Neighbourhood analysis of competition between two Namaqualand ephemeral plant species

M.A. Oosthuizen, M.W. van Rooyen* and G.K. Theron

Department of Botany, University of Pretoria, Pretoria, 0002 Republic of South Africa

By using attributes of neighbours, such as number, size and distance, investigators have developed neighbourhood competition models that are able to predict plant performance of an individual in a plant population. A non-linear neighbourhood model proposed by Silander & Pacala (1985) was applied to performance data (i.e. total above-ground dry mass) of *Dimorphotheca sinuata* and *Ursinia cakilefolia*, two Namaqualand ephemeral species. The best neighbourhood size was sought by varying the neighbourhood size and plotting an interference index against dry mass. The non-linear model was then fitted to the data and the r^2 values determined for each neighbourhood. Correlations between performance (total above-ground dry mass) and different interference indices were much higher in mixtures than in monocultures for both species. Number of neighbours seemed to be the best predictor of performance for both *D. sinuata* and *U. cakilefolia* in mixtures. In monoculture, the best correlations were obtained when the distance of the neighbours was also taken into account. Even so, these correlations accounted for less than 50% of the variation in plant mass. Although these neighbourhood models may be useful in describing the inter-individual effects of interference on Namaqualand ephemeral species, it may be difficult to apply these results in the field.

Keywords: Competition, *Dimorphotheca sinuata*, neighbourhood analysis, number of neighbours, performance, predict, *Ursinia cakilefolia*.

*To whom correspondence should be addressed.

Introduction

Most studies on plant competition have focused on the effect of mean density on performance or yield in plant populations, assuming that it is an effective description of the state of the population without considering individual variation (Silander & Pacala 1985). Plants only compete for resources with those individuals immediately surrounding them and not with all the members of the population (Harper 1977). The intensity of competition faced by each individual is therefore determined by the number of neighbours within a particular area (Fowler 1984).

The importance of spatial patterns and processes in plant community dynamics has been widely recognized (Czárán & Bartha 1992; Hara & Wyszomirski 1994). By using attributes of neighbours, such as number, size, distance and spatial arrangement, investigators have developed neighbourhood models of competition that can predict plant performance of an individual in a plant population (Mack & Harper 1977; Waller 1981; Weiner 1982; Watkinson *et al.*1983; Pacala & Silander 1985; Silander & Pacala 1985; Benjamin & Hardwick 1986; Hara 1988; Bonan 1991, 1993). Other aspects which need to be taken into consideration in the use of these models are the form of the relationship between performance and competition (Weiner 1984; Goldberg 1987); the time interval over which performance is related to local crowding (Liddle *et al.* 1982; Mithen *et al.* 1984); the type of competition among plants (Goldberg 1987; Goldberg & Fleetwood 1987); the degree of competition among plants and the conditions under which growth occurred (Bonan 1993). Although plant size is most often used as a measure of plant performance (Mack & Harper 1977; Fowler 1984; Firbank & Watkinson 1985,1987; Pacala & Silander 1987; Goldberg 1987; Goldberg & Fleetwood 1987), it may not be appropriate, because plant size is not independent among target and neighbour plants (Mead 1968; Fowler 1984; Firbank & Watkinson 1987).

Although spatial competition models have an intuitive appeal and seem to be more realistic than non-spatial ones, the proportion of variation (expressed as a percentage) explained by the

models ranges from nearly 0% to approximately 90% depending on the models and species examined (Hara & Wyszomirski 1994). The objective of this study was to investigate whether the performance of *Dimorphotheca sinuata* DC. and *Ursinia cakilefolia* DC., grown in monocultures and mixtures with each other, was determined by the spatial distribution of neighbouring plants, and whether a neighbourhood model could be used to predict the performance of these plants. Both species are annual herbs that occur abundantly in Namaqualand, especially in old fields or otherwise disturbed vegetation. The mass floral displays created by these species under favourable conditions attract thousands of tourists to the area annually. Although both species occur in mixed stands, they often produce patches where one species dominates. Experimental studies have indicated *D. sinuata* as the stronger competitor (Oosthuizen *et al.* 1996; Rösch 1996) being able to suppress the growth of *U. cakilefolia*. Both species germinate over a relatively broad range of temperatures, *Dimorphotheca sinuata* having a slightly faster germination rate and a higher final germination percentage (Beneke *et al.* 1993).

Materials and Methods

Achenes of *Dimorphotheca sinuata* and *Ursinia cakilefolia* were sown in $360 \times 360 \times 190$ mm pots in monocultures and mixtures, at a density of 240 achenes per pot (representing approximately 1 850 achenes per m²) in monoculture and 120 achenes per species per pot in mixture. Each treatment was replicated four times. Seedling emergence varied between pots and as seedlings were not thinned to a constant density after emergence, density varied between pots. All plants received tap water daily and once a week Arnon and Hoagland's complete nutrient solution (Hewitt 1962). After approximately six months, all plants were harvested, and the specific position of each plant was noted on a grid and numbered accordingly. The total number of inflorescences per plant were counted, whereafter all plants were divided into reproductive and vegetative plant parts and dried for one week at 60°C before determining the dry mass. For each plant the number of neighbours and distance to

neighbours in neighbourhood radii, ranging from 2 cm to 10 cm, were determined from the grids.

The following attributes of a focal plant and its neighbours were studied from the grid and the dry mass data:
(a) number of neighbours;
(b) distance to neighbours; and
(c) distance and total above-ground dry mass of neighbours.

A neighbourhood is regarded as a circle of fixed radius (r) around each plant and from this an interference or crowding index for plant neighbourhoods can be calculated (Mack & Harper 1977; Silander & Pacala 1985). Only plants with a complete neighbourhood circle, with a radius of 10 cm, were included in the analyses. The simplest interference index was taken as the number of neighbours in the circle (Silander & Pacala 1985). The interference index was then plotted against the total above-ground dry mass of the focal plant. A non-linear model was fitted to the data, using the STATGRAPHICS (Statgraphics 5.0, 1989, STSC, Inc., U.S.A.) computer program. The model (adapted from Silander & Pacala 1985) used, was:

$$S = M/(1 + CW)$$

where S = total above-ground dry mass of the focal plant; M = a constant, the maximum total above-ground dry mass produced by a plant with no neighbours (i.e. singly grown plant); C = a decay constant; W = a variable, the crowding or interference index.

Results

Only total above-ground dry mass is discussed as performance parameter in this study, since dry mass of the inflorescences as well as total number of inflorescences yielded essentially the same results.

Number of neighbours

The number of neighbours in the neighbourhood was used to determine the interference index. The neighbourhood radius (r) ranged from 2 to 10 cm, and only individuals with a complete neighbourhood size of 10 cm were used. The best neighbourhood size, i.e. that which minimizes the residual sum of squares for a given model, was sought by systematically varying the r and

plotting the interference index against the above-ground dry mass of the focal plant. The non-linear model of Silander & Pacala (1985) was fitted to the data and the r^2 values determined for each neighbourhood. That neighbourhood size which yielded the highest r^2 value was taken as the best predictor radius.

The highest r^2 values for *D. sinuata* in a monoculture and mixture were obtained at a radius of 7 cm, accounting for 24.39% and 56.57% of the variation in dry mass of the focal plant in a monoculture and mixture respectively (Table 1). The highest r^2 values for *U. cakilefolia* were obtained at a radius of 5 cm in a monoculture and 3 cm in a mixture, accounting for 33.14% and 56.24% of the variation in dry mass in a monoculture and mixture (Table 1).

Distance to neighbours

Pielou (1960) found that competitive interference between individual plants was directly related to their distance apart. An interference index that weights each neighbour by its distance from the focal plant was therefore also used to study the effect of within-neighbourhood distance (Silander & Pacala 1985):

$$W = \sum_{i=1}^{N} (1 - d_i/r)^\theta$$

with d_i = distance of neighbour i from focal plant; r = neighbourhood radius; θ = weighting constant.

When d approaches r, the effect of distance is minimized, while it is maximized when d approaches 0. When the weighting constant (θ) is equal to 0, the index is the same as the number of neighbours, but when it increases, nearer neighbours are weighted more than remote neighbours (Silander & Pacala 1985). The above-ground dry mass of the focal plant was plotted against this interference index and the nonlinear model fitted to the data and the highest r^2 values sought.

In the case of *D. sinuata* in a monoculture at $r = 7$ cm, the r^2 values at $\theta = 0.5$ were slightly higher ($r^2 = 0.27$) than when only number of neighbours was used (Table 2). In general, lower r^2

Table 1 Results of a neighbourhood analysis relating the above-ground dry mass of the focal plant to the number of neighbours in a neighbourhood of a particular size. The r^2 values were determined by fitting the non-linear function $S = M/(1 + CW)$ (Silander & Pacala 1985) to the data of *Dimorphotheca sinuata* and *Ursinia cakilefolia* in monoculture and mixture

| Neighbour-hood radius (cm) | r^2 values | | | |
| | Dimorphotheca sinuata | | Ursinia cakilefolia | |
	Monoculture	Mixture	Monoculture	Mixture
2	0.0002	0.1296	0.0679	0.4253
3	0.0339	0.1331	0.2838	0.5624
4	0.0201	0.2927	0.2375	0.0303
5	0.0611	0.2341	0.3314	0.0084
6	0.0928	0.3926	0.2069	0.1466
7	0.2439	0.5657	0.1401	0.0919
8	0.1761	0.3697	0.0517	0.1104
9	0.1038	0.2813	0.0234	0.4638
10	0.1176	0.1110	0.0444	0.0716

Table 2 Results of a neighbourhood analysis relating the above-ground dry mass of the focal plant to the number of neighbours weighted by the distance to the focal plant. The r^2 values were determined by fitting the non-linear function $W = \sum (1 - d_i/r)^\theta$ (Silander & Pacala 1985) to the data of *Dimorphotheca sinuata* in a monoculture and mixture

| Neigh-bour hood radius (cm) | r^2 values | | | | | |
| | Monoculture | | | Mixture | | |
	$\theta = 0.5$	$\theta = 1.0$	$\theta = 2.0$	$\theta = 0.5$	$\theta = 1.0$	$\theta = 2.0$
2	0.0018	0.0038	0.0060	0.0634	0.0513	0.0366
3	0.0179	0.0017	0.0038	0.0000	0.0001	0.0038
4	0.0185	0.1030	0.0001	0.1037	0.0579	0.0195
5	0.0266	0.0125	0.0002	0.0511	0.0342	0.0150
6	0.0585	0.0373	0.0022	0.0469	0.0309	0.0601
7	0.2746	0.2065	0.0397	0.0060	0.0081	0.0108
8	0.2086	0.1585	0.0366	0.0001	0.0015	0.0084
9	0.1741	0.1438	0.0363	0.0170	0.0011	0.0056
10	0.2467	0.2090	0.0736	0.0033	0.0000	0.0065

values were obtained as θ increased and the best predictor radius increased to 10 cm (Table 2). In a mixture, the best predictor radius of *D. sinuata* decreased (from 7 to 3 cm), with much lower r^2 values than when only number of neighbours was considered as the interference index (Table 2). However, in the case of *U. cakilefolia*, distance to neighbours yielded a higher correlation with dry mass of the focal plant in a larger neighbourhood than when only number of neighbours was considered (Table 3). The highest correlation ($r^2 = 0.44$) was obtained when θ = 0.5 (Table 3). In a mixture, the best predictor radius remained 3 cm and the percentage of variation explained by the model (when θ = 0.5) was not higher than when only number of neighbours was used (Table 3). In the case of *U. cakilefolia* in a mixture, close neighbours tend to have a proportionately greater effect on the performance of the focal plant (increased θ) in larger neighbourhood sizes than in smaller neighbourhoods.

Distance as well as total above-ground dry mass of neighbours

An interference index that weights each neighbour by its distance from the focal plant as well as its total above-ground dry mass was also used in the neighbourhood analysis:

$$W = \sum_{i=1}^{N} (1 - d_i/r)\, w_i$$

with w_i = total above-ground dry mass of neighbour i; d_i = distance of neighbour i from focal plant; r = neighbourhood size.

The best predictor radii of *D. sinuata* gave low r^2 values in both a monoculture and mixture, accounting for less than 10% of the variation in biomass of the focal plant (Table 4). The r^2 values obtained for *U. cakilefolia* in a monoculture and mixture remained virtually unchanged compared to when only number of neighbours was used (Table 4).

Discussion

Correlations between the performance of the focal plant (i.e. total above-ground dry mass) and the different interference indices showed mixed results, with the variation in individual performance accounted for by the interference indices ranging from 0.60% to 56.57%.

On the whole, the correlations in this study were much higher in mixtures than in monocultures for both species. Number of neighbours seemed to be the best predictor of performance of both *D. sinuata* and *U. cakilefolia* in mixtures. Including other parameters, such as distance to and mass of neighbours, reduced the values of r^2 in the case of *D. sinuata*, while it had no effect for *U. cakilefolia*. These correlations in the mixtures (accounting for up to 56% of the variation) were obtained without taking the identity of the neighbouring plant into account. Various studies have indicated that it is the biomass and not the identity of the neighbours that determines target performance (Goldberg & Fleetwood 1987; Miller & Werner 1987; Gaudet & Keddy 1988). However, in other studies involving old-field annual species, it was found that neighbour identity and not just neighbour plant biomass determined target plant performance (McConnaughay & Bazzaz 1990; Tremmel & Bazzaz 1993).

In monoculture, the best correlations were obtained when the distance to the neighbours was also taken into account. Even so, these correlations accounted for less than 50% of the variation in plant mass of the focal plant.

On the whole, the best predictor radius for *D. sinuata* was larger than for *U. cakilefolia*. According to Silander & Pacala (1985) most of the interference among plants occurs over distances within the best radius (optimal neighbourhood size) or less. They reasoned that neighbours outside the neighbourhood radius of the focal plant had a net positive effect on that plant by depressing the growth of the closer neighbours. The optimal neighbourhood radius of *U. cakilefolia* was smaller than that of *D. sinuata* and this may be related to their competitive abilities. In a replacement series evaluation of the two species, *D. sinuata* had a higher competitive ability than *U. cakilefolia* (Oosthuizen et al. 1996).

In a review on neighbourhood analyses, Bonan (1993) found that the amount of variation in individual plant performance,

Table 3 Results of a neighbourhood analysis relating the above-ground dry mass of the focal plant to the number of neighbours weighted by the distance to the focal plant. The r^2 values were determined by fitting the non-linear function $W = \sum (1 - d_i/r)^\theta$ (Silander & Pacala 1985) to the data of *Ursinia cakilefolia* in a monoculture and mixture

| Neighbour-hood radius (cm) | r^2 values | | | | | |
| | Monoculture | | | Mixture | | |
	θ = 0.5	θ = 1.0	θ = 2.0	θ = 0.5	θ = 1.0	θ = 2.0
2	0.1120	0.1283	0.0950	0.4253	0.4253	0.4253
3	0.1173	0.2059	0.0389	0.5584	0.5409	0.4866
4	0.1856	0.2640	0.0734	0.1412	0.2444	0.3535
5	0.4176	0.4223	0.2421	0.0510	0.0939	0.1585
6	0.4401	0.4353	0.2502	0.1693	0.2652	0.3999
7	0.3520	0.3444	0.2112	0.0996	0.2008	0.3193
8	0.3110	0.2512	0.1971	0.1341	0.2229	0.3216
9	0.1950	0.1330	0.1632	0.3963	0.4569	0.4661
10	0.2458	0.1657	0.1457	0.2110	0.3090	0.3927

Table 4 Results of a neighbourhood analysis relating the above-ground dry mass of the focal plant to the number of neighbours weighted by distance and mass of neighbours. The r^2 values were determined by fitting the non-linear function $W = \sum (1 - d_i/r)\, w_i$ to the data of *Dimorphotheca sinuata* and *Ursinia cakilefolia* in monoculture and mixture

| Neighbour-hood radius (cm) | r^2 values | | | |
| | *Dimorphotheca sinuata* | | *Ursinia cakilefolia* | |
	Monoculture	Mixture	Monoculture	Mixture
2	0.0001	0.0172	0.1292	0.4253
3	0.0003	0.0106	0.1481	0.5600
4	0.0001	0.0569	0.1296	0.2472
5	0.0002	0.0634	0.3115	0.0776
6	0.0135	0.0720	0.2579	0.0533
7	0.0846	0.0466	0.2358	0.2228
8	0.0122	0.0127	0.0388	0.2116
9	0.0247	0.0313	0.0001	0.3438
10	0.0574	0.0131	0.0027	0.4812

accounted for by indices of local crowding ranged from 0% to 91%. Sixty per cent of the analyses accounted for less than one-half of the total variation in individual plant performance (Bonan 1993). The low correlation between performance and competition indices can be attributed to the relative importance of non-competitive factors in determining individual plant size (Mack & Harper 1977; Waller 1981; Liddle *et al.* 1982; Silander & Pacala 1985; Goldberg 1987; Firbank & Watkinson 1987) and limitations in the understanding of the effects of competition and spatial patterns on growth (Firbank & Watkinson 1987; Miller & Weiner 1989).

The effects of neighbours can also be obscured by being confounded with that of emergence order. The effect of this on the size and subsequent fate of an individual has been observed in many plant populations (Fowler 1984; Miller 1987). Ross & Harper (1972) found that emergence date accounted for 95% of the variance in plant mass and that there was no consistent relationship between the size of an individual and the size and number of its neighbours.

Hara & Wyszomirski (1994) tried to explain why a neighbourhood effect was apparent in some species and models and negligible in others. They found that the degree of competitive asymmetry determined the size–structure dynamics of plant populations. They concluded that spatial pattern is important at low densities, irrespective of whether competition is symmetric or asymmetric. However, at high densities, spatial pattern is nearly immaterial under strongly asymmetric competition, while it is much more pronounced under symmetric competition.

Bonan (1993) suggested that correlations between growth and local crowding at a given point in stand development mix both competitive response and competitive effect (Bonan 1993). A target plant is also its neighbours' neighbour, thereby reflecting both response to competition from neighbours and its effect on the growth of neighbours.

Although the effect of inter-individual interference on the performance of Namaqualand ephemeral species in experimentally grown mixtures can be described with the use of neighbourhood models, its application is of limited scope. Under field conditions small-scale heterogeneity in the habitat is likely to affect the outcome of competition, as the competitive interactions among the species can change along moisture, nutrient and CO_2 gradients (Fowler & Antonovics 1981; Turkington & Aarssen 1984; Fowler 1988; McConnaughay & Bazzaz 1990). The effects of germination and emergence time will also probably be exaggerated under field conditions, obscuring the relationship between the size of the focal plant and the number or distance of its neighbours.

According to Hara & Wyszomirski (1994), the degree of competitive asymmetry greatly affects the process and outcome of interactions between individuals. Competition between the two species chosen for this study is asymmetric (Oosthuizen *et al.* 1996) and a future study should investigate the relationships between two competitive symmetric species. Under crowded conditions, a population undergoing strongly asymmetric competition is a stable system little affected by spatial patterns, whereas a population undergoing symmetric competition is an unstable system highly sensitive to the spatial distribution pattern as well as to changes in physiological and morphological parameters caused by environmental fluctuations (Hara 1993). Asymmetric competition works as a structuring force for plant communities, whereas symmetric competition is not a structuring force but does bring about diversity (Hara 1993).

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