

Competition effects and responses to variable numbers of neighbours in two tropical savanna grasses in Venezuela

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ABSTRACT. In a garden experiment we monitored tillering and flowering for target plants of two grass species, surrounded by one to five neighbours and compared them with control plants growing alone. We analysed the results using a non-linear regression. The species differed markedly in their seasonal patterns of growth but these differences faded when growing with two or more neighbours. The presence of neighbours had a significant depressing effect on both tillering and flowering in both species. Effects and responses were strongly asymmetrical concerning species and mode of growth. *Andropogon semiberbis* is in disadvantage against *Trachypogon plumosus* concerning vegetative growth. However, *T. plumosus* is strongly affected in its reproductive growth by competition not only from *A. semiberbis* but also from conspecific neighbours. We conclude that the complexity of interactions between effects and responses as well as vegetative and reproductive growth could have a net result of competitive equivalence or compensating competitive abilities of these two species.

KEY WORDS: *Andropogon semiberbis*, coexistence, competitive ability, growth, neighbourhood, phenology, population, reproduction. *Trachypogon plumosus*.

INTRODUCTION

Graminoids are the dominant growth form in Neotropical savannas and grasslands. Their relative importance seems to vary according to physical factors such as seasonal water availability, soil textures, topography, etc. (Frost *et al.* 1986, Silva & Sarmiento 1976) and to other factors such as fire and grazing (McNaughton 1985, Silva *et al.* 1990, 1991). It is likely that competition plays a role in temporal and spatial changes in the structure of these ecosystems, although this has received little attention. Large extensions of Neotropical seasonal savannas are dominated by a few bunch grass species, especially by *Trachypogon plumosus* (Humb. & Bonpl.) Ness (Sarmiento 1983a), which occupies a wide range of habitats (Silva & Sarmiento 1976). In contrast, in other savanna areas these species coexist with several other grasses. They differ in their architectural and phenological patterns, and these differences may partially explain

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coexistence (Sarmiento 1983b, Silva 1987). In an attempt to correlate architecture and phenology with competitive abilities (Raventós & Silva 1988), we found that the erect growth form was competitively superior over the basal growth form since its effects on other species were strongest and its responses to other species were weakest. Also, competitive interactions were strongly asymmetrical and phenological differences did not play any role.

McNaughton (1992) suggested that seemingly simple interactions between grass and herbivore could be very complex. The complex nature of competition among plants has been largely ignored, possibly because of the emphasis on the effects of high densities in agricultural plots and the methodology of replacement series (Connolly 1986). Competition as a community process is being re-evaluated and both questions and experimental designs to test competitive effects are being reformulated (Keddy 1989).

To explore these interactions among savanna grasses, we are developing an experimental study within the framework of the Programme Responses of Savannas to Stress and Disturbance of the International Union of Biological Sciences (Frost *et al.* 1986). This study involves detailed monitoring of target plants under various treatments. In this paper we present the results of an experiment on the effects and responses of two common savanna grass species when growing with a variable number of neighbours in intra- and interspecific combinations. Both species are important components of the herbaceous layer and grow together along catenas from medium- to very well-drained soils in the Western Llanos of Venezuela (Silva & Sarmiento 1976).

METHODS

The study was conducted in an experimental area protected from grazing and fire at the 'UNELLEZ' Botanical Garden, in the city of Barinas, Venezuela (38° N, 70° 12' W). The original vegetation of the area was a typical wooded savanna (Silva *et al.* 1971). Climate is strongly isothermal with a mean annual temperature of 27°C. In contrast, rainfall is strongly seasonal with a rainy season from May to November and a dry season from January to March.

Table 1. Annual precipitation (mm) during 1989 and 1990 in Barinas.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
89	3	21	11	14	216	169	189	78	246	234	56	33
90	7	11	67	51	251	186	354	102	155	394	168	16

December and April are transitional (Table 1). Mean annual rainfall is 1700 mm.

Species

The species used in the experiment were *Andropogon semiberbis* (Ness) Kunth and *Trachypogon plumosus*. *A. semiberbis* is a late-blooming species (November)

with an erect architecture whose short rhizomes rise above the ground exposing their lateral meristems. *T. plumosus*, blooming in mid-season (September), is distinguished by an erect architecture with significant vegetative reproduction by means of long shallow rhizomes. Several previous reports on growth, demography and responses to fire of this species are available (Silva & Ataroff 1985, Silva & Castro 1989, Silva *et al.* 1990, 1991).

Field methods

In June 1989 adult plants were randomly removed from a near-by intact savanna to obtain transplants of five tillers each. To ensure transplant success, *A. semiberbis* (A) plants were clipped at 5 cm height and *T. plumosus* (T) plants were clipped at 25 cm height, after planting as explained below. We removed all previous vegetation from the experimental plot (50 m × 30 m) by mechanical means, and squared the plot into 1 m × 1 m. Target plants (*A. semiberbis* or *T. plumosus*) were sown at the square centre, in combination with a number (1–5) of surrounding plants of the associate species, either *T. plumosus* or *A. semiberbis*. These neighbours were planted 2 cm from the base of the target plant. Control target plants, growing without associate plants, were also similarly planted. The combinations and the controls were randomly distributed in the plot. Combinations with 2–5 neighbours were replicated twice and combinations with one neighbour as well as the controls were replicated five times. During the following 2½ months we monitored the transplants weekly to replace dead plants. There were no more deaths after September, and we started measuring number of tillers, phenology and number of flowering tillers of the target plants. At the end of October the plants had reached a similar height. These two months were considered as the stabilization period, and field data were collected from November 1989 to October 1990 for further analysis. During the experiment, all plant invaders were mechanically removed from the plots.

Statistical analysis

The experiment can be considered as a neighbourhood version of a density series experiment. Therefore, the method of analysis applied is a non-linear regression between the performance of the target plant and the number of neighbours. With our data we can evaluate this performance with vegetative or reproductive growth. Consequently, we plotted either the total number of tillers per target plant (Figure 3) or the number of reproductive tillers per plant (Figure 5) versus the number of neighbours. This relationship was concave for all the cases examined, and was fitted to a non-linear model using a SAS statistical routine (NLIN procedure, Marquardt algorithm, Ray 1982). The model used is

$$P = \frac{M}{1 + c_{ij}n}$$

where P is the number of vegetative or reproductive tillers per plant; M is the

number of vegetative or reproductive tillers per plant when growing without neighbours; C_{ij} is the competition index of the effects of species j upon species i and n is the number of neighbour plants, the independent variable of the experiment.

We used the non-linear regression of vegetative growth to estimate the values of M and C_{ij} for each month in the four possible combinations of species (AA, AT, TT, TA). We used the coefficients of determination and the distribution of the residuals as a criterion to compare the estimated parameters of the function (see Pacala & Silander 1987, Silander & Pacala 1985, Weiner 1982, 1984).

To compare the effects of neighbours on the maximum and final size of target plants, we used an unbalanced one-way ANOVA. The data were unbalanced because there were five replicates for the control plants and for the one-neighbour treatment, whereas in the other treatments there were only two replicates. Means were compared using the Bonferroni multiple range test.

RESULTS

Vegetative growth

Seasonal patterns of growth. The seasonal patterns of growth of the two species were clearly different when the plants had no competitors but the differences were concealed when plants were growing with two or more neighbours (Figures 1 and 2). *A. semiberbis* growing unaccompanied (Figure 1) showed a pattern of two clearly different phases: a sustained increase in numbers from November to April, which coincides with the end of rains and the dry season (Table 1), and a consistent decrease during the following rainy period. In April, plants reached a maximum number of tillers (MS), an average of 35 times the initial number of five tillers per plant. During the second phase, the number of tillers declined to reach a final plant size (FS), 17 times the initial number of tillers.

In contrast, plants of *T. plumosus* growing alone (Figure 2) showed a pattern of four clearly different phases: (1) two periods of about a twofold increase in numbers of tillers: (i) from November to January, which coincides with the end of rains and beginning of the dry season, and (ii) from April to June, which corresponds to the onset and the beginning of the rainy season; (2) two periods with very restricted growth or a slight decrease in number of tillers: (i) from February to April, concurring with mid- and late dry season, and (ii) from June to October, corresponding with the wettest phase of the rainy season (Table 1). The maximum plant size, attained in June, was 53 times the initial size of five tillers, and the final size was 42 times the initial number of tillers.

Maximum size. In intraspecific competition MS in both species is significantly depressed by any number of associate plants ($P < 0.0001$, Table 2). Furthermore, plants growing with one neighbour attained higher sizes compared with those growing with more than one neighbour ($P < 0.05$). Beyond two, the addition of more neighbours made no further significant differences in MS. In interspecific competition the pattern is slightly different for the two target species.

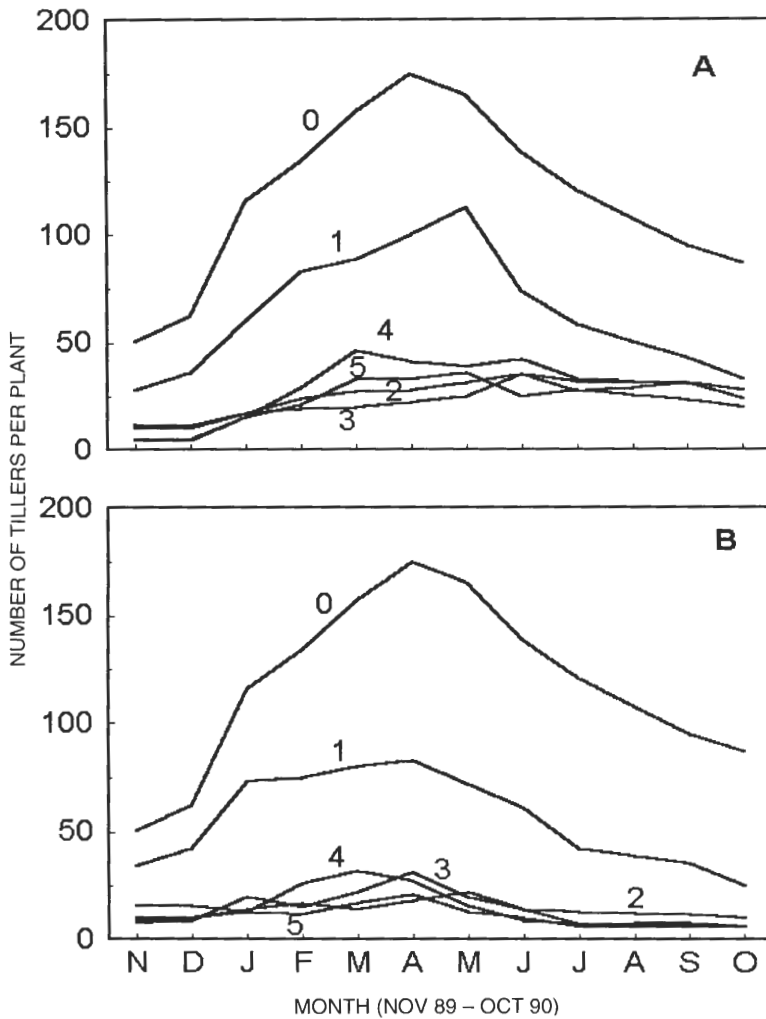


Figure 1. Changes in mean number of tillers per plant in *A. semiberbis* growing alone or with a variable number of neighbours. (A) Intraspecific competition with *A. semiberbis*; (B) interspecific competition with *T. plumosus*. (0) Control, plants growing alone; (1-5), target plants in association with one to five neighbours.

In *A. semiberbis*, the response is similar to that of intraspecific competition. In *T. plumosus*, MS is significantly higher when growing alone or with one neighbour than when growing with two or more neighbours, ($P < 0.004$).

Final size. With *A. semiberbis*, FS was significantly reduced in all combinations (Table 2), but there were no significant effects of increasing number of neighbours ($P > 0.05$). However, in interspecific combinations the reduction in FS was at least three times higher than in intraspecific combinations. In all cases, the target plants increased in size from the initial five tillers. FS was significantly correlated with MS ($r = 0.79$). FS of *T. plumosus* target plants (Table 2) in intraspecific competition was significantly decreased in the presence of neighbours, but does not

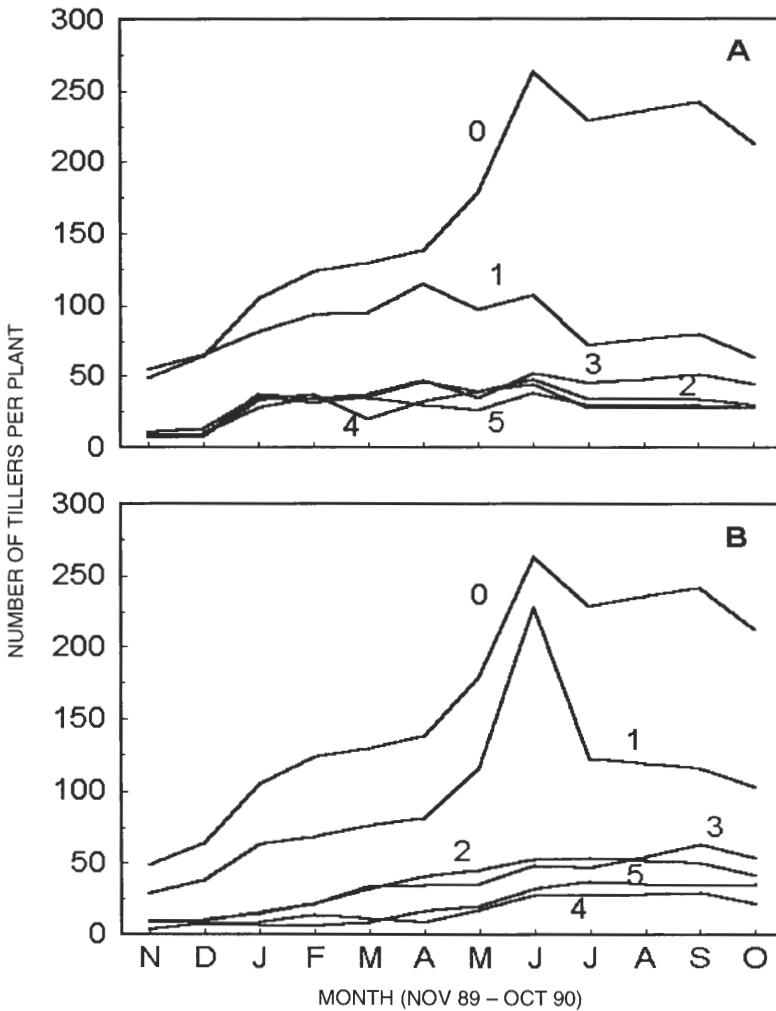


Figure 2. Changes in mean number of tillers per plant in *T. plumosus* growing alone or with a variable number of neighbours. (A) Intraspecific competition with *T. plumosus*; (B) interspecific competition with *A. semiberbis*. (0) Control, plants growing alone; (1)–(5) target plants in association with one to five neighbours.

show a clear trend. In interspecific competition, the one-neighbour treatment FS did not decrease significantly but it was significantly reduced with the addition of two or more neighbours. All target plants increased in size from the initial five tillers, and as in *A. semiberbis*, FS depends on MS ($r = 0.86$).

The model. The coefficients of determination of the non-linear regressions were high and very significant ($P < 0.001$) in all combinations and months (see Appendix). In most cases, the residuals seem to be in conformity with the assumption of normality. Figure 3 shows the last month values (October) and the fitted curves as an example.

Table 2. Effects of number of neighbours of different species on maximum (M) and final (F) size (number of tillers per plant) of *Andropogon semiberbis* (a) and *Trachypogon plumosus* (b). Average sizes with common superscript on each horizontal line do not differ significantly ($P < 0.05$). In parentheses, the standard deviation. Associate species in second column are: A = *A. semiberbis*; T = *T. plumosus*.

(a) Target = *A. semiberbis*

Size	With	Number of neighbours					
		0	1	2	3	4	5
M	A	175 (25)	100 (26) ^a	28 (3) ^a	29 (4) ^a	41 (1) ^a	33 (3) ^a
F	A	96 (27)	33 (23) ^a	25 (5) ^a	36 (4) ^a	25 (1) ^a	21 (4) ^a
M	T	175 (25)	74 (44) ^a	21 (3) ^b	31 (27) ^{ab}	22 (9) ^b	18 (14) ^b
F	T	96 (27)	19 (8) ^a	6 (1) ^a	6 (3) ^a	6 (1) ^a	10 (1) ^a

(b) Target = *T. plumosus*

Size	With	Number of neighbours					
		0	1	2	3	4	5
M	A	282 (80)	107 (36)	48 (13) ^a	52 (7) ^a	44 (14) ^a	38 (7) ^a
F	A	206 (80)	87 (2) ^{ab}	33 (2) ^a	51 (3) ^b	29 (3) ^a	28 (3) ^a
M	T	282 (80) ^a	223 (73) ^{ab}	52 (12) ^b	49 (24) ^b	28 (0) ^b	30 (1) ^b
F	T	206 (80) ^a	110 (27) ^{ab}	50 (14) ^c	63 (25) ^{bc}	30 (0) ^c	32 (3) ^c

Competitive index. Competitive effects of *A. semiberbis* showed little variation throughout the period, with most values lower than the unity (Figure 4). In contrast, the effects of *T. plumosus* showed a broad variation, with similar pattern but different magnitudes in the two types of combinations. In interspecific competition, values were higher than two, except in the first two months. Conversely, in intraspecific competition the values were higher than one only in the three final months of the experiment.

Reproductive growth

The model. The application of the non-linear model to the reproductive performance of the plants (Figure 5) rendered different results from the vegetative growth (Table 3). With *A. semiberbis* as a target species, competitive effects were two to three times lower, the level of significance of the fitted regression was lower and the coefficient of determination was half the value than in the case of *T. plumosus* as a target (Table 3). As in the vegetative model, the residuals seem to be in conformity with the assumption of normality.

Correlation to vegetative growth. In both species the number of flowering tillers was significantly correlated to maximum size (MS) and to final size (FS). In *A. semiberbis*, correlation coefficients were: with MS, $r = 0.72$ and with FS, $r = 0.65$. In *T. plumosus*, correlation coefficients were: with MS, $r = 0.89$ and with FS, $r = 0.91$.

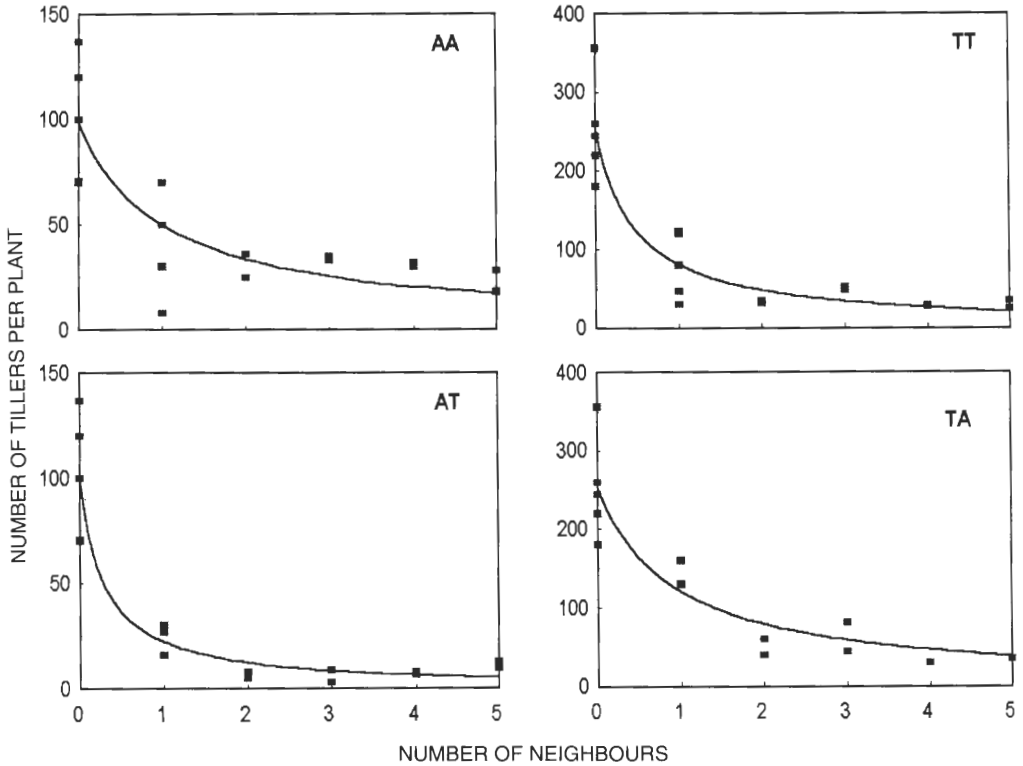


Figure 3. Number of tillers per target plant in the last month of the experiment (October) as a function of number of neighbours and the corresponding fitted regression curve, for each combination AA, AT, TT, TA. First letter denotes the target species and second the neighbour species. A = *A. semiberbis*; T = *T. plumosus*.

DISCUSSION

Andropogon semiberbis showed a remarkable increase in the number of tillers during the end of the rains and the dry period, indicating that production of new tillers was higher than mortality. During the following rainy season, tiller numbers decreased, indicating that tiller mortality was higher than tiller production during that period. Previous phenological studies have shown that tiller production by this species increases at the end of the rainy season and continues on during the dry season (Silva & Ataroff 1985). Also, our observations showed that tiller mortality was more prevalent during the wet season, when most of the aerial biomass growth took place. This plant self-thinning may reflect competition for light between tillers of the same plant, as well as the deleterious effects of shading and excessive moisture on the growth of this species (Silva *et al.* 1991).

The phenology of *T. plumosus* is different from that of *A. semiberbis* in that there was no increase in tillers during the last phase of the dry season and there was a significant increase in tillers during the first part of the rainy season, followed by a plateau. This suggests that self-thinning is not as

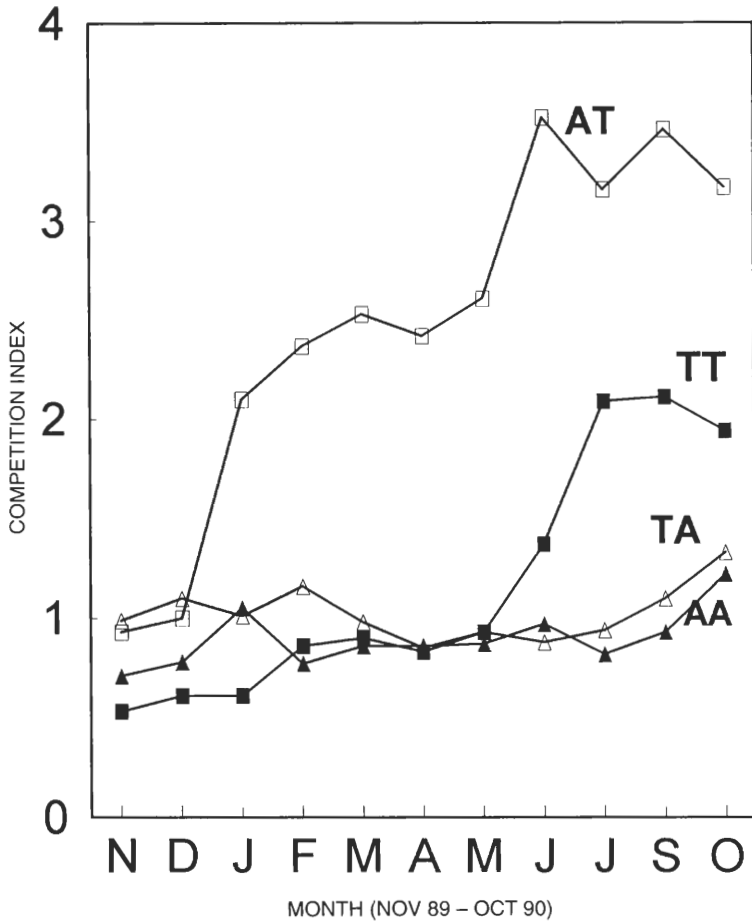


Figure 4. Values of the competition index (C_{ij}) throughout the year, estimated from the fitted regressions, for each combination AA, AT, TT, TA. First letter denotes the target species and second the neighbour species. A = *A. semiberbis*; T = *T. plumosus*.

important in *T. plumosus* as in *A. semiberbis*. Tiller self-thinning also operates in another savanna tall grass species, *Hypparrena filipendula* (Coughenour *et al.* 1985a) but is absent in the medium-stature *Themeda triandra* (Coughenour *et al.* 1985b).

Our results confirm previous findings of temporal asynchrony of vegetative and reproductive phenology between these two species. Asynchrony has been pointed out as a possible explanation for their coexistence (Sarmiento 1983b, Silva & Ataroff 1985). However, the presence of associate plants resulted in a remarkable decrease in plant growth in both species in intra- and interspecific combinations. Suppression by neighbours could be interpreted as being the result of interplant root competition during the dry season and increasing competition for light during the wet season, since aerial biomass was relatively small during the dry season and very large during the wet season.

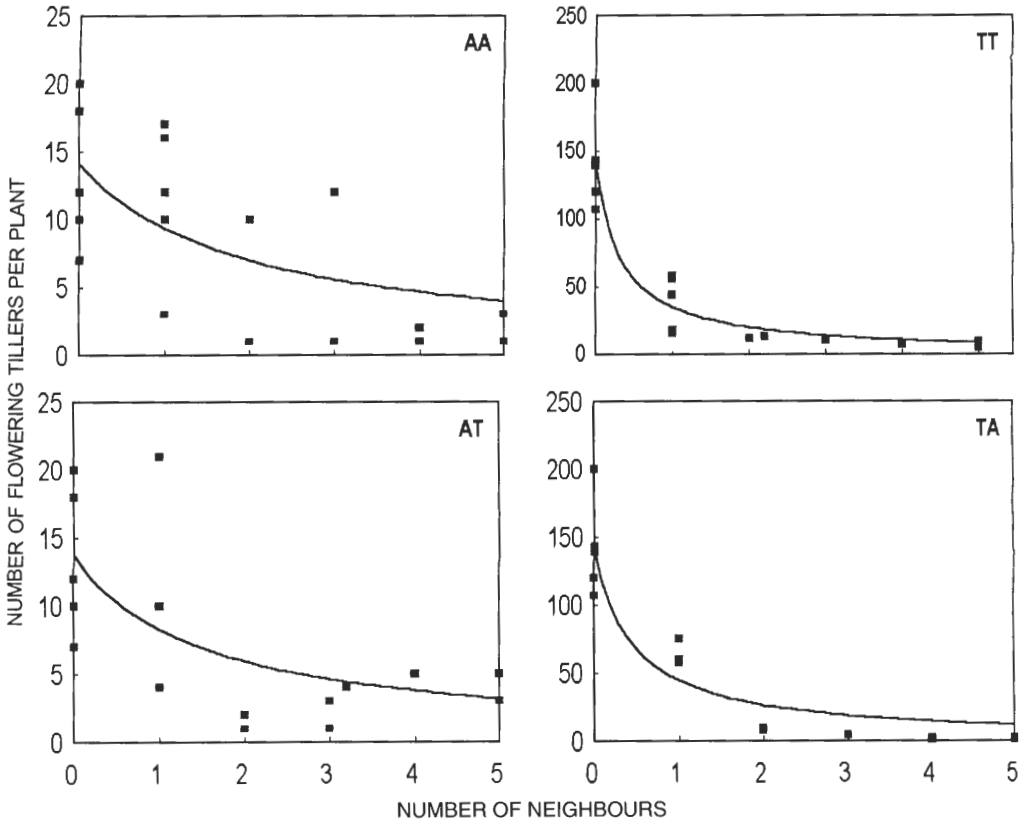


Figure 5. Number of flowering tillers per target plant as a function of number of neighbours and the corresponding fitted regression curve, for each combination AA, AT, TT, TA. First letter denotes the target species and second the neighbour species. A = *A. semiberbis*; T = *T. plumosus*.

The non-linear model explained much of the variance of our experimental results in vegetative as well as reproductive growth. These neighbourhood effects may be an expression of the reciprocal-yield law at the individual level (Weiner 1982). Our results are consistent with previous reports from studies of annual plant species (Silander & Pacala 1985, Weiner 1982, 1984), although in our case we have estimated the changes in the model parameters throughout the year. Whilst the parameter M is reflecting the changes in the surrounding physical environment, the competition index C_{ij} shows the variations in the effects of neighbours, which in turn reflects the seasonal changes in their condition. In our experiment, the estimated values of M for the vegetative model were essentially identical to the values measured in plants growing in the field without neighbours. The two species differed greatly in the behaviour of their competitive effects, estimated by the index C_{ij} . The major fluctuations in *T. plumosus* could be interpreted as the result of the changes in number of tillers throughout the year, since they resemble the growth curve of this species shown

Table 3. Values of competitive index (C_{ij}): (I) average value of monthly estimates from vegetative performance; (II) estimated from reproductive performance of plants and the correspondent regression coefficient (R^2); standard error in parentheses. First letter of the combination is the target species, second letter is the associate species.

(I) Vegetative performance

	AA	AT	TT	TA
C_{ij}	0.89 (0.04)	0.47 (0.26)	1.16 (0.18)	1.02 (0.04)

(II) Reproductive performance

	AA	AT	TT	TA
C_{ij}	0.59 (0.35)	0.69 (0.41)	3.05 (0.96)	2.20 (0.51)
R^2	0.40**	0.45**	0.88***	0.87***

** $P < 0.01$; *** $P < 0.001$.

in Figure 2. However, the same cannot be said about the behaviour of competitive effects of *A. semiberbis*, which changed little.

The effects on reproductive growth were as important as the effects on plant size. In *A. semiberbis*, the presence of neighbours reduced blooming as much as tenfold. In *T. plumosus*, the reduction was more dramatic as blooming was decreased to as low as 2%. The application of the non-linear model to reproductive growth rendered different results from the vegetative model, suggesting that competition between these plant species may be a complex process.

To interpret our results, we use the distinction between effect and response as components of competition as suggested by Goldberg (1990). Individuals of different species can be ranked in competitive ability either by how strongly they suppress other individuals (net competitive effect) or by how little they respond to the presence of competitors (net competitive response). We distinguished the response of each species to a different competitor (AA v. AT and TT v. TA) from the effect of each competitor species on a different target species (AA v. TA and TT v. AT) by comparing the indices of competition presented in Table 3. Effects and responses were strongly asymmetrical concerning species and mode of growth.

In *A. semiberbis*, effects and responses differed depending on mode of growth. In vegetative growth the effects are similar and close to 1.0 in intra- and interspecific combinations. The responses behaved exactly the opposite, vegetative response was two times higher in interspecific than in intraspecific combinations and reproductive response was low and similar in both mixtures.

Effects on vegetative growth of *T. plumosus* were two times higher in interspecific than in intraspecific mixtures. However, the effects on reproductive growth

are four times higher in intraspecific than in interspecific combinations. Responses in vegetative growth are similar and close to one in both mixtures, whereas responses in reproductive growth are slightly higher in intraspecific than interspecific combinations.

Summarizing, *A. semiberbis* is in disadvantage against *T. plumosus* concerning its vegetative growth. However, *T. plumosus* is strongly affected in its reproductive growth by competition not only from *A. semiberbis* but also from conspecific neighbours. In the field, *A. semiberbis* consistently produces a high number of seeds per plant, whereas *T. plumosus* has a very low annual seed yield and an important clonal growth (Silva & Ataroff 1985).

The suggestion that similar species could coexist because interspecific competition is approximately equal to intraspecific competition (Aarssen 1983, 1985) should take into account the complexities arising from the distinction between effects and responses as well as vegetative and reproductive growth. Our results suggest that this complexity could have a net result of competitive equivalence or compensating competitive abilities of these two similar species, in the sense of Goldberg (1990), and may be playing a role in savanna community composition.

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Appendix follows on next page.

APPENDIX

Values of M and C_{ij} estimated from the non-linear regression, for each combination of target (first letter) and neighbour (second letter) species. All regressions are significant at $P < 0.001$.

	Month	M	Std error	C_{ij}	Std error	R^2
AA	11	43.67	3.92	0.71	0.21	0.76
	12	53.67	4.56	0.78	0.22	0.77
	1	113.55	10.08	1.05	0.3	0.76
	2	130.52	13.53	0.77	0.27	0.68
	3	154.63	12.21	0.86	0.23	0.78
	4	166.24	12.23	0.86	0.21	0.81
	5	168.93	10.76	0.87	0.1	0.84
	6	140.79	12.92	0.97	0.3	0.72
	7	107.41	10.28	0.82	0.26	0.67
	9	94.73	10.47	0.93	0.35	0.58
10	95.13	8.85	1.22	0.39	0.71	
AT	11	43.88	3.09	0.93	0.24	0.82
	12	1.85	3.31	1	0.23	0.86
	1	111.8	7.3	2.1	0.64	0.88
	2	126.72	7.2	2.37	0.66	0.91
	3	152.24	7.17	2.53	0.6	0.93
	4	163.71	6.88	2.42	0.5	0.97
	5	166.45	4.89	2.61	0.39	0.97
	6	140.81	9.49	3.52	1.44	0.89
	7	107.66	7.13	3.16	1.2	0.89
	9	99.62	7.38	3.46	1.55	0.87
10	96.05	7.25	3.17	1.38	0.87	
TT	11	52.44	7.13	0.53	0.25	0.54
	12	63.49	8.63	0.61	0.28	0.55
	1	113.14	11.58	0.61	0.21	0.62
	2	140.6	11.86	0.86	0.24	0.74
	3	148.73	12.18	0.9	0.25	0.77
	4	156.95	8.99	0.83	0.16	0.86
	5	172.53	9.98	0.93	0.18	0.87
	6	247	15.51	1.37	0.3	0.86
	7	232	22	2.09	0.79	0.76
	9	250	17.8	2.11	0.6	0.85
10	236	15.93	1.94	0.59	0.87	
TA	11	48.41	3.85	0.99	0.3	0.82
	12	59.55	6.41	1.1	0.46	0.72
	1	114.18	12.96	1.01	0.45	0.71
	2	141.87	13.21	1.16	0.42	0.79
	3	149.63	13.47	0.98	0.33	0.78
	4	159.2	14.12	0.85	0.28	0.78
	5	172.53	9.83	0.93	0.18	0.87
	6	252.71	24.49	0.88	0.32	0.75
	7	234.98	24.8	0.94	0.37	0.7
	9	253.01	18.25	1.1	0.3	0.84
10	236	15.74	1.33	0.35	0.87	