*Journal of Ecology* 2005 93, 384–394

## Plant strategies and trait trade-offs influence trends in competitive ability along gradients of soil fertility and disturbance

### R.W.S. FYNN, C.D. MORRIS\* and K.P. KIRKMAN

Grassland Science, School of Biological and Conservation Sciences, and \*Agricultural Research Council – Range and Forage Institute, University of KwaZulu-Natal, Private Bag X01, Scottsville 3209, Pietermaritzburg, South Africa

### Summary

1 We present evidence of trade-offs in competitive ability among five perennial  $C_4$  grass species at different levels of soil fertility and disturbance in a garden experiment in KwaZulu-Natal, South Africa.

2 Our goals were to examine plant strategy theory, using grass species that differed widely in various traits and in their response to environmental influences. More specifically, we wished to examine whether the importance of competition was less in low fertility or regularly disturbed environments (stressed environments) than in more fertile or undisturbed conditions, and whether species made trade-offs in competitive ability along such stress gradients.

**3** The trend in the competitive ability of two species in mixture along a soil fertility gradient tended to be inversely related if one had narrow and the other broad leaves or they differed in height, providing strong evidence for trait trade-offs. Thus, a tall broad-leaved species, *Panicum maximum*, was the most competitive species in fertile subplots, whereas a tall narrow-leaved species, *Hyparrhenia hirta*, was the most competitive species in infertile subplots, but no difference in competitive ability across a fertility gradient was observed when both species in a mixture had similar traits.

**4** Regular cutting altered competitive interactions amongst species resulting in a short species, *Themeda triandra*, having a greater competitive effect on neighbours and a better response to neighbours in cut than in the less stressed uncut treatments, suggesting a trade-off for competitive ability in regularly disturbed habitats. However, cutting only improved the performance of *T. triandra* against *P. maximum* in infertile subplots.

**5** We demonstrated that for some, but not all, mixtures of species, competitive hierarchies may reverse along gradients of soil fertility and disturbance. Moreover, soil fertility and disturbance may interact in their effect on competitive interactions. Thus, soil fertility and disturbance form the major axes of an ecological framework for understanding plant competitive interactions.

*Key-words*: competitive hierarchy, ecological theory, garden experiment, limiting resources, response ratio

*Journal of Ecology* (2005) **93**, 384–394 doi: 10.1111/j.1365-2745.2005.00993.x

### Introduction

Habitat fertility and disturbance have been recognized in conceptual and predictive models as major underlying determinants of plant community organization (Grime 1973, 1977; Huston 1979; Tilman, 1982, 1988). Indeed, many empirical studies have demonstrated the importance of habitat fertility, disturbance and their interaction on plant community organization (Gibson *et al.* 1993; Gaudet & Keddy 1995; Fuhlendorf & Smeins 1997; Collins *et al.* 1998; Kirkman 2002; Osem *et al.* 2002; Wilson & Tilman 2002; Foster *et al.* 2004; Fynn *et al.* 2004; Osem *et al.* 2004).

Although competition has been invoked as an important determinant of plant species distribution

© 2005 British Ecological Society Correspondence: Richard W. S. Fynn (tel. +27 33 2605505; fax +27 33 2605708; e-mail fynn@ukzn.ac.za).

**385** *Plant strategies and competitive ability*  and abundance along fertility gradients (Grime 1973, 1979; Tilman 1988; Austin 1990; Gaudet & Keddy 1995), its importance at the opposite extremes of these gradients has become a source of intense debate amongst ecologists (Tilman 1987; Campbell & Grime 1992; Grace 1993). Competition is considered by one school of thought to have negligible influence on the structuring of plant communities in low fertility habitats but for all resources (space, light, nutrients and moisture) to increase in importance with increasing habitat fertility (Grime 1973; Grime 1977).

A contrary view is that species make trade-offs in competitive ability along fertility gradients, with some being more competitive in infertile than fertile habitats and *vice versa* (Tilman 1988). Competition for soil resources should then be relatively more important in infertile habitats, and for light and aerial space in fertile habitats.

Despite much examination of trends in competition intensity and in the competitive ability of different species along fertility gradients (Campbell & Grime 1992; Wedin & Tilman 1993; Wilson & Tilman 1993; Gaudet & Keddy 1995; Twolan-Strutt & Keddy 1996; Cahill 1999; Keddy *et al.* 2002; Rajaniemi 2002; Rajaniemi *et al.* 2003; MacDougall & Turkington 2004), the debate over plant strategies on fertility gradients still awaits resolution.

Another unresolved question is the relative importance of equilibrial and non-equilibrial mechanisms as determinants of community organization under various disturbance regimes (Suding & Goldberg 2001). Non-equilibrial models assume that disturbance reduces the intensity of competitive interactions, thereby reducing the ability of strong competitors to exclude less competitive species (e.g. Huston 1979). By contrast, equilibrial models assume trade-offs in competitive ability in disturbed or undisturbed conditions (sensu Tilman 1988) and disturbance is thought to alter competitive interactions amongst species through differential effects on nutrient loss rates, by increasing light availability and alteration of the soil abiotic environment (Tilman 1988; Berendse & Elberse 1990; Tilman 1990a; Suding & Goldberg 2001; MacDougall & Turkington 2004). Very little understanding exists on the influence of disturbance on competitive interactions, and especially on how this may interact with habitat productivity (Goldberg & Barton 1992), but recent studies have begun to shed light on relations between productivity, disturbance and competitive interactions (Proulx & Mazumder 1998; Suding & Goldberg 2001; Osem et al. 2002; Osem et al. 2004). Plant traits may be useful predictors of the response of species to environmental factors and to competitors because they may represent specific functional adaptations to various constraints (e.g. Goldberg 1996; Westoby 1998; Craine et al. 2002; Lavorel & Garnier 2002). Trait trade-offs that species may make in dealing with specific constraints may influence a species' ability to compete under different conditions (Tilman 1988; Goldberg 1996; Suding et al. 2003).

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394 Thus, a knowledge of which trait trade-offs influence competitive ability along specific environmental gradients should enable greater general predictive ability (Tilman 1990b; Suding *et al.* 2003).

Our aim was to examine plant strategy theory using five perennial C4 grass species that differ in habitat preferences, ecological responses and traits (low to high specific leaf area, short to tall) in an experiment that manipulated fertility, moisture availability, habitat productivity and disturbance. In order to clarify some of the issues in the debate on the role of habitat fertility, disturbance and competition in structuring plant communities, we aimed to (i) determine whether competitive interactions amongst species were affected by different limiting soil resources (soil moisture and nutrients), (ii) examine whether the competitive hierarchy in various species mixtures became reversed along gradients of soil fertility and disturbance, and (iii) determine which trait trade-offs resulted in a differentiation of competitive ability among species on different environmental gradients.

### Methods

#### STUDY SITE

The experiment was established in December 2002 at the Neil Tainton arboretum (29°40′ E, 30°24′ S) on the campus of the University of KwaZulu-Natal, Pietermaritzburg, South Africa. Mean annual rainfall for Pietermaritzburg is 844 mm, with most of the rain falling in summer between November and March. Summers are hot (maximum mean monthly temperature of 28.2 °C in February and March), while winters are mild with occasional frost (minimum mean monthly temperature of 2.9 °C in June). The growing period is controlled by temperature and rainfall, with most annual dry-matter production occurring between October and April, and peak growth rates between December and February.

### CHOICE OF SPECIES

The species used in this experiment were native perennial  $C_4$  grasses chosen for their wide variation in morphological traits (Table 1) and different responses to various environmental influences.

Themeda triandra (Forssk.) is a relatively short, narrow-leaved species that generally dominates grasslands on well-drained relatively infertile soils that are burnt or mown regularly (Fynn 2004). It appears to be intolerant of litter accumulation in the absence of disturbance (Belsky 1992). Hyparrhenia hirta (L.) is a tall, narrowleaved species that generally favours well-drained stony or sandy soils. It often dominates abandoned cultivated fields. Aristida junciformis (Trin. & Rupr.) is a species of medium height with extremely erect narrow, needlelike leaves. It may dominate grasslands on very infertile soils or increase under prolonged selective grazing or

 Table 1
 Selected morphological traits of the species used in the experiment when grown in a glasshouse in sand culture with a 110% Hoaglands nutrient solution for 2 months (R. W. S. Fynn, unpublished data)

	Leaf area (cm <sup>2</sup> )	SE	Specific leaf area (cm <sup>2</sup> g <sup>-1</sup> )	SE	Height class (mm)*	Maximum leaf height (mm)	SE	Maximum leaf width (mm)	SE	Root : shoot ratio	SE
Aristida junciformis	258.73	36.09	38.38	13.75	100-200	450.00	40.41	2.17	0.17	0.24	0.02
Eragrostis curvula	1418.62	403.61	54.20	6.92	200 - 400	816.67	68.88	7.17	0.44	0.20	0.05
Hyparrhenia hirta	1812.59	160.58	78.60	8.87	400 - 800	1353.33	66.67	6.67	0.67	0.22	0.02
Panicum maximum	3919.84	216.02	154.00	2.89	400 - 800	1376.67	132.96	24.33	2.73	0.14	0.01
Themeda triandra	958.99	162.48	89.14	9.85	100 - 200	536.67	151.91	7.00	0.58	0.30	0.05

\*Height class in which maximum leaf area occurs; SE = standard error.

with long-term protection from disturbance (Fynn 2004). *Eragrostis curvula* (Schrad.) is a relatively tall, narrow-leaved and strongly tufted species that invades and dominates grassland fertilized with nitrogen (Fynn 2004) and increases in abundance in grassland that is burnt or mown only infrequently (Fynn 2004). *Panicum maximum* (Jacq.) is a tall, broad-leaved species that often dominates grassland on deep-fertile soils near rivers or under leguminous trees in grassland on less fertile soils or open grassland fertilized with nitrogen (N) plus phosphorus (P) (Fynn 2004).

#### EXPERIMENTAL DESIGN

The outdoor split-plot garden experiment was designed to examine the effect of disturbance, soil fertility and soil moisture on competitive interactions among species, with irrigation as whole-plots and fertilization as subplots with three blocked replications (Table 2). The site had been sprayed with herbicide and cultivated using a disk to kill the existing vegetation (lawn grasses dominated by *Paspalum notatum*). To maintain treatment integrity, irrigated plots were separated from non-irrigated plots by 4-m walkways and fertilized subplots from non-fertilized subplots by 2-m walkways. The 2- and 4-m-wide walkways were maintained as lawns but the 0.75-m-wide walkways between quadrats (see below) were kept free of vegetation.

Species mixture and monoculture plantings, crossed with two cutting treatments, were randomly allocated to 25 experimental  $0.5 \times 0.5$  m quadrats within each subplot. The species mixtures were: (i) all species separately in pairwise competition with *T. triandra* (*T. triandra* was used as a baseline species in mixtures because it is one of the most common species in local grasslands); (ii) *H. hirta* in competition with *E. curvula* (tall narrow-leaved species vs. tall narrow-leaved species); and (iii) *H. hirta* in competition with *P. maximum* (tall narrow-leaved species vs. tall broad-leaved species).

All quadrats in the experiment were cut at the end of the first season (end of April 2003) to remove old dead material, allowing for new growth during the second season. The cutting height was 50 mm above the soil surface, which removed most of the foliage of all species. In the no cutting (control) quadrats, vegetation was not cut during the growing season, otherwise nonselective cutting was applied every 2 weeks (six cuts) between December and April of the 2002/2003 growing season and each month (three cuts) between November and February of the 2003/2004 growing season.

In the irrigated treatments, quadrats were watered with a mist spray irrigation system (each quadrat had its own spray terminal) once a day for half an hour to ensure water was not limiting. In the fertilized treatments, fertilizer was applied to quadrats three times during the growing season at a rate of 94 g m<sup>-2</sup> per dressing of 2:3:2 NPK fertilizer.

Species were grown from seed in seedling trays before planting into quadrats. Species were planted in monoculture or mixture quadrats of 16 plants (eight of each species in mixture quadrats) comprising four rows of four plants spaced 50 mm apart. In mixture quadrats, each row consisted of two plants of each species, alternating to ensure that each was evenly dispersed throughout the quadrat. Consequently, any individual within a mixture quadrat was surrounded by an even distribution of interspecific and conspecific neighbours to ensure that each species experienced symmetric competition with respect to the number of interspecific neighbours. Quadrats were regularly weeded to remove unwanted species.

# DETERMINATION OF ENVIRONMENTAL PROPERTIES

Twenty-five systematically located 35 cm<sup>3</sup> soil samples, taken at the end of the second season from the surface 50 mm in each subplot (A–L; Table 2), were pooled by subplot and air dried. The bulked samples were analysed for total N using a LECO nitrogen analyser, ammonium bicarbonate extractable P, organic matter using dichromate oxidation and clay content using the pipette method. Soil depth was determined as the mean of four systematically located auger points in each subplot. The percentage stone cover on the soil surface was estimated visually. Values obtained for soil fertility of a subplot should represent the inherent fertility of that subplot because sampling was done in the walkways between quadrats and should not therefore be influenced by the fertilization treatment.

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394

### Plant strategies and competitive ability

387

Treatm	ent allocation			Soil prope	erties					Production in u	ncut monocul	ture plots (g plo	t <sup>-1</sup> )	
					Stone		Organic							
2	F	ŀ	Rep.	Depth	cover	Clay	matter	Z (	P	s		Ē	Ē	
Plot	Fertilize	Irrigate	stratum	(mm)	(%)	(%)	(%)	(mg kg ')	(mg kg ')	P. maximum	H. hirta	I. trianara	E. curvula	A. Junciformis
A	1	0	1	353	15	18.8	2.57	1400	6	962.69	562.53	173.35	484.34	217.14
В	0	0	1	288	10	26.39	4.87	2200	2	361.45	634.47	257.28	46.35	289.93
C	0	1	1	303	80	20.65	5.35	2700	9	1216.08	2422.62	1067.54	613.38	926.81
D	1	1	1	318	65	20.85	4.33	2300	7	1026.07	1482.15	930.46	865.00	830.77
Щ	1	1	2	348	65	16.96	4.13	2000	6.5	1826.74	1575.86	1323.08	861.35	1348.24
Ĺ	0	1	2	285	15	25.42	5.42	2800	10	1729.11	1933.98	884.24	460.84	676.37
Ċ	0	0	2	355	10	25.21	5.42	2400	8.5	408.73	1258.57	293.73	210.14	714.47
Η	1	0	2	333	10	26.69	5.48	2600	17	1608.99	1199.10	337.01	288.51	511.18
I	0	0	.0	365	10	26.51	7.86	3700	16.3	1875.69	1013.32	328.94	217.04	489.24
ſ	1	0	6	360	15	26.71	6.09	3300	18.5	1546.1	543.29	601.22	489.03	351.66
К	1	1	ю	305	10	28.31	7.32	3500	20.5	3427.05	1614.41	1162.12	1041.01	1593.01
L	0	1	Э	315	10	24.89	6.37	3100	12.5	4690.32	2096.23	1312.74	1712.60	1769.60

SPECIES SAMPLING METHOD

Sampling of species biomass in the various mixture and monoculture quadrats was done at the end of the second growing season (late March 2004) and data therefore represent the outcome after two seasons of competition and experimental effects. Each species in a quadrat (mixture or monoculture) was clipped at 50 mm above the soil surface, bagged and dried at 90 °C to constant mass and weighed. In quadrats where the amount of a species was too large to fit into paper bags for drying, the fresh material of that species was weighed, and this weight was converted to dry mass using the moisture content determined from a representative grab sample.

### DATA ANALYSES

A formal analysis of the effects of various environmental factors on competitive interactions and the competitive ability of various species requires quantification of how the strength of interspecific competition for a species in a specific mixture varied relative to the strength of intraspecific competition (biomass in monoculture) along a specific environmental gradient. Using the ratio of the response of a species in mixture to its response in monoculture (Hedges et al. 1999; Weigelt & Jolliffe 2003) has advantages over the relative competition intensity index because it is symmetrical for competitive and facilitative interactions and does not impose a ceiling on the maximum possible competition intensity (Goldberg et al. 1999; Weigelt & Jolliffe 2003). Thus, increasing values of the response ratio along an environmental gradient would indicate that the strength of interspecific competition was decreasing relative to intraspecific competition for a species in a specific mixture along that environmental gradient. Inversely related trends in the strength of interspecific relative to intraspecific competition for two species in mixture along an environmental gradient would indicate that these species had opposing competitive strategies along this gradient. To meet statistical assumptions it has been advocated that the response ratio be log transformed (Hedges et al. 1999). Thus all statistical analyses were conducted on the log of the response ratio [ln (response ratio + 1)], where a value of one was added to cater for subplots where competitive exclusion had resulted in zero values for the response ratio. The number of individuals of a species planted in a quadrat differed for monoculture and mixture quadrats (16 in monoculture vs. eight in mixture). Thus, the response of a species consisted of the mean dry-matter production of eight individuals of a species if it was a mixture quadrat and of 16 individuals of a species if it was a monoculture quadrat, to ensure a standardized comparison of performance in mixture vs. monoculture.

All data analyses were performed using GENSTAT 5 (Anonymous 1993). Analysis of variance (split-plot design) was used to examine whether the response ratio of each species in the various species mixtures was

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394 Table 2 Treatment and environmental characteristics of whole-plots and subplots of the competition experiment at the N.M. Tainton Arborretum

influenced by the whole-plot irrigation and subplot fertilization treatments (i.e. was the competitive performance of different species affected differently by different limiting soil resources).

Multiple linear regression with groups was used to test whether the intercepts and slopes of the line differed in the relation between the response ratio of two species in mixture and inherent variation in total soil N and extractable soil P. Testing for a difference in slope is equivalent to testing for a species-environment interaction. Significant differences for both the slope and intercept terms indicate that the competitive abilities of the two species under examination are inversely related along a specific environmental gradient (especially if the fitted lines of the response ratios of the two species are crossed over along the gradient). This would be unequivocal evidence that the two species have made opposing trade-offs for competitive ability along that environmental gradient. The response ratio was examined in relation to soil N and P because these two nutrients have a major effect on plant composition in local grasslands (Fynn 2004).

The model used in the analysis was:  $\ln(\text{response} \text{ratio} + 1) = \text{constant} + \text{soil N or soil P + species + soil N or soil P × species, with species as a factor. A similar model was used to determine how cutting and soil N or P may alter the proportion of a species in a mixture quadrat: Proportion of a species in a quadrat = constant + soil N or soil P + cutting treatment + soil N or soil P × cutting treatment, with cutting treatment as a factor.$ 

Paired *t*-tests were used to determine if cutting resulted in a change in the response ratio of a species in a specific mixture relative to uncut treatments. Paired comparisons consisted of the response ratio of a species in a specific mixture in the cut and uncut treatments of a specific subplot. Multiple linear regression was used to determine if the effect of cutting on the response ratio interacted with soil N or P. The model to examine this was: ln (response ratio + 1) = constant + soil N or soil P + cutting treatment + soil N or soil P × cutting treatment, with cutting treatment as a factor.

Two-way analysis of variance, with cutting treatment and species as factors, was used to test for a cuttingspecies interaction on the response ratios of the two species in the specific mixture under examination. A significant cutting × species interaction would be evidence that there had been a reversal or shift in the competitive hierarchy between cut and uncut treatments. The response ratio of T. triandra in the cut treatment could not be calculated in subplot A (Table 2), owing to the failure of its cut monoculture. Thus, to examine the effect of cutting on the response ratio of T. triandra, the paired t-tests were done using 11 instead of all 12 subplots and a missing value for the response ratio of T. triandra in subplot A was included in the two-way analysis of variance. Simple linear regression was used to determine if the slope of the fitted lines of the response ratio of a species or their proportion in quadrats along N or P gradients differed significantly from zero.

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394

### Results

# EFFECT OF FERTILIZATION AND IRRIGATION ON COMPETITIVE ABILITY

Irrigation had no effect on the response ratio of any of the species in any mixture, whether or not N or P was included as a covariate in the analysis (Table 3). The only significant effects of fertilization on the response ratio were for *P. maximum* in the *P. maximum* vs. *H. hirta* mixture and *H. hirta* in the *H. hirta* vs. *T. triandra* mixture, and these disappeared when inherent soil N or soil P was included as a covariate (Table 3). Thus, it is apparent that the steep pre-existing gradient in soil fertility across the experiment (Table 2) had a greater effect than that of applied fertilizer on competitive interactions amongst species.

# TRENDS IN COMPETITIVE ABILITY ALONG SOIL FERTILITY GRADIENTS

Strong differences in the trends of response ratios of two species in a mixture are apparent along inherent gradients of extractable soil P and to some extent total soil N. For example, there were highly significantly different slopes and intercepts of the response ratios (P < 0.001) of *H. hirta* and *P. maximum* in the *H. hirta*-P. maximum mixtures along a gradient of extractable soil P (Fig. 1b) and to a smaller degree along a gradient of total soil N (Fig. 1a). Moreover, the crossing over of the fitted lines (Fig. 1b) indicates that there was a complete reversal of the competitive hierarchy between H. hirta and P. maximum along the soil P gradient. Significant differences in slope of the line (P = 0.027) and almost so for the intercept (P = 0.066) of the response ratios of H. hirta and P. maximum show that there was a shift in the competitive hierarchy for these species along the soil N gradient (Fig. 1a). Apart from the subplot with the lowest soil N the competitive hierarchy appeared to reverse along the N gradient (Fig. 1a). No such reversals of the competitive hierarchy were observed in any other species mixture (Fig. 1c-h), although significant differences in the slope of the lines of the response ratios indicate that T. triandra became increasingly more competitive against P. maximum (P = 0.003; Fig. 1d) and *H. hirta* (P = 0.042; Fig. 1f) as soil P levels declined. Themeda triandra had on average larger response ratios than A. junciformis (P = 0.015; Fig. 1g,h) but non-significant slope and intercept values (P > 0.05) indicate that there was no shift in the competitive hierarchy along the N or P gradients for the T. triandra-A. junciformis mixtures (Fig. 1g,h).

The tall narrow-leaved *H. hirta* almost completely eliminated the tall broad-leaved *P. maximum* in subplots with low soil N or P (proportional biomass of *H. hirta* in a quadrat close to 1; Figs 2a and 3a), whereas the reverse has occurred in subplots with high soil N or P. In one of the low N subplots, however, *P. maximum* performed uncharacteristically well (Fig. 3a). The Table 3 F ratios and probabilities for analysis of variance of the effect of irrigation and fertilization treatments with or without covariates on the response ratios of various species in specific species mixtures

		Response ratio of <i>P. maximum</i> in the <i>P. maximum</i> vs. <i>H. hirta</i> mixture			Response ratio of <i>P. maximum</i> in the <i>P. maximum</i> vs. <i>T. triandra</i> mixture			Response ratio of <i>H. hirta</i> in the <i>T. triandra</i> vs. <i>H. hirta</i> mixture			Response ratio of <i>A. junciformis</i> in <i>T. triandra</i> vs. <i>A. junciformis</i> mixture			
		Covariate			Covariate			Covariate	;		Covariate			
Source of variation	d.f.	None	Ν	Р	None	Ν	Р	None	Ν	Р	None	Ν	Р	
Rep stratum		14.97*			0.01			1.49			1.29			
Covariate	1		12.9	656.49*		0.2	0.04		3.6	15		6.87	2.17	
Residual	1		70.35	0.09		0.01	0.31		0.45	0.09		0.17	0.78	
Irrigation	1	1.82	23.1	5.72	1.25	1.95	10.69	0.93	0.32	0.38	0.54	0.21	0.97	
Covariate	1		64.34	3.08		1.05	56.29		0.37	0.01		0.01	0.9	
Residual	1	0.62	0.01	0.24	2.15	1.7	0.06	2.09	2.32	3.18	0.07	0.11	0.08	
Fertilization	1	14.06*	7.52	4.6	0	0.04	0.23	7.78*	3.73	4.68	2.08	0.76	2.6	
Irrigation × Fertilization	1	0.96	0.73	0.43	0.11	0.11	0	0.26	0.22	0.1	0.06	0.04	0.34	
Covariate	1		0.01	0.16		0.23	0.38		0.05	0.08		0.12	0.92	
Residual	3													
Total	11													

\*P < 0.05.

Note, the effect of irrigation and fertilization on the response ratios of species in all other mixtures was non-significant.



**Fig. 1** Trends in the response ratio (mixture biomass/monoculture biomass) for various species in specific mixtures along a gradient of total soil nitrogen and extractable soil phosphorus. Mixtures: *P. maximum* vs. *H. hirta*, a, b; *P. maximum* vs. *T. triandra*, c, d; *H. hirta* vs. *T. triandra*, e, f; *T. triandra* vs. *A. junciformis*, g, h. DI and DS = *P*-values for the difference in *y* axis intercept and slope of the lines, respectively, in the relation between the response ratios of two species in a specific mixture and soil nitrogen or phosphorus. AD = *P*-values for the average difference in the response ratios of the two species.

short species, *T. triandra*, was eliminated by the taller *P. maximum*, and almost replaced by the taller *H. hirta*, in subplots with high soil N or P, whereas it persisted in lower fertility subplots (Figs 2b,c and 3b,c). By contrast, the two shorter narrow-leaved species *T. triandra* and *A. junciformis* (Table 1) occupied approximately equal proportions of the biomass of quadrats (Figs 2e and 3e) regardless of soil N or P.

### EFFECT OF CUTTING ON COMPETITIVE INTERACTIONS AMONGST SPECIES

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394 Compared with uncut quadrats, cutting did not have a significant effect on the proportion of *H. hirta* in a quadrat when in mixture with *P. maximum* (Figs 2a and 3a). However, relative to uncut quadrats, cutting



Fig. 2 Proportions of *H. hirta* and *T. triandra* in specific species mixtures in uncut and cut plots along a gradient of soil phosphorus. DI and DS = *P*-values for the difference in *y* axis intercept and slope of the lines, respectively, in the relation between the proportion of a species in a plot and soil phosphorus. AD = *P*-values for the average difference in the proportion of a species in cut and uncut plots. PMA = *P. maximum*; HHI = *H. hirta*; TTR = *T. triandra*; ECU = *E. curvula*; AJU = *A. junciformis.* 

increased the proportion of *T. triandra* in mixture with *P. maximum* in subplots with low soil N or P (Figs 2b and 3b) and greatly increased the proportion of *T. triandra* in mixture with *H. hirta* (Figs 2c and 3c), *E. curvula* (Figs 2d and 3d) and *A. junciformis* (Figs 2e and 3e).

These dramatic changes in the proportion of T. triandra in cut compared with uncut quadrats appear to be related to changes in its competitive effect on other species and in its response to competitors under cutting. For example, the response ratio for H. hirta in the H. hirta-T. triandra mixtures is lower in cut than uncut treatments (P = 0.001; Table 4), indicating that it performed worse in mixture with T. triandra (relative to its performance in monoculture) in cut treatments. Importantly, there were highly significant speciescutting interactions for the response ratios in the H. hirta-T. triandra, E. curvula-T. triandra and A. junciformis-T. triandra mixtures (Table 4). The response ratios reveal that the competitive hierarchy was completely reversed for H. hirta and T. triandra between cut and uncut treatments, with H. hirta having the higher response ratio in uncut treatments and T. triandra in cut treatments (P < 0.001; Table 4).

Table 4 Mean values of the response ratio in uncut and cut treatments and P values for the species × cutting interaction and the difference in y axis intercept and slope of the lines, respectively, in the relation between the response ratio of a species and extractable soil phosphorus or total soil nitrogen

			Mean re	sponse rat	tio	Nitrogen		Phosphorus	
Mixture	Species × cutting interaction	Species	Uncut	Cut	Paired <i>t</i> -test (one tail)	Intercept	Slope	Intercept	Slope
P. maximum-H. hirta	0.815	P. maximum	0.710	0.870	0.058	0.171	0.287	0.009	0.03
		H. hirta	0.507	0.627	0.092	0.653	0.511	0.596	0.274
P. maximum-T. triandra	0.389	P. maximum	1.020	1.070	0.348	0.478	0.404	0.795	0.947
		T. triandra	0.233	0.423	0.010	0.098	0.212	0.047	0.358
H. hirta-T. triandra	< 0.001	H. hirta	0.960	0.670	0.001	0.657	0.76	0.486	0.414
		T. triandra	0.265	0.873	< 0.001	0.889	0.401	0.203	0.386
E. curvula-T. triandra	0.013	E. curvula	0.506	0.283	0.113	0.336	0.197	0.992	0.504
		T. triandra	0.858	1.194	0.027	0.563	0.274	0.929	0.18
A. junciformis-T. triandra	< 0.001	A. junciformis	0.491	0.346	0.080	0.899	0.81	0.449	0.966
		T. triandra	0.769	1.121	0.003	0.337	0.771	0.143	0.978

Significant P values (P < 0.05) are in bold.

Moreover, T. triandra had a higher response ratio in cut than in uncut treatments in the various species mixtures (P < 0.05; Table 4). This indicates that T. triandra has a better competitive response (response to competitors) in cut than uncut treatments. The significantly

DI: 0.586

Hvparrhenia hirta

DI: 0.517

O Uncut

Cut

Themeda triandra

Uncut

Cut

different intercept (P < 0.05; Table 4) for the fitted lines of the response ratios T. triandra and P. maximum in cut and uncut treatments indicates that cutting interacted with soil fertility in its effects on competitive interactions between these species.

### Discussion

### EFFECT OF FERTILIZATION AND IRRIGATION ON COMPETITIVE ABILITY

Despite the first two growing seasons experiencing only 84 and 66%, respectively, of average rainfall, irrigation had no effect on competitive interactions amongst species (Table 3). There do not therefore appear to be any tradeoffs in competitive ability along gradients of soil moisture availability amongst these species. This may be because none of the grass species used in this experiment occur commonly in wet habitats. Only a few subcanopy species in a New Jersey oldfield have been shown to be limited by water rather than nutrients (Carson & Pickett 1990). This suggests that shifts in the importance of soil moisture and soil nutrients as limiting resources in wet and dry seasons (sensu Knapp et al. 1998) are unlikely to have a large effect on competitive interactions amongst species characteristic of relatively well-drained soils.

Fertilization affected competitive interactions amongst some species but appeared to have less influence than inherent soil fertility, such as total soil N and extractable soil P (Table 3). Temporal pulses in fertility following fertilization may not have been able to compensate for nutrient deficiencies in subplots with inherently low soil fertility, whereas N and P may not have been limiting in the more fertile subplots.

### TRENDS IN COMPETITIVE ABILITY ALONG SOIL FERTILITY GRADIENTS

Panicum maximum and H. hirta showed clear evidence of trade-offs in competitive ability along a gradient

© 2005 British Ecological Society, Journal of Ecology, 93, 384-394



Fig. 3 Proportions of H. hirta and T. triandra in specific species mixtures in uncut and cut plots along a gradient of soil nitrogen. DI and DS = P-values for the difference in y axis intercept

and slope of the lines, respectively, in the relation between the

proportion of a species in a plot and soil nitrogen. AD = P-

values for the average difference in the proportion of a species

in cut and uncut plots. PMA = P. maximum; HHI = H. hirta;

TTR = T. triandra; ECU = E. curvula; AJU = A. junciformis.

of soil phosphorus and to some extent soil nitrogen (Figs 1a,b, 2a and 3a). Trends in the response ratios for these species were inversely related, crossing over midway along the soil N and P gradient (Fig. 1a,b). *Hyparrhenia hirta* was nearly eliminated by *P. maximum* in subplots with high soil N and P, whereas the reverse occurred in subplots with low soil P and most subplots with low soil N (Figs 2a and 3a). Other studies have also demonstrated that species may be inversely related in their competitive abilities along fertility gradients (Wedin & Tilman 1993).

Panicum maximum may have performed uncharacteristically well in the subplot with the lowest soil N (relative to other subplots with low soil N; Fig. 1a) because this subplot did not have the lowest soil P (Table 2). This subplot aside, there is a clearer separation of the response ratios and reversal of the competitive hierarchy along N than P gradients (Fig. 1a,b). A long-term (54 years) grassland fertilization experiment at Ukulinga, South Africa, revealed that the competitive ability of P. maximum was strongly influenced by an interaction of N and P. Panicum maximum was unable to dominate plots fertilized with N or P only (i.e. where the other nutrient remained limiting) but dominated plots fertilized with the highest level of N plus P (Fynn 2004). Soil phosphate may be an important determinant of community organization (Olsson & Tyler 2004). In contrast, H. hirta declined strongly in abundance with increasing levels of N fertilization (Fynn 2004). Hyparrhenia hirta is well known for its dominance of abandoned cultivated lands on infertile soils where long-term ploughing may result in a loss of over 50% of total soil N (Schimel et al. 1985). Thus, H. hirta appears to be a good competitor in infertile habitats.

Inversely related trends of the response ratios of species in various mixtures along soil N and P gradients tended to occur only when species differed strongly in various traits, such as leaf width or height, Thus, the tall broad-leaved *P. maximum* crossed over with the tall narrow-leaved *H. hirta* and taller species, such as *P. maximum* and *H. hirta*, had a competitive advantage over the shorter *T. triandra*, especially in fertile subplots (Fig. 1c–f), whereas the more similar *T. triandra* and *A. junciformis* (Table 1) showed no response (Fig. 1g,h).

Thus, it appears that trade-offs in height and leaf width, traits predicted to be important for competitive ability (Huston & Smith 1987; Tilman 1988; Goldberg 1996; Westoby 1998), resulted in inversely related competitive abilities along the fertility gradient, in accordance with mathematical predictions (Tilman 1988). This result contradicts models advocating a single competitive strategy in plants (Grime 1977, 1979).

Specific leaf area and leaf life span tend to be inversely related (Craine *et al.* 2002; Wright *et al.* 2002), and, as leaf life span and nutrient loss rates are inversely related (Berendse & Elberse 1990; Chapin 1980), this may affect trade-offs related to specific leaf area. Empirical studies (Berendse & Elberse 1990) and mathematical theory (Tilman 1990a) have shown that nutrient loss rates are a critical determinant of the ability of a species to compete for a limiting soil resource. This is consistent with the observation that species characteristic of infertile habitats tend to have long tissue life spans (Chapin 1980; Berendse & Elberse 1990; Craine *et al.* 2002).

However, species with low specific leaf area will have slow growth rates (Chapin 1980), which will reduce their competitive ability in fertile habitats (MacDougall & Turkington 2004). Narrow-leaved species are likely to be less shade-tolerant than broad-leaved species, a trait that is critical for tiller initiation (Everson et al. 1988) or seedling survival in shaded habitats (Goldberg 1996; MacDougall & Turkington 2004). It appears, however, that in the absence of cutting, a tall growth form was an important trait for competitive ability, even in infertile subplots, because the tall narrow-leaved H. hirta was more competitive than shorter narrow-leaved species in infertile subplots (Fig. 1). Similarly, a species of medium height, Schizachyrium scoparium, was shown to be the most competitive species on infertile soils in Minnesota (Wedin & Tilman 1993).

# EFFECT OF CUTTING ON COMPETITIVE INTERACTIONS AMONGST SPECIES

Regular cutting was shown to alter quadrat composition (Figs 2 and 3) through a shift in the competitive hierarchy (equilibrial mechanism) rather than by reducing competitive interactions (non-equilibrial mechanism). In contradiction to the predictions of Suding & Goldberg (2001), alteration of neighbourhood structure by regular cutting resulted in a reversal of the competitive hierarchy for *H. hirta* and *T. triandra* and a shift in the hierarchy for other species (Table 4). These effects, however, may be contingent on soil fertility because, when in mixture with *P. maximum*, cutting only improved the performance of *T. triandra* in infertile subplots (Figs 2 and 3, Table 4).

Short grasses (e.g. *T. triandra*) generally lose fewer nutrients than taller grasses under mowing or cutting, which may give the shorter species a competitive advantage (Berendse & Elberse 1990) when competing for a limiting soil nutrient (Tilman 1990a). Species relative abundance in infertile habitats was shown to be negatively correlated with the degree of tissue loss to herbivores (Reader 1998). Therefore, nutrient loss rate may provide a unifying link that is able to account for competitive ability on both fertility and disturbance gradients.

These results are in accordance with patterns of composition in two long-term (54 years) burning and mowing and fertilization experiments at Ukulinga, South Africa, where *T. triandra* dominated over *E. curvula* in all plots burnt annually in spring or winter or mown annually in summer, but was replaced by *E. curvula* in infrequently disturbed and undisturbed plots, where soil N accumulates, or in plots mown annually in summer but fertilized with N (Fynn 2004). In other

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394 Plant strategies and competitive ability words, cutting only reduced the competitive ability of the taller species, *E. curvula*, in infertile sites, as observed for *P. maximum* in this experiment (Figs 2b and 3b).

Themeda triandra appears to be intolerant of litter accumulation in the absence of disturbance (Belsky 1992), which may result from a trade-off for competitive ability in regularly disturbed environments (high loss environments) where litter accumulation is low and light availability is high. Tolerance-based competitive strategies are best expressed in undisturbed habitats where litter accumulates, whereas T. triandra appears to show a suppression-based competitive strategy requiring regular disturbance to reduce shading and remove litter, of which such species are intolerant (MacDougall & Turkington 2004). The observation that T. triandra becomes more competitive under a form of stress, such as cutting, is again inconsistent with models advocating a single competitive strategy in plants (Grime 1977, 1979).

#### Conclusion

Species appeared to be differentiated in competitive ability along a fertility gradient through trade-offs in leaf width, specific leaf area and height, whereas tradeoffs in maximum leaf height and height of maximum leaf area allocation appeared to result in species being differentiated in competitive ability on a disturbance gradient. However, the effect of disturbance on competitive ability may be contingent upon soil fertility. Thus, soil fertility and disturbance appear to form the major axes of an ecological framework for understanding and predicting the outcome of competition between species.

### Acknowledgements

We are grateful to Jerry Naiken for overseeing the management of the experiment and to Freedom Linda and Mpumulane Ngcobo for technical assistance. Comments of two anonymous referees and David Gibson and Lindsay Haddon have greatly improved this manuscript.

#### References

- Anonymous (1993) Genstat 5.3. Reference Manual. Clarendon Press, Oxford.
- Austin, M.P. (1990) Community theory and competition in vegetation. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 215–239. Academic Press, San Diego, California.
- Belsky, A.J. (1992) Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, **3**, 187–200.
- Berendse, F. & Elberse, W. (1990) Competition and nutrient availability in heathland and grassland ecosystems. *Per*spectives on Plant Competition (eds J.B. Grace & D. Tilman), and 0.2, 116 Academic Pares, San Diago, California.

© 2005 British Ecological Society, *Journal of Ecology*, **93**, 384–394

- pp. 93–116. Academic Press, San Diego, California. Cahill, J.F. (1999) Fertilization effects on interactions between
- above- and belowground competition in an oldfield. *Ecology*, **80**, 466–480.

- Campbell, B.D. & Grime, J.P. (1992) An experimental test of plant strategy theory. *Ecology*, 73, 15–29.
- Carson, W.P. & Pickett, S.T.A. (1990) Role of resources and disturbance in the organization of an old-field plant community. *Ecology*, **71**, 226–238.
- Chapin, F.S. III (1980) The mineral nutrition of wild plants. Annual Review of Ecology and Systematics, 11, 233–260.
- Collins, S.L., Knapp, A.K., Briggs, J.M., Blair, J.M. & Steinauer, E.M. (1998) Modulation of diversity by grazing and mowing in native Tallgrass Prairie. *Science*, 280, 745– 747.
- Craine, J.M., Tilman, D., Wedin, D., Reich, P., Tjoelker, M. & Knops, J. (2002) Functional traits, productivity and effects on nitrogen cycling of 33 grassland species. *Functional Ecology*, 16, 563–574.
- Everson, C.S., Everson, T.M. & Tainton, N.M. (1988) Effects of intensity and height of shading on the tiller initiation of six grass species from the highland sourveld of Natal. *South African Journal of Botany*, 54, 315–318.
- Foster, B.L., Dickson, T.L., Murphy, C.A., Karel, I.S. & Smith, V.H. (2004) Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. *Journal of Ecology*, 92, 435–449.
- Fuhlendorf, S.D. & Smeins, F.E. (1997) Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science*, 8, 819–828.
- Fynn, R.W.S. (2004) Determinants of community composition and diversity in KwaZulu-Natal mesic grasslands: evidence from long-term field experiments and pot and plot competition experiments. PhD thesis. University of KwaZulu-Natal, Pietermaritzburg.
- Fynn, R.W.S., Morris, C.D. & Edwards, T.J. (2004) Effect of burning and mowing on grass and forb diversity in a long-term grassland experiment. *Applied Vegetation Science*, 7, 1–10.
- Gaudet, C.L. & Keddy, P.A. (1995) Competitive performance and species distribution in shoreline plant communities: a comparative approach. *Ecology*, **76**, 280–291.
- Gibson, D.J., Seastedt, T.R. & Briggs, J.M. (1993) Management practices in tallgrass prairie: large- and small-scale experimental effects on species composition. *Journal of Applied Ecology*, **30**, 247–255.
- Goldberg, D.E. (1996) Competitive ability: definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society London, B*, **351**, 1377–1385.
- Goldberg, D.E. & Barton, A.M. (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist*, **139**, 771–801.
- Goldberg, D.E., Rajaniemi, T., Gurevitch, J. & Stewart-Oaten, A. (1999) Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology*, **80**, 1118–1131.
- Grace, J.B. (1993) The effects of habitat productivity on competition intensity. *Trends in Evolution and Ecology*, **8**, 229–230.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, 242, 344–347.
- Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, **111**, 1169–1194.
- Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*. John Wiley and Sons, Chichester.
- Hedges, L.V., Gurevitch, J. & Curtis, P. (1999) The metaanalysis of response ratios in experimental ecology. *Ecology*, 80, 1150–1156.
- Huston, M.A. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.
- Huston, M.A. & Smith, T. (1987) Plant succession: life history and competition. *American Naturalist*, **130**, 168–198.

### 393

Keddy, P.A., Nielsen, K., Weiher, E. & Lawson, R. (2002) Relative competitive performance of 63 species of terrestrial herbaceous plants. *Journal of Vegetation Science*, 13, 5–16.

- Kirkman, K.P. (2002) The influence of various types and frequencies of rest on the production and condition of sourveld grazed by sheep or cattle. 1. Proportional species composition. *African Journal of Range and Forage Science*, **19**, 55–62.
- Knapp, A.K., Briggs, J.M., Blair, J.M. & Turner, C.L. (1998) Patterns and controls of above-ground nett primary production in tallgrass prairie. *Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie* (eds A.K. Knapp, J.M. Briggs, D.C. Hartnett & S.C. Collins), pp. 193–221. Oxford University Press, Oxford.
- Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, 16, 545–556.
- MacDougall, A. & Turkington, R. (2004) Relative importance of suppression-based and tolerance-based competition in an invaded oak savanna. *Journal of Ecology*, 92, 422–434.
- Olsson, P.A. & Tyler, G. (2004) Occurrence of non-mycorrhizal plant species in south Swedish rocky habitats is related to exchangeable soil phosphate. *Journal of Ecology*, 92, 808– 815.
- Osem, Y., Perevolotsky, A. & Kigel, J. (2002) Grazing effect on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology*, **90**, 936–946.
- Osem, Y., Perevolotsky, A. & Kigel, J. (2004) Site productivity and plant size explain the response of annual species to grazing exclusion in a Mediterranean semi-arid rangeland. *Journal of Ecology*, **92**, 297–309.
- Proulx, M. & Mazumder, A. (1998) Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrientrich ecosystems. *Ecology*, **79**, 2581–2592.
- Rajaniemi, T.K. (2002) Why does fertilization reduce plant species diversity? Testing three competition-based hypotheses. *Journal of Ecology*, **90**, 316–324.
- Rajaniemi, T.K., Allison, V.J. & Goldberg, D.E. (2003) Root competition can cause a decline in diversity with increased productivity. *Journal of Ecology*, **91**, 407–416.
- Reader, R.J. (1998) Relationship between species relative abundance and plant traits for an infertile habitat. *Plant Ecology*, **134**, 43–51.

Schimel, D.S., Coleman, D.C. & Horton, K.A. (1985) Soil

organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma*, **36**, 201–214.

- Suding, K.N. & Goldberg, D.E. (2001) Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology*, 82, 2133–2149.
- Suding, K.N., Goldberg, D.E. & Hartman, K.M. (2003) Relationships among species traits: separating levels of response and identifying linkages to abundance. *Ecology*, 84, 1–16.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.
- Tilman, D. (1987) On the meaning of competition and the mechanisms of competitive superiority. *Functional Ecology*, 1, 304–315.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton.
- Tilman, D. (1990a) Mechanisms of plant competition for nutrients: the elements of a predictive theory of competition. *Perspectives on Plant Competition* (eds J.B. Grace & D. Tilman), pp. 117–141. Academic Press, San Diego, California.
- Tilman, D. (1990b) Constraints and tradeoffs: toward a predictive theory of competition and succession. *OIKOS*, 58, 3–15.
- Twolan-Strutt, L. & Keddy, P.A. (1996) Above- and belowground competition intensity in two contrasting wetland plant communities. *Ecology*, 77, 259–270.
- Wedin, D. & Tilman, D. (1993) Competition among grasses along a N gradient: initial conditions and mechanisms of competition. *Ecological Monographs*, 63, 199–229.
- Weigelt, A. & Jolliffe, P. (2003) Indices of plant competition. *Journal of Ecology*, **91**, 707–720.
- Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.
- Wilson, S.D. & Tilman, D. (1993) Plant competition and resource availability in response to disturbance and fertilization. *Ecology*, 74, 599–611.
- Wilson, S.D. & Tilman, D. (2002) Quadratic variation in oldfield species richness along gradients of disturbance and nitrogen addition. *Ecology*, 83, 492–504.
- Wright, I.J., Westoby, M. & Reich, P.B. (2002) Convergence towards higher leaf mass per area in dry and nutrient-poor habitats has different consequences for leaf life span. *Journal* of Ecology, **90**, 534–543.

Received 13 September 2004 revision accepted 24 November 2004 Handling Editor: David Gibson