Nearest-neighbour analysis and the prevelance of woody plant competition in South African savannas

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Abstract

Inter- and intra-specific competition has long been regarded as a significant determinant of the structure and function of woody plant communities in African savannas. The most widely used approach to detect the presence or absence of competition has been the use of nearest-neighbour methods. Although several studies have been published reporting the presence of competition in *Acacia* dominated communities, less than 20 plots have been sampled across all these studies. Results from broad-leaved communities are variable, and also based on a small sample number. Consequently, this study sought to assess the prevalence of competition from a large number of savanna sites (45), and to identify abiotic and biotic factors characterising sites with competition relative to those without. Using the nearest-neighbour method only four sites (9.3%) indicated the presence of inter-specific competition; two were *Acacia* dominated communities (18.2% of *Acacia* sites) and two were broad-leaved communities (7.7%). These four sites had a significantly higher mean annual rainfall and fewer woody species than sites without inter-specific competition. There were also significant relationships between the inter-specific competition index and the dominance index and the number of species at a site. In terms of intra-specific competition only ten of the 31 sites tested revealed a significant correlation between nearest-neighbour distance and summed canopy volume of the two neighbours. Seven were for *Acacia* species (55.6% of the *Acacia* species comparisons) and three were for broad-leaved species (21.4% of the broad-leaved species comparisons). Sites lacking evidence of intra-specific competition were at a significantly lower slope position and had a smaller proportion of small stems. The lower prevalence of competition in South African savannas detected in this study using the same method as previous studies is discussed, and the appropriateness of nearest-neighbour analysis is examined.

Introduction

Competition between the woody and herbaceous components is frequently invoked as one of the major processes influencing the structure and function of African savannas (Knoop and Walker 1985; Stuart-Hill and Tainton 1989; Teague and Smit 1992; Scholes and Walker 1993; Scholes and Archer 1997). It has also been argued that competition between trees may be a significant determinant of woody community structure and productivity (Smith and Goodman 1986; Teague and Smit 1992; Scholes and Walker 1993).

The presence or absence of competitive interactions between plants can be determined in a number of ways (Keady 1989; Tilman and Kareiva 1997). For woody plants across a range of biomes, including savannas, it has been inferred from the spatial distribution of individuals within the community (Phillips and MacMahon 1981; Fowler 1986; Midgley and Watson 1992). In southern African savannas the most common approach has been nearest-neighbour methods which assume that competitive interference be-

tween neighbouring plants, if present, will be manifest through a reduction in the size of one or both of the competing neighbours. If there is a significant correlation between the distance separating the two neighbouring plants and the sum of their sizes (usually canopy cover), then competition is inferred (Pielou 1962).

In savannas, Smith and Walker (1983) analysed four bottomland sites and concluded that inter- and intra-specific competition played a role in spacing *Acacia* communities, but did not regulate broad-leaved communities. Smith and Grant (1986) determined from nearest-neighbour analysis that intra-specific competition occurred within the two dominant broad-leaf species at a single plot at Nylsvley; whilst Smith and Goodman (1986) demonstrated intra- and inter-specific competition in the spacing of two *Acacia* species at three sample sites. Intra-specific competition was also detected in this manner at three sites by Gutierrez and Fuentes (1979) for *A. caven* in Chile. Grundy et al. (1994) using the same approach detected intra-specific competition at three out of five sites for *Brachstegia spiciformis*, and two out of five sites for *Julbernardia globifera* at Marondera, Zimbabwe.

Although from a relatively small number of plots, it is consistent from the above studies that intra- and inter-specific competition is prevalent within savanna communities dominated by *Acacias*. Results for the broad-leaved species or communities are inconclusive, and also are based on a relatively small sample number. Thus, the oft stated importance of woody plant competition in southern African savannas rests on a poor sample size and variable results.

In light of the significance placed on competition in southern African savannas, but the small sample size of the above studies, and the inconclusive evidence resulting from broad-leaved savannas, I undertook a study to determine: (i) the prevalence of intra- and inter-specific competition across a range of South African savanna communities, using the same methods as previous workers (nearest-neighbour methods), and (ii) whether or not particular site factors are correlated with the presence or absence of competition.

Methods

I measured between 30 and 40 randomly selected nearest-neighbour pairs in 45 plots at 22 localities (1-3 plots per locality) around the South African biome during July 1994 (Figure 1). The sites were these set up previously by Shackleton (1997) as permanent plots for monitoring woody productivity. Each stem had been marked with a number during 1992 or 1993. For each pair, the number of the point tree was randomly selected from a list of all numbered trees in the plot. The nearest-neighbour to it was then measured. Stems less than 1 m tall were not considered. For each pairing the following were recorded: (i) The distance (rounded to the nearest 10 cm), between the point tree and its nearest neighbour using a 25 m tape-measure. Generally, inter-neighbour distances were less than 5 m, but it was variable because of differences in plant density within the 45 plots, ranging from 0.3 m to 9.0 m. (ii) The circumference of each tree at 35 cm above ground level using a 1 mm graduated tape. (iii) The height of each tree (to the nearest 10 cm). For trees less than four metres this was done using a ranging pole with 10 cm graduations. For trees taller than four metres, the height was determined via trigonometric conversion after measuring the angle to the top of the tree from a recorded distance away from the tree (Shackleton 1993). (iv) The height (to the nearest 10 cm) of the base of the canopy above ground level using a tape-measure. (v) The length of the long and short axis of each canopy, using a tape-measure (to the nearest 10 cm). (vi) The species.

In the previous year, I recorded a number of abiotic characteristics at each site (Shackleton 1997). These included latitude, longitude, altitude (all taken using a GPS), aspect (compass), slope (Abney level), landscape position (topland, mid-slope or bottomland), mean annual rainfall (local records), and soil depth (A and B horizons separately, and total) (using an extendable soil auger). Soil samples (A and B horizons separately) were taken at five places throughout the plot, mixed, and analysed for texture (Bouyoucos hydrometer method), stones (% volume), organic carbon (Walkley-Black), CEC (atomic absorption), Ca, Mg, Na, K, P (Ambic I extraction followed by AA spectroscopy), N (Keldjahl), nitrogen mineralisation (anaerobic incubation), and extractable acidity. Biotic site characteristics recorded included woody plant species richness, dominance (Simpson's index), competition index (r^2 value from the regression of nearest-neighbour analysis), density of stems greater than 75 cm tall, basal area per hectare, biomass (using Rutherford (1979) general allometric equation), and proportion (%) of small stems (< 10.1 cm circumference).
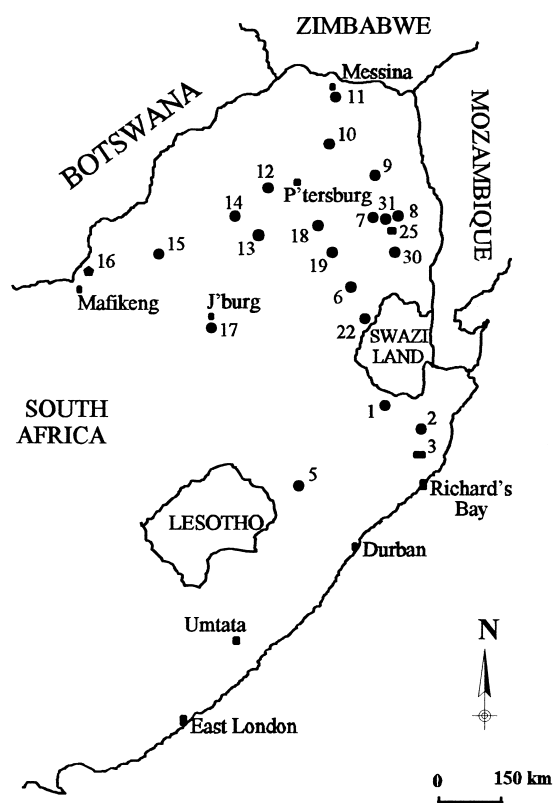
Figure 1. Geographical distribution of sample localities within the South African savanna biome.

The size of each canopy was calculated from the above dimensions, on an area (= Π *(length of long axis * length of short axis)/4*) and volume basis (= *area * (canopy height - canopy base)*). The sum of the areas, and the sum of the volumes of the two neighbouring trees were both regressed against the distance between the two trees for all the pairs (30-40), irrespective of species identities, within that plot, following the approach of Pielou (1962) and the nearest-neighbour studies cited above. For plots where at least five of the nearest-neighbour pairings were between trees of the same species, the regression between inter-neighbour distance and sum of canopy area or volume was repeated to determine the presence of absence of intra-specific competition. Two of the sites were mono-specific sites dominated by a single *Acacia* species. These were assessed for intra-specific interactions only. Thus, sample size for analysis of inter-specific competition was 43 (11 *Acacia* dominated communities; 26 broad-leaved communities; 6 mixed), and for intra-specific competition it was 31 (18 *Acacia* species; 12 broad-leaved species; 1 microphyllous, non-*Acacia*).

Given the large number of regressions performed and the low proportion of sites that indicated a significant relationship, a Monte-Carlo procedure was performed to ascertain whether the small number of sites with significant regressions was simply due to chance. A total of 900 Monte-Carlo samples were generated.

The abiotic and biotic characteristics of sites demonstrating a significant competitive effect were compared to those sites where competition was not significant, by means of a T-test. The difference between using canopy area or canopy volume was tested via a paired T-test on the r values from the regressions of summed area and interplant distance.

Results

Inter-specific competition

Only four of the 43 sites (9.3%) indicated a significant relationship between summed canopy area and the distance between nearest neighbours (Figure 2, Table 1). Two were *Acacia* dominated communities (18.2% of *Acacia* sites) and two were broad-leaved communities (7.7%). Analysis using canopy area resulted in significantly higher r^2 values (T = 2.66; d.f. = 42; p < 0.01) than canopy volume (mean r^2 for canopy area based regressions was 0.097, and for canopy volume regression it was 0.060). Results from the 900 Monte-Carlo generated samples indicated a significant chance relationship in only 4% of the sample, as compared to the 9.3% obtained from this study.

Comparison of the four sites where inter-specific competition was inferred relative to the other sites, indicated no differences in site variables other than mean annual rainfall and number of woody species (Table 2). Sites with inter-specific competition were at higher rainfall (p < 0.05) than those without and had fewer woody species (p < 0.05).

There were also significant relationships between the inter-specific competition index (significant or not) and (i) the dominance index, and (ii) the number of species at a site, summarised as:

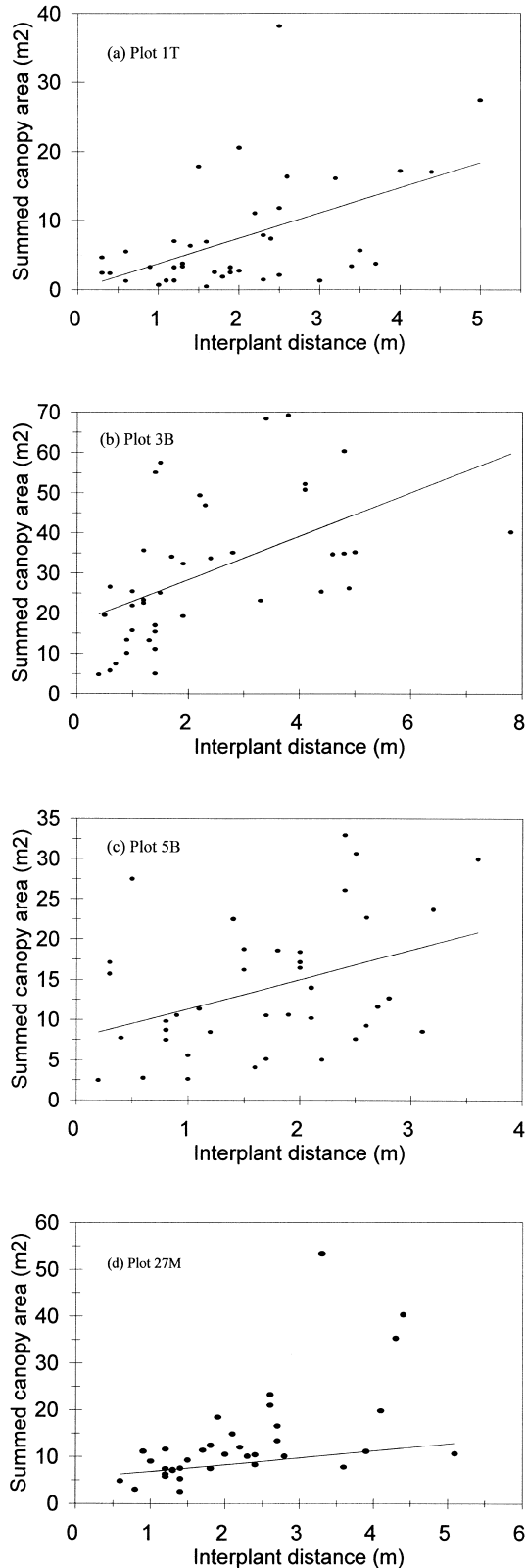Competition index = 0.319(Dominance index)
+ 0.00218($r^2 = 0.11; p < 0.05; n = 45$)

Figure 2. Scatter plots of sites with inter-specific competition.

Competition index = -0.0187(No. of species)
$+ 0.351 (r^2 = 0.19; p < 0.005; n = 45)$

Intra-specific competition

There was no significant difference in mean r^2 values (T = 1.65; d.f. = 30; p > 0.05) between using canopy area or canopy volume (0.328 and 0.281, respectively). However, on a canopy area basis only six of the 31 intra-specific analyses showed a significant competitive effect, whereas using canopy volume, ten of the 31 analyses resulted in a significant relationship with nearest-neighbour distance (Table 3). Of the ten sites indicating a significant correlation between the interplant distance of the dominant species and the summed canopy volume, seven were *Acacia* species (55.6% of the *Acacia* species comparisons) and three were broad-leaved species (21.4% of the broad-leaved species comparisons). Of the six sites with significant results based on canopy area, four were *Acacia* species and two were broadleaved species (Figure 3).

Sites with intra-specific competition differed from those without in terms of slope position and the proportion of small stems (< 10.1 cm circumference) (Table 4). Those with competition tended to be higher up a slope and have a higher proportion of small stems than sites without.

Discussion

The results from this study indicate that evidence for competition (based on nearest-neighbour analysis) as a determinant of savanna woody community structure is not as prevalent as previously suggested. Intra-specific competition seems more prevalent than inter-specific competition (32% and 9% of sites, respectively), which corroborates findings from similar studies in other environments (Yeaton and Cody 1976; Yeaton et al. 1977; Midgley and Watson 1992). However, the generality of this conclusion has been questioned by Goldberg and Barton (1992), who argued that very few studies have the correct statistical design to test this. Of those that had, there were few consistent trends. Competition was more prevalent in

Table 1. The r and p values for the regression between inter-specific nearest-neighbour distance and canopy area or volume for each sample plot.

Locality no. (Fig 1)	Plot	No. of pairs	Canopy area		Canopy volume	
			r	p	r	p
1	1B	38	0.162	>0.05	0.095	>0.05
	1T	40	0.503	<0.001	0.464	<0.005
2	2B	40	0.197	>0.05	0.107	>0.05
	2T	34	−0.106	>0.05	−0.111	>0.05
3	3B	40	0.525	<0.001	0.424	<0.01
	3T	34	0.274	>0.05	0.317	>0.05
	4T	32	−0.114	>0.05	−0.085	>0.05
5	5B	40	0.396	<0.05	0.076	>0.05
	5T	40	0.212	>0.05	0.073	>0.05
6	6M	37	−0.177	>0.05	−0.124	>0.05
	6T	36	0.121	>0.05	−0.125	>0.05
7	7M	37	0.050	>0.05	0.120	>0.05
	7T	39	0.211	>0.05	0.174	>0.05
8	8B	32	0.079	>0.05	0.063	>0.05
	8T	32	0.058	>0.05	−0.106	>0.05
9	9B	40	−0.018	>0.05	−0.102	>0.05
	9T	32	−0.060	>0.05	−0.077	>0.05
10	10B	32	−0.092	>0.05	−0.137	>0.05
	10T	37	0.221	>0.05	0.049	>0.05
11	11B	40	0.061	>0.05	0.037	>0.05
	11T	36	0.197	>0.05	0.215	>0.05
12	12B	37	−0.060	>0.05	−0.026	>0.05
	12T	32	0.158	>0.05	0.289	>0.05
13	13B	39	−0.016	>0.05	−0.065	>0.05
	13T	40	−0.118	>0.05	−0.100	>0.05
14	14B	35	0.091	>0.05	−0.033	>0.05
	14T	34	−0.149	>0.05	−0.165	>0.05
15	15B	35	−0.056	>0.05	−0.109	>0.05
	15M	35	−0.294	>0.05	−0.292	>0.05
16	16M	36	0.022	>0.05	0.131	>0.05
17	17M	30	0.021	>0.05	0.165	>0.05
18	18B	40	0.296	>0.05	0.186	>0.05
	18T	40	0.160	>0.05	0.053	>0.05
19	20T	38	0.145	>0.05	0.098	>0.05
22	21T	40	0.141	>0.05	0.168	>0.05
	22T	39	0.116	>0.05	0.138	>0.05
25	25M	33	0.041	>0.05	0.024	>0.05
	26M	34	0.283	>0.05	0.326	>0.05
	27M	36	0.582	<0.001	0.492	<0.005
30	30B	30	0.083	>0.05	−0.19	>0.05
	30T	34	−0.061	>0.05	−0.012	>0.05
31	31B	34	−0.064	>0.05	−0.157	>0.05
	31T	33	0.168	>0.05	0.160	>0.05

Acacia communities and within *Acacia* species than broad-leaf communities or species. This is in general agreement with previous studies (Smith and Walker 1983). The absence of detectable competition within most of the sites examined is contrary to most previous studies in southern African savannas, especially

Table 2. Comparison of site attributes for sites with (n = 4) and without (n = 39) inter-specific competition using a T-test. (Soil data for A-horizon).

Variable	Sites with competition	Sites without competition	T	p
Competition index (see methods)	0.507	0.056	6.27	<0.0001
Altitude (m.a.s.l.)	585.0 ± 152.6	853.3 ± 67.1	1.61	n.s.
Aspect (^{0})	240.3 ± 75.2	175.8 ± 16.5	0.84	n.s
Slope position	2.8 ± 0.5	2.5 ± 0.2	0.56	n.s.
Slope angle(^{0})	6.4 ± 3.3	6.2 ± 1.0	0.05	n.s
Mean annual rainfall (mm)	733 ± 25.3	635 ± 26.6	2.67	<0.05
Basal area (m²/ha)	11.3 ± 4.4	12.7 ± 1.7	0.31	n.s
Biomass (t/ha)	18.5 ± 4.9	36.0 ± 8.0	1.87	n.s
Dominance index (see methods)	0.43 ± 0.04	0.36 ± 0.04	1.29	n.s
No. of woody species	8.8 ± 1.4	12.7 ± 0.8	2.49	<0.05
Stem density	1 726 ± 644	1 614 ± 191	0.17	n.s
Proportion small stems (%)	18.8 ± 7.7	24.5 ± 2.5	0.70	n.s
Total soil depth (m)	1.1 ± 0.6	0.6 ± 0.1	0.75	n.s
Cation Exchange Capacity (meq)	13.4 ± 4.4	9.1 ± 1.1	0.95	n.s
Organic carbon (%)	1.2 ± 0.4	1.1 ± 0.1	0.26	n.s
Nitrogen	11.5 ± 3.7	13.9 ± 1.3	0.63	n.s
Nitrogen mineralisation	25.8 ± 9.4	24.7 ± 2.6	0.11	n.s
Clay (%)	35.8 ± 4.4	19.3 ± 1.6	1.10	n.s
Sand (%)	49.0 ± 15.6	69.1 ± 2.2	1.28	n.s
Silt (%)	15.3 ± 3.2	11.5 ± 0.9	1.13	n.s

Acacia communities (Smith and Walker 1983; Smith and Goodman 1986), and summaries from other biomes (Fowler 1986; Goldberg and Barton 1992). However, recently Rathogwa (2000) in examining inter-specific and intra-specific competition for two savanna tree species reported that competition was detected at only a minority of the sites. Intra-specific competition was evident in 36% of *Colophospermum mopane* sites (22 samples), and 50% of *Androstachys johnsonii* sites (20 plots). The was no evidence of inter-specific competition between the two species where they occurred in mixed stands (8 plots). Thus, the recent results of Rathogwa (2000) and my study, both based on large sample sizes, indicate that competition is not as prevalent in southern African savannas as preciously thought. This requires examination in terms of analysis of what is different at those few sites that did indicate the presence of competition relative to the sites that did not, or a critical scrutiny of the nearest-neighbour method.

In terms of the characteristics of sites exhibiting inter-specific competition relative to those that did not, the only difference was that competitive sites were at higher mean annual rainfall than sites without, and had a lower number of species. However, these differences were not exclusive, as there were some sites without competition that had a higher mean annual rainfall than some of the sites where competition was inferred. Thus, no threshold level of mean annual rainfall could be identified above which inter-specific competition begins to assume a prominent role in savanna community structure and function. Higher rainfall sites commonly have a higher basal area or biomass (Shackleton 1997), which will serve to increase the likelihood of competitive effects. However, in this study, there was no statistical difference in biomass or basal area between sites exhibiting inter-specific competition and sites that did not.

Differentiation of sites with and without intra-specific competition was evident on the basis of slope position and the proportion of small stems. In southern African savannas on weathered granites, slope position has a strong correlation with soil texture (and hence available soil moisture) and nutrient status due to the development of catenas (Scholes 1997). Upper slopes are characterised by shallow, sandy, dystrophic soils, whilst bottomlands typically have deeper, clay, euthrophic soils. It is more likely that the effects of slope position on intra-specific competition are manifest through the effect of slope position on soil moisture and fertility than slope position *per se*. However, no specific differences were found in terms of soil

Table 3. The r and p values for the regression between intra-specific nearest-neighbour distance and canopy area or volume for each sample plot.

Locality no. (Fig 1)	Plot	No. of pairs	Species	Canopy area		Canopy volume	
				r	p	r	p
1	1B	10	*Acacia nilotica*	− 0.229	> 0.05	− 0.310	> 0.05
	1T	12	*Faurea saligna*	0.1957	>0.05	0.063	>0.05
2	2B	8	*Acacia burkeii*	0.662	>0.05	0.672	<0.05
	2T	22	*Bolosanthus speciosus*	0.367	>0.05	0.378	>0.05
3	3B	8	*Acacia nilotica*	0.444	>0.05	0.413	>0.05
	3T	14	*Acacia nilotica*	0.475	>0.05	0.548	<0.5
	4T	8	*Euclea schimperii*	0.918	<0.001	0.919	<0.001
5	5B	19	*Acacia tortilis*	0.347	>0.05	−0.145	>0.05
	5T	7	*Acacia tortilis*	0.065	>0.05	−0.088	>0.05
6	6T	5	*Syzygium cordatum*	0.297	>0.05	0.171	>0.05
8	8T	7	*Combretum apiculatum*	0.296	>0.05	−0.246	>0.05
9	9B	14	*Colophospermum mopane*	− 0.256	>0.05	−0.231	>0.05
	9T	17	*Colophospermum mopane*	0.046	>0.05	0.067	>0.05
10	10T	13	*Acacia gerrardii*	0.581	<0.05	0.624	<0.05
12	12B	5	*Faurea saligna*	0.161	>0.05	0.116	>0.05
13	13B	6	*Acacia burkeii*	−0.296	>0.05	−0.115	>0.05
	13T	17	*Lannea discolor*	0.089	>0.05	−0.045	>0.05
14	14T	8	*Combretum apiculatum*	0.537	>0.05	0.640	<0.05
15	15B	10	*Acacia nilotica*	0.189	>0.05	0.008	>0.05
16	16M	18	*Acacia robutsa*	0.287	>0.05	0.454	<0.05
17	17M	17	*Acacia caffra*	0.257	>0.05	0.243	>0.05
	17T	32	*Acacia caffra*	0.654	<0.001	0.654	<0.001
18	18B	11	*Acacia tortilis*	0.587	<0.05	0.661	<0.05
	18T	36	*Acacia grandicornuta*	0.127	>0.05	0.069	>0.05
19	19B	33	*Acacia karroo*	0.501	<0.005	0.459	<0.01
22	21T	6	*Acacia caffra*	0.374	>0.05	0.254	>0.05
	22T	6	*Faurea speciosa*	0.622	>0.05	0.614	>0.05
25	25M	5	*Combretum collinum*	0.658	>0.05	0.693	>0.05
	26M	7	*Dichrostachys cinerea*	0.038	>0.05	0.183	>0.05
	27M	23	*Terminalia sericea*	0.651	< 0.001	0.578	< 0.005
30	30T	15	*Combretum apiculatum*	0.446	>0.05	0.455	>0.05

texture or indices of nutrient status between sites with and sites without intra-specific competition. Stands with a relatively high proportion of small stems tended to have significant competitive interactions as measured through nearest-neighbour analysis. Once again though, this was not an precise categorisation, with several plots without intra-specific competition having higher densities than plots with competition. Thus, a high density of small stems possibly predisposes a site to intra-specific competition, but other factors are required before this is realised. It has been observed that stands of dense, small individuals become progressively less dense with time through what is known as self-thinning, which is taken as an indication of competition (Peet and Christensen 1987).

However, Grundy et al. (1994) found that competition was not evident in stands dominated by smaller stems, but was present between larger trees.

The relationships between inter-specific competition and the dominance index and woody plant species richness indicate that competition increases with decreasing species number, suggesting a change from inter-specific to intra-specific competition, and that the latter plays a more prominent role than inter-specific competition. This is corroborated by the higher prevalence of intra-specific competition from the results of this study. The greater the number of species, the less the dominance and the greater the niche separation within the community.
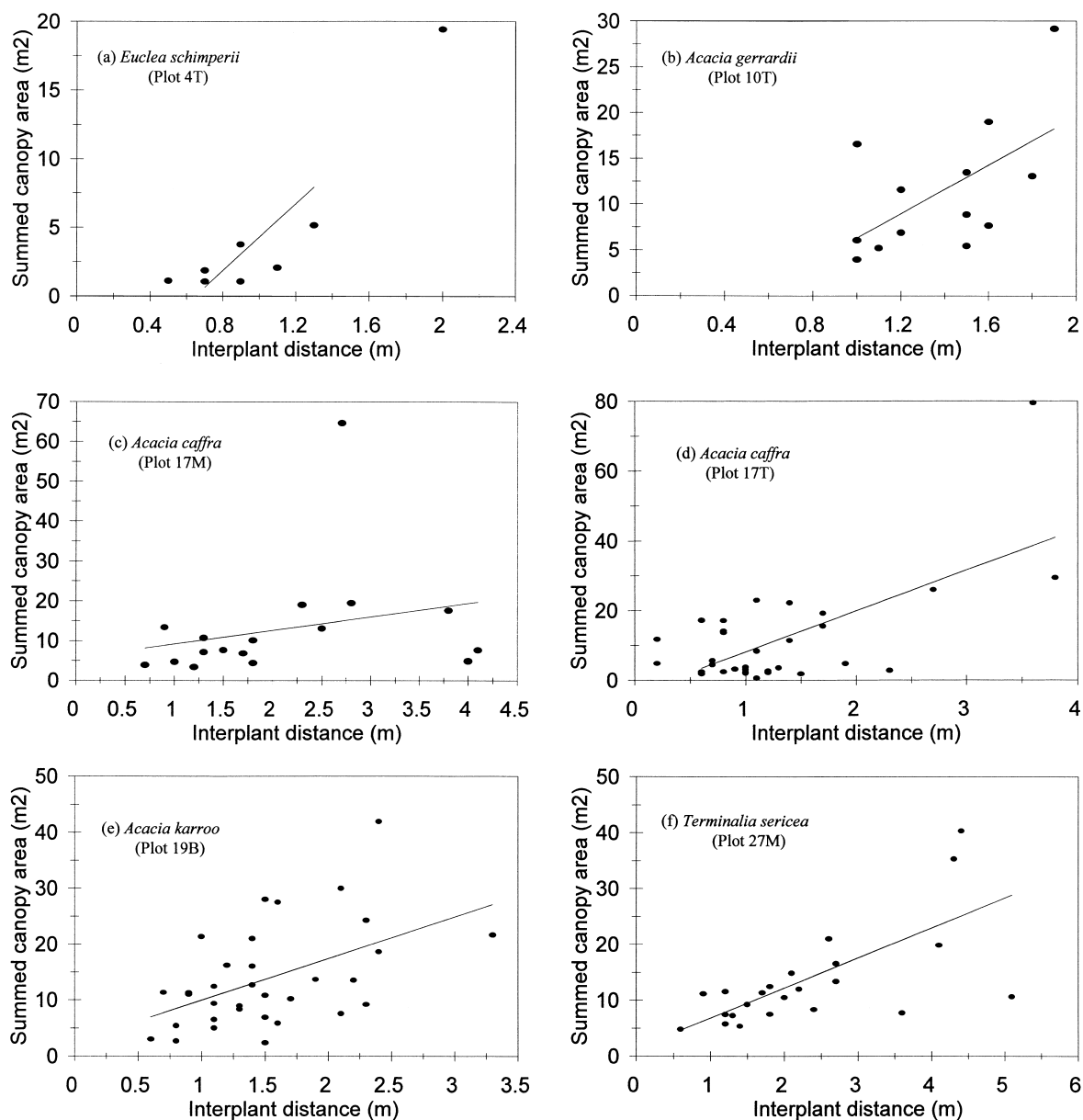
Figure 3. Scatter plots of sites with intra-specific competition.

The method used here was the same as that used in previous studies in southern Africa where competition was inferred for most savanna woody communities. The low proportion of sites displaying competition in this study relative to previously published work, particularly *Acacia* communities, begs a critical analysis of the method, and whether or not it is more applicable in some situations than others. In this regard I discuss four potential problems with nearest-neighbour analysis as an approach to determine the presence or absence of competition.

Application of nearest neighbour analysis

Canopy area versus canopy volume

Canopy area has been the dependent variable most commonly used by previous authors. In this study, it generally provided higher r^2 values than canopy volume in the regressions of summed areas, or volumes, against interplant distance. However, is it perhaps simplistic to measure tree canopy growth responses in the horizontal dimension only. It is well accepted

Table 4. Comparison of site attributes for sites with (n = 6) and without (n = 25) intra-specific competition using a T-test. (Soil data for A-horizon).

Variable	Sites with competition	Sites without competition	T	p
Competition index (see methods)	0.360 ± 0.15	0.081 ± 0.03	2.41	< 0.05
Altitude (m.a.s.l.)	1 033 ± 240.2	798 ± 63.1	0.95	n.s
Aspect (^{0})	168.3 ± 53.3	183.3 ± 17.3	0.27	n.s
Slope position	1.7 ± 0.3	2.6 ± 0.2	2.52	< 0.05
Slope angle (^{0})	8.7 ± 3.1	5.8 ± 0.9	0.86	n.s
Mean annual rainfall (mm)	690 ± 92.4	636 ± 24.9	0.56	n.s
Basal area (m²/ha)	18.7 ± 9.6	11.6 ± 1.1	0.73	n.s
Biomass (t/ha)	61.9 ± 46.4	30.2 ± 4.9	0.68	n.s
Dominance index (see methods)	0.50 ± 0.12	0.35 ± 0.03	1.24	n.s
No. of woody species	10.0 ± 2.6	12.7 ± 0.7	1.02	n.s
Stem density	2 886 ± 814	1 430 ± 151	1.96	n.s
Proportion small stems (%)	36.9 ± 3.8	21.9 ± 2.5	3.26	< 0.01
Total soil depth (m)	0.7 ± 0.3	0.7 ± 0.1	0.04	n.s
Cation Exchange Capacity (meq)	15.6 ± 3.7	8.6 ± 1.0	1.83	n.s
Organic carbon (%)	1.5 ± 0.4	1.0 ± 0.1	1.07	n.s
Nitrogen	17.8 ± 4.1	13.1 ± 1.2	1.11	n.s
Nitrogen mineralisation	36.2 ± 12.2	23.0 ± 2.1	1.07	n.s
Clay (%)	21.2 ± 2.4	20.9 ± 2.3	0.10	n.s
Sand (%)	67.0 ± 4.1	67.4 ± 2.8	0.07	n.s
Silt (%)	12.3 ± 2.5	11.8 ± 0.9	0.21	n.s

that trees competing for light allocate more resources to increase vertical dimensions than horizontal dimensions. There is no reason to doubt why the same should not apply for woody savanna communities. If two individuals compete a range of response strategies may result, and especially in dense vegetation, an increase in canopy height as opposed to canopy spread is probable. Therefore, in dense stands measurement of canopy area during a nearest-neighbour analysis to detect competition will tend to decrease the probability of a significant relationship between the sum of canopy size (areas) and distances, whereas canopy volume will not. The degree of canopy overlap in stands measured in the previous studies relative to those in this study is unknown, but could be one contributor to different results.

Another drawback of canopy area, or spread, is that species differ with respect to their inherent canopy architecture. Some savanna woody species are characterised by a spreading canopy, i.e. favouring horizontal growth (e.g. *Acacia sieberiana, Acacia tortilis, Pterocarpus angolensis*), whilst others are noted for their relatively tall and narrow growth from (e.g. *Faurea saligna, Pterocarpus rotundifolius*) (Figure 4). Therefore, attempts to detect inter-specific competition using nearest-neighbour analysis based

on canopy area in communities where both types of species are present will be confounded by the influence of canopy architecture. This problem would not apply to analysis of intra-specific competition. Canopy volume accounts for both horizontal and vertical dimensions of the canopy and should therefore is recommended over canopy area, although results from this study do not support this argument. The extent and density of the rooting system would possibly be the best measure, but is fraught with methodological problems.

Temporal dynamics

Nearest-neighbour analysis is based upon a snapshot of the current situation of the spatial arrangement of individuals in the community. It fails to interpret these within the context of the temporal dynamics, which can be marked within savannas, which are inherently variable systems (Scholes and Walker 1993; Scholes and Archer 1997; Higgins et al. 2000). A typical example is provided in Figure 5. At time zero two large mature trees are present (*A* and *B*), and are far enough apart not to compete at the time of measurement (a number of years in the future, as they continue to grow, they may be competing). Sometime later (time
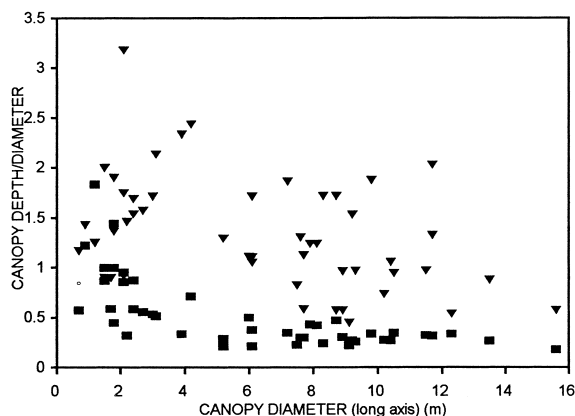
Figure 4. Canopy height:width ratio for two species with contrasting architecture (■ - *Pterocarpus angolensis*; ▼ - *Faurea saligna*).

t1), another plant *C* is recruited into the space between *A* and *B*. Nearest-neighbour measurements now may well conclude that competition is present as the sum of canopy sizes of *A* and *C*, or *B* and *C*, is less than that between *A* and *B* and the interplant distance is smaller. The interpretation is that *C* is stunted because of the competitive effects of its neighbours. If by chance, plant *C* is of a species that has an inherently faster growth rate than species *A* or *B*, and soon attains a comparable size, remeasurement of the nearest-neighbour dimensions several years later (t2) may well provide a picture that leads to the interpretation that no competition is occurring relative to t1 since the sum of the canopy size is greater. This example serves to illustrate that the determination of the presence or absence of competition through nearest-neighbour methods is highly dependent upon the temporal timing of the potential pairings at that time only. Recruitment and mortality will continually interfere with the nature of existing competitive or non-competitive nearest-neighbour interactions, as perhaps will phenological patterns of the competing neighbours. In a review of 89 published articles on plant competition Goldberg and Barton (1992) found only one, on algal communities, that had directly tested changes in competitive effects through time.

This problem may potentially be addressed by analysis of relative growth rates (RGR) between neighbouring trees (Penridge and Walker 1986; Duncan 1991), rather than canopy size. However, this too has its problems, including (i) the time required to obtain an adequate measure of RGR in a variable savanna environment, and (ii) RGR is dependent on the size and species of the tree (Shackleton 1997). Moreover, testing this hypothesis using growth rate data for
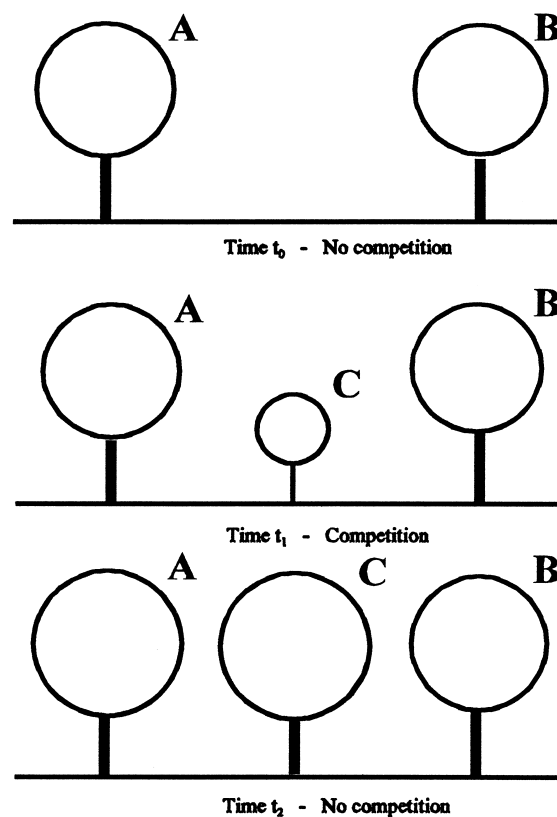

Figure 5. Schematic representation of the problems of nearest-neighbour analysis with temporal change in competitive interactions (see text for details).

those four plots where nearest-neighbour analysis suggested inter-specific competition was present, failed to corroborate the presence of competition at those plots (Shackleton 1997). Grundy et al. (1994) found no relationship between interplant distance and combined RGR for *Julbernardia globifera*, but one did exist for *Brachystegia spiciformis*.

Exclusion of the smallest size classes

In most of the studies cited, as well as this study, the nearest-neighbour analysis is confined to established stems larger than a specified minimum, frequently 1 m tall. The smallest stems are excluded from the analysis. Yet it is the smallest stems that are possibly most vulnerable to adverse abiotic and biotic factors as evident in the higher mortality rates of small stems relative to big stems (Duncan 1991; Shackleton 1997). Such factors, including competition from neighbours, may lead to the death of a newly recruited plant within one or two seasons after establishment (the

equivalent of competitive exclusion), or restrict it to a small size with frequent shoot die-back (Milton 1987; Chidumayo 1992a, 1992b) until a change in circumstances allows it grow though into a larger size class (Higgins et al. 2000). Competition with herbaceous plants is also important at the seedling stage (Bush and van Auken 1990; McPherson 1993; Davis et al. 1998). Thus, the current application of nearest-neighbour studies to detect competition are possibly at an incorrect resolution and should be focussed on, or certainly include, the smallest individuals. A high proportion of small stems was important in differentiating sites with significant intra-specific competitive interactions in this study, but not so in the study of Grundy et al. (1994).

Consideration of the nearest-neighbour only

The basic assumption of the nearest-neighbour approach is that the closer together two individuals are, the stronger the degree of competition between them. However, this need not necessarily be so since the assumption ignores the sizes of the two individuals to one another relative to other adjacent trees. For example, a relatively large tree (*C*) in the vicinity of a small tree (*A*) could be expected to have a greater influence on the small tree (*A*) than another small tree that is closer (*B*). The nearest neighbour pair is *A* and *B*, but the strongest competitive interference is *A* and *C*. It may well be that *C*s nearest neighbour is not *A*, and therefore the competitive influence of *C* is never measured. This may be addressed by measuring more than one nearest-neighbour per point tree, for example the nearest tree in each 90° quadrant around the point tree. Grundy et al. (1994) recognised this, and in their study if the point tree was large (>5 m), and the nearest-neighbour was small (<5 m) they measured the closest large tree (>5 m) rather than the closest nearest neighbour. Rathogwa (2000) compared results of using only the nearest neighbour with using a sum of sizes of the three nearest neighbours. When only the nearest neighbour was used competition was inferred at only 36% of sites. Yet, when the three nearest neighbours were used, competition was not inferred at any of the sites.

The result of the above inadequacies of the nearest-neighbour methodology is that it probably underestimates the prevalence of competition, certainly in savannas. The 'stochastic' nature of some of these problems (such as temporal dynamics, and the role of non-neighbours) may contribute to some of the differences between this study and previous work, or result in all studies using this approach having a large Type II error component, and thus finding significant relationships by chance alone, especially given the small sample sizes of previous studies. The Monte-Carlo analysis of this study indicated this was not the case. Within a caveat of perhaps an imprecise methodology, which has also been used by previous workers in southern African savannas, the results of this study suggest that niche separation in both spatial and temporal planes between species and within species is generally greater than previously argued. Alternatively, if competition is occurring, its impact is relatively low, both at the level of specific pairs of trees, as well as the community as a whole. It may occur on a spatial as well as a temporal dimension. It is necessary to obtain a predictive capacity in this regard, so that the role of competition can be accurately determined for specific sites and species, rather than generalised from a limited number of studies.

There are a number of alternatives to the nearest neighbour method including pattern analysis (also based on nearest-neighbour distances), transplant or removal studies, analysis of relative growth rates, modelling of available resource pools and demonstration of direct interference (Keady 1989; Grace and Tilman 1990). Nearest-neighbour approaches remain attractive because they are simple and rapid. Yet, the inadequacies identified indicate that it requires modifications. These should not unduly compromise the simplicity and speed. To that end, I suggest that future studies employing the nearest-neighbour approach measure more than one nearest-neighbour, include all stems (even the smallest ones), and use canopy volume instead of canopy area. Other methodologies allowing examination of temporal dynamics through growth rates or reproductive success would be preferable, but are time consuming and costly in a naturally variable environment such as savannas.

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