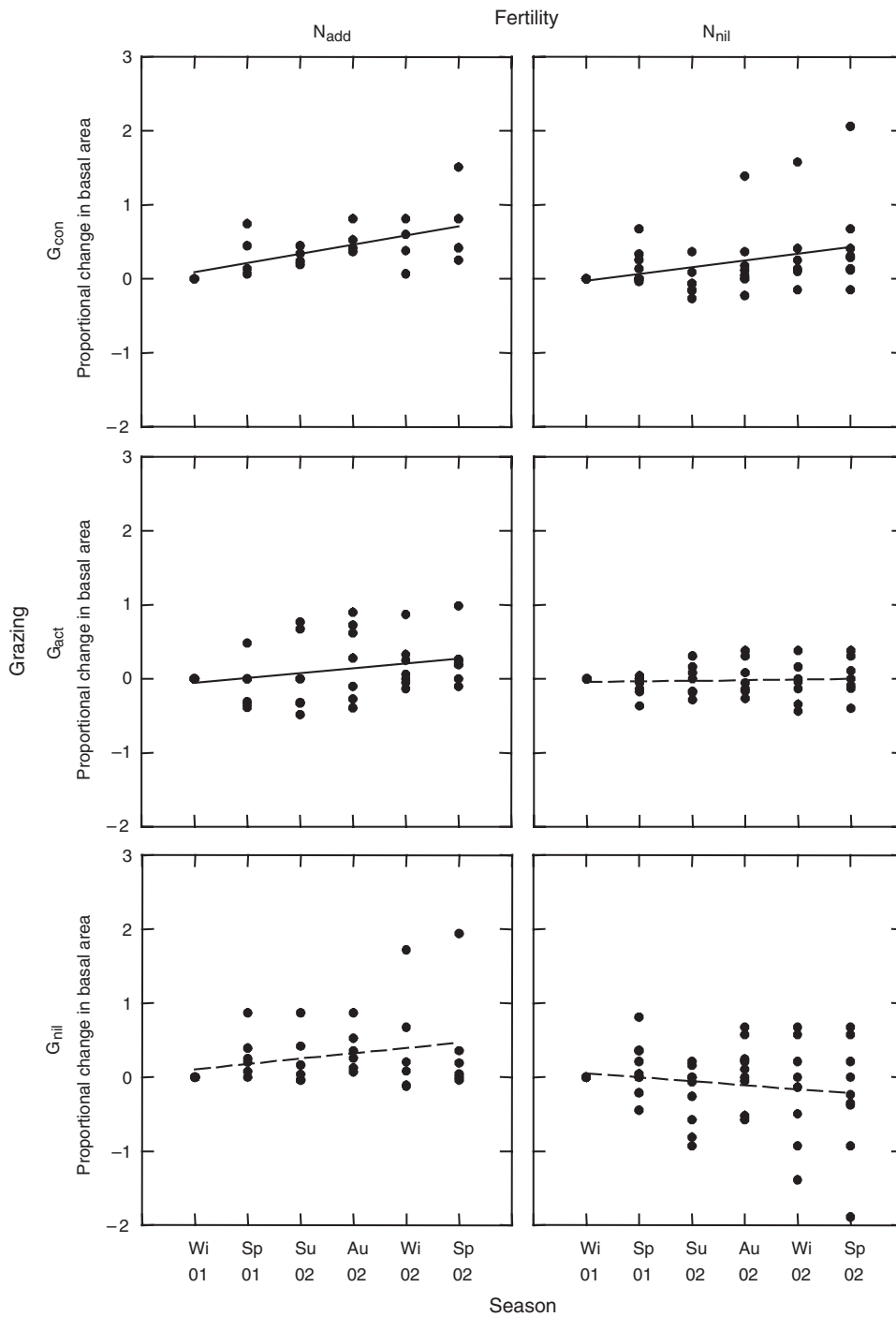
There were statistically significant grazing  $\times$  fertility interactions between regression slopes. Two of the  $N_{add}$  fertility grazing treatments had a slope  $> 0$  ( $P < 0.05$ ), the exception being the  $G_{nil}$  treatment, indicating an increase in basal area (Fig. 1, Table 5). The  $G_{con}$   $N_{nil}$  treatment also had a slope  $> 0$  ( $P < 0.05$ ); however, the remaining grazing treatments in the  $N_{nil}$  fertility treatments, such as the  $N_{add}$   $G_{nil}$  treatment, did not have slopes significantly different from zero. The  $N_{nil}$   $G_{nil}$  treatment had a negative slope (Table 5), indicating that the basal area of *N. trichotoma* plants in this treatment decreased over the experimental period, although not significantly.

##### The effect of initial plant size on basal area change

A non-linear relationship was detected between initial plant size and plant response over the experimental period (data not presented). Most of the change in basal area occurred in *N. trichotoma* plants with an initial basal area  $< 500$  mm<sup>2</sup>.

**Table 5.** Slope, probability that the slope is significantly different from zero, and  $R^2$  of linear regressions between the standardised basal area of *N. trichotoma* ( $BA \ln(H_x/H_1)$ , where  $H_1$  is the basal area at the first harvest and  $H_x$  is the basal area at measurement  $X$ ), and grazing, fertility, and grazing  $\times$  fertility (Fig. 1) over time  
n.s., Not significant

Grazing	Fertility	Slope	P-value	$R^2$
$G_{con}$		0.102	$< 0.001$	0.171
$G_{act}$		0.036	n.s.	
$G_{nil}$		-0.003	n.s.	
	$N_{add}$	0.081	$< 0.001$	0.111
	$N_{nil}$	0.012	n.s.	
$G_{con}$	$N_{add}$	0.123	$< 0.01$	0.361
	$N_{nil}$	0.091	$< 0.05$	0.125
$G_{act}$	$N_{add}$	0.065	$< 0.05$	0.090
	$N_{nil}$	0.008	n.s.	
$G_{nil}$	$N_{add}$	0.072	n.s.	
	$N_{nil}$	-0.054	n.s.	



**Fig. 1.** Relationship between the standardised basal area of *N. trichotoma* ( $BA \ln(H_x/H_1)$ , where  $H_1$  is the basal area at the first harvest and  $H_x$  is the basal area at measurement  $X$ ), and grazing  $\times$  fertility over time. Solid lines represent linear regressions that are significantly different from zero ( $P < 0.05$ ) and the dashed lines are not significantly different.

The standardised basal area [ $\ln(H_6/H_1)$ ] of plants that were initially  $< 500 \text{ mm}^2$  was used for a REML analysis (Table 6). Grazing did not have a significant effect, but fertility and grazing  $\times$  fertility interactions were significant. The  $N_{add}$  treatments had a greater increase in basal area than those that

did not have N added. The most notable grazing  $\times$  fertility interaction was in the  $G_{nil} N_{add}$  treatment where basal area increased significantly compared with the  $G_{nil} N_{nil}$  treatment, which actually decreased. No significant difference was found at the other grazing intensities between fertility treatments.

**Table 6. Mean standardised basal area [ $\ln(H_6/H_1)$ ] of *N. trichotoma* plants < 500 mm<sup>2</sup> for different grazing, fertility, and grazing × fertility treatments**

Values followed by the same letter are not significantly different in the average variance of differences from the REML model

Grazing	Fertility		Total grazing
	N <sub>add</sub>	N <sub>nil</sub>	
G <sub>con</sub>	1.16b	1.05b	1.09a
G <sub>act</sub>	0.48bc	0.35bc	0.43a
G <sub>nil</sub>	1.94a	-0.16c	0.26a
Total fertility	0.95a	0.35b	0.59

### *N. trichotoma* seed production

In 2001 or 2002, there were no differences among treatments in the amount of seed per plant or seed per cm<sup>2</sup> of basal area, although there was approximately twice the amount of seed produced in 2001 compared with the drier year 2002. In 2001, seed yields ranged from 81 554 to 390 seeds per plant, averaging 16 606 ± 2984. In 2002, seed yields ranged from 55 680 to 0 seeds per plant, averaging 8797 ± 1849.

### Discussion

In the 2 years of this study, there was little change in the biomass of adult *N. trichotoma* plants, except when herbicide was applied, which caused complete mortality. However, changes in soil fertility and grazing regimes among treatments had an effect on pasture composition, with *N. trichotoma*, AG, and C3IP grasses all increasing with increased soil fertility, whereas C4NP and, to lesser extent, C3NP grasses decreased. While standing biomass of *N. trichotoma* did not change significantly there was some evidence of competition affecting adult plants, particularly smaller plants (<50 cm<sup>2</sup>). Basal area of *N. trichotoma* plants decreased or remained the same in the G<sub>act</sub> and G<sub>nil</sub> treatments when no fertiliser was added, but increased in the G<sub>con</sub> treatment and where fertiliser was added, except in the G<sub>nil</sub> treatment.

### Grazing

The aim of the G<sub>act</sub> and G<sub>nil</sub> grazing treatments was to increase the competitiveness of surrounding perennial native grasses by reducing the effect of selective grazing by sheep. The most obvious effect of these strategies was an increase in the C4NP grass component compared with G<sub>con</sub>, a treatment typical of current grazing practices in *N. trichotoma*-infested pastures. While the higher biomass of C4NP grasses did not directly affect the cover or biomass of *N. trichotoma* overall, effects on the basal area of individual plants were detected. For example, the basal area of *N. trichotoma* plants in continuously grazed plots increased with time, whereas the plants in the other grazing treatments did not change significantly.

This change in basal area can be explained by considering the resources available under the different grazing systems. Removing large amounts of plant material by grazing, lowers the resource consumption of the grazed plant species, thereby making more resources available to the ungrazed plant species, which in turn affects competitive interactions (Hulme 1996).

Since *N. trichotoma* is an unpalatable plant, it was not grazed, in contrast to the surrounding pasture species in the continuously grazed treatment. This gave *N. trichotoma* a competitive advantage over treatments where grazing was controlled. Preferential grazing is one of the predominant mechanisms that cause compositional change as continuous grazing pressure increases (Anderson and Briske 1995; Bullock *et al.* 2001). Moretto and Distel (1997, 1999) found that *N. trichotoma* was not as competitive as the palatable species *Nassella clarazii* (Ball) Barkworth, but rather it was grazing that resulted in the dominance of *N. trichotoma* in mixed grasslands in Argentina. A similar pattern was observed in this experiment in Australia.

A long-term experiment by Rawes (1981) demonstrated that the unpalatable species *Juncus squarrosus* L. was eliminated when grazing was excluded for 24 years. This present study was only for 2 years and a longer period may be necessary to more fully determine treatment effects. Over the experimental period there was very little change in the basal area of larger plants in all treatments. Plants maintained senescent material, which effectively masked the underlying competitive effects on *N. trichotoma*. Also, it is likely that once plants reach a mature size (>500 mm<sup>2</sup>), tiller recruitment within the plant is diverted into replacing senescing material in the centre rather than into the expansion of basal area, unless resource levels are dramatically increased, further masking changes in the plant.

### Soil fertility

There was some evidence to support the hypothesis that reduced grazing pressure and soil fertility (sucrose addition) increased the competitiveness of C<sub>4</sub> native perennial grasses (Wedin and Tilman 1996; Wedin 1999), but not to an extent that had any marked effect on the *N. trichotoma* abundance. The alternative hypothesis, that the unpalatable species would not be able to respond to fertility as well as the more palatable native grasses, was rejected because adult *N. trichotoma* plants responded positively to increased soil fertility in all grazing treatments, indicating that *N. trichotoma* was able to use higher soil fertility conditions even though it has a higher tissue density than most native species (Campbell 1960). This contradicted the finding of Craine *et al.* (2001) that high-tissue-density species are less common as fertility and disturbance increase. Chapin *et al.* (1993) suggested that N uptake by unpalatable species is low and therefore they could not respond to elevated levels of N with increased growth as quickly as species with a lower tissue density. However, this was not supported by Distel *et al.* (2003) who found that *Nassella* species that have a high tissue density might also have high absorption capacities when they are adapted to resource-rich microsites. Also Badgery *et al.* (2005) reported that *N. trichotoma* has a similar growth rate to the native perennial grasses found in the current experiment.

In the N<sub>min</sub> treatment, available N was reduced and both the C3NP and C4NP grasses had a higher biomass than in the higher fertility treatments and a higher frequency than in the N<sub>add</sub> fertility treatment. Although there was no statistically significant change in *N. trichotoma* biomass or cover at lower soil fertility, there were effects on individual *N. trichotoma* plants in the N<sub>nil</sub> fertility treatments. Measurements of individual plants



in the  $N_{\min}$  treatment may have provided further evidence of this pattern because a substantial reduction in size of *N. trichotoma* plants in the  $N_{\min}$  treatment was observed when *T. australis* plants were immediately adjacent. However, this was not reflected in the biomass measurements of the sward. Nevertheless, this suggested that, over the long term, *N. trichotoma* could be out-competed in lower fertility environments when grazing is removed.

### Herbicide

As previously reported by Campbell *et al.* (1979), flupropanate was very effective against *N. trichotoma* plants, but there was severe collateral damage to the C4NP and in particular C3NP grasses. Damage to native grasses recorded in this experiment was similar to that found by Keys and Simpson (1993) and Campbell and Van de Ven (1996). *Austrodanthonia* spp. and *M. stipoides* were severely affected by flupropanate. *T. australis* and *B. macra* were also affected, but not as severely. The forbs *H. radicata* and *A. vulgaris* tolerated flupropanate and dominated standing biomass in the first measurement 6 months after the herbicide was applied. The standing biomass of different species continued to change in some treatments up to 18 months after the herbicide had been applied. The delayed sustained action of flupropanate means it can take up to 12 months to kill adult plants completely (M. H. Campbell, pers. comm.).

To explain the change in standing biomass it is important to identify how this disturbance affected the grassland. Disturbance may alter vegetation either directly through the survival of individuals or indirectly by changing the resource levels that affect individual plants in a patch (Hobbs 1991). Direct disturbance caused by the herbicide initially almost entirely killed C3NP and substantially reduced C4NP. However, C4NP continued to decrease 18 months after the herbicide application, long after the residual effect of the herbicide had subsided. The continued reduction was not as pronounced in the  $N_{\min}$  treatment, suggesting that the effect on C4NP grasses was at least partly associated with changes in soil fertility resulting from the herbicide application. Annual grasses, which are more competitive at higher soil fertility than are native perennial grasses (Groves *et al.* 2003), continued to increase proportionally 18 months after the herbicide had been applied. Competition from these species probably reduced the growth of C4NP. Even though soil fertility was not directly measured at the herbicide level of the experiment, it can be expected that available soil nutrients would have substantially increased as a result of the herbicide treatment, due to decomposition of plant material, with this indirectly affecting the biomass of C4NP grasses. The response of C4NP grasses to fertility in this experiment and as a result of the herbicide treatment agrees with that reported by Wedin and Tilman (1996) and Lane and BassiriRad (2002), in that  $C_3$  grasses responded better to N addition than  $C_4$  grasses.

### Implications for management

Large adult *N. trichotoma* plants are relatively biologically inert i.e. they change in size slowly and, in our experiment, the population of adult plants in most treatments remained relatively constant. There was no recorded mortality of these

plants over the experimental period except where herbicide was applied and very few young plants achieved a mature size.

With only a slight and/or slow effect of native grasses on adult *N. trichotoma* plants it was unlikely that this would be a successful management technique to reduce *N. trichotoma* populations in the short term. However, competition is likely to be critical in limiting the invasion of new *N. trichotoma* seedlings (Badgery *et al.* 2008). Other selective forms of management, such as spot spraying, wick-wiper, or chipping, which target adult plants but do not affect surrounding pastures, are likely to be required for successful *N. trichotoma* control in native pastures.

Results from the fertility treatments highlight 2 main implications for the use of soil fertility manipulations in adult *N. trichotoma* plants. First, if fertiliser is applied to pasture where few competitive perennial grasses (e.g. *P. aquatica*) are present to use the added nutrients, it is likely that the response of native perennial grasses will not be sufficient to out-compete adult *N. trichotoma* plants. Furthermore, while annual grasses and legumes show a strong response to increased soil fertility, their effect on adult *N. trichotoma* plants is likely to be minimal because of their short (autumn–spring) life-cycle, but they could be effective in preventing *N. trichotoma* seedling establishment (Badgery *et al.* 2008). At naturally higher fertility sites, *N. trichotoma* is more likely to invade rapidly and persist unless there is a dense perennial pasture to prevent it. At naturally lower fertility sites, invasion may still occur, but at a slower rate, and so a lower proportion of perennial native grasses may be needed to prevent invasion than at higher soil fertility. However, it is likely to be easier to maintain a competitive pasture under grazing at higher rather than lower soil fertility.

Flupropanate effectively killed adult *N. trichotoma* plants but the collateral damage to native perennial grasses also altered grassland composition and so re-invasion is likely to occur irrespective of what grazing management or soil fertility treatments are imposed. Using lower rates of flupropanate will not maintain native species, such as *Austrodanthonia* spp. and *M. stipoides*, since they are susceptible at half the recommended rate (0.75 kg a.i./ha) (Keys and Simpson 1993), but *B. macra* may be maintained at this rate (Campbell and Van de Ven 1996). Rates as low as 0.56 kg a.i./ha have effectively controlled *N. trichotoma* (Campbell 1997) but it is uncertain if these rates would have less effect on native grasses species. Glyphosate, a knock-down herbicide, can be applied at a time when the dominant grasses are not actively growing, i.e. mid-summer for  $C_3$  native grasses or mid-winter for  $C_4$  native grasses, to minimise collateral damage and maintain a reasonable ground cover and biomass of perennial grasses to prevent re-invasion (L. Ayres and B. Verbeek, pers. comm.).

Effective management will only be achieved with integrated strategies that effectively control *N. trichotoma*, while maintaining a competitive perennial pasture to prevent seedling re-invasion. However, further experiments would clarify the application of these results in a wider range of environments and through different climatic cycles.

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