Competitive interactions between the perennial shrub *Leipoldtia constricta* and an annual forb, *Gorteria diffusa*

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Competitive interactions were studied between individuals of the perennial shrub, *Leipoldtia constricta* L. Bol., and an annual forb, *Gorteria diffusa* Thunb. in the winter rainfall region of the Karoo using nearest-neighbour analysis. Strong competitive interactions were measured between intraspecific and interspecific nearest-neighbour pairs. In particular, the size and reproductive potential of the annual forb was reduced whenever it established next to the perennial shrub. This reduction was greater than that occurring intraspecifically among individuals of the annual forb. Despite this effect, more annuals established close to the perennial shrub, presumably as the result of the latter's multiple-stemmed growth habit which traps soil at its base providing a 'safe site' for germination and establishment.

Kompeterende interaksie was ondersoek tussen individue van die meerjarige struik *Leipoldtia constrictor* L. Bol. en die eenjarige kruid *Gorteria diffusa* Thunb. wat in die winterreënvalstreek van die Karoo deur gebruik te maak van die naaste-individu-analise. Sterk kompeterende interaksies is waargeneem tussen intraspesifieke en interspesifieke naaste-individu-pare. Die grootte en voorplantingspotensiaal van die eenjarige kruid het drasties afgeneem wanneer hierdie plant langsaan die meerjarige struik gevestig was. Nieteenstaande hierdie invloed het meer eenjarige plante hulle in die nabyheid van die meerjarige struik gevestig. Hierdie verskynsel was moontlik as gevolg van die meerstammige groeiwyse van die meerjarige struik wat daartoe gelei het dat grond teen die basis van die stamme opgehoop het. Dit het dan gedien as 'n gunstige omgewing vir die kieming en vestiging van die saad.

Keywords: Interspecific competition, intraspecific competition, Karoo, Mesembryanthemaceae, reproductive potential, seedling establishment

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Introduction

Quantitative studies of plant distribution patterns suggest that biotic interactions are important in determining the structure of arid and semi-arid plant communities (Fowler 1986). Evidence of intraspecific and interspecific competition has been inferred from correlations between nearest-neighbour distances and plant sizes (Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977; Phillips & MacMahon 1981). Such results have been attributed in areas of low rainfall to competition between neighbouring plants for available water (Woodell *et al.* 1969). The experimental removal of all surrounding nearest neighbours, resulting in less negative xylem water potentials of the central plant, has demonstrated clearly that these patterns are caused by root competition for available soil moisture (Fonteyn & Mahall 1978, 1981; Robberecht *et al.* 1983; Ehleringer 1984). These investigations have been largely confined to perennial plants, despite the fact that annuals are known to be a successful component of these communities; their success being dependent upon the exploitation of resources during periods when the environment is suitable for completion of their life-cycles and their remaining dormant when it is not (Pattern 1978; Inouye *et al.* 1980). When such studies consider the interaction between perennials and annuals the emphasis is usually upon putative allelopathic effects of the perennials (Muller 1953; Friedman *et al.* 1977).

In this study we describe the interactions between a perennial succulent shrub, *Leipoldtia constricta* L. Bol. (Mesembryanthemaceae), and an annual forb, *Gorteria diffusa* Thunb. (Asteraceae), in disturbed semi-arid regions of the winter rainfall region of the Namaqualand Karoo. Specifically we ask:

1. do interactions occur between intraspecific pairs of *L. constricta* and *G. diffusa*?
2. do interspecific interactions occur between individuals of *L. constricta* and *G. diffusa*?
3. what effect, if any, do such interspecific interactions have on the reproductive potential of the annual species? and
4. is there a stronger effect on the reproductive potential of the annual forb from the perennial shrub than from the annual itself?

Study area

The study area is located in the winter rainfall region of Namaqualand in the north-western Cape, South Africa, 3 km east of Springbok (29°10′S, 17°53′E). The study area lies on a gentle 1–2, east-facing slope at 1 000 m elevation. The soils of the study area are derived from granite and are sandy. The mean annual rainfall for a 73-year period at Springbok is 224 mm (Weather Bureau 1965). Temperatures at the nearest long-term recording station, O'Kiep (29°36′, 17°52′E, elevation 927 m), averaged over a 21-year period are for annual maximum, 24.3°C, and for annual minimum 10.9°C (Weather Bureau 1965).

The vegetation consists of a low, sparse cover of both succulent and non-succulent annuals and perennial shrubs. The dominant species are the low perennial succulent shrub, *Leipoldtia constricta*, and a small annual forb, *Gorteria diffusa. Leipoldtia constricta* is a multiple-branched shrub growing up to 60 cm high with succulent leaves up to 2.5 cm long. *Gorteria diffusa* is a daisy growing up to about 30 cm high. Both species are widely distributed over rocky slopes and disturbed fields of the Namaqualand Karoo (le Roux & Schelpe 1988). Minor elements are *Aptosimum leucorrhizum* (E. Mey.) Phill., *Cheiridopsis candidissima* N.E. Br., *Eriochephalus ericoides* (L.f.) Druce, *Euphorbia dregeana* E. Mey. ex Boiss, *Galenia africana* L., *Hermannia trifurca* L., *Lampranthus suavissimus* (L. Bol.) L. Bol., *Osteospermum hyoseroides* (D.C.) Norl., *Pentzia incana* (Thunb.) Hutch., *Pharnaceum* sp., *Salsola kahlii* L., *Sarcocaulon crassicaule* Rehm, *Tetragonia fruiticosa* L. and *Whiteheadia bifolia* (Jacq.) Bak.

Methods

Plant canopy cover was measured by the line intercept method (Grieg-Smith 1983) along five randomly placed 5-m lines. Total cover was calculated as the mean percentage (± *S.E.*) of the line covered by vegetation along each line transect. The relative abundances of the dominant species were estimated as the average percentage of the total vegetation coverage along each line transect.

Measurement of intraspecific and interspecific interactions were made using the nearest-neighbour technique of Pielou (1960, 1962) and following the operational definitions of Yeaton & Cody (1976). In this method the distance between a randomly chosen individual and its nearest neighbour is recorded and the size of each measured and summed. If negative interactions (i.e. competition) are occurring, a positive correlation will occur between these two parameters (Pielou 1962). These measurements are made only in relatively homogeneous and continuous vegetation for pairs of individuals not occurring in or separated by drainage lines. Furthermore these measurements are made only if no individual of another species is growing such that its canopy intersects a straight line between the intra- or interspecific pair of individuals being measured.

Three sets of measurements were made for randomly chosen individuals of *Leipoldtia constricta* and *Gorteria diffusa*. Nearest-neighbour distances for the multiple-stemmed *L. constricta* were measured as the distance between the centers of the two canopies and the size of each roughly spherical individual measured as its diameter. For the single-stemmed *G. diffusa*; nearest-neighbour distances were measured from stem to stem and the size measured as (1) the diameter of the canopy and (2) the number of flowers (including developing buds and seed heads). For both species, the plant diameter of an individual is measured as the average of the length of its long axis and the maximum width of the canopy perpendicular to that length. Interspecific interactions were measured for *G. diffusa* individuals growing within a 1-m radius from the centre of each *L. constricta* shrub. *Leipoldtia constricta* shrubs were chosen randomly to serve as the central plant and the diameter, number of flowers and distance to the centre of the shrub's canopy were recorded for each individual of *G. diffusa* present within the 2-m wide circle. Average values for diameter, number of flowers and distance from the central *L. constricta* were calculated and used in the regression analyses for the interspecific case. The intensity of competition between intraspecific pairs of annuals and perennials and between intra- and interspecific pairs was determined by comparing the correlation coefficients for each regression line (Steel & Torrie 1960). Individuals were chosen for all analyses by selecting points, obtained from a random-number table, along a 50-m tape laid over the veld. The first individual of a target species, intersected by walking a line to the right or left of the tape, was selected and measurements made of its size and the distance to and size of its nearest neighbour. This procedure was allowed until at least 90 intraspecific pairs for each species were measured and 50 *L. constricta* chosen for the estimation of interspecific interactions, necessitating the movement of the 50-m tape several times.

The diameters, reproductive status (i.e. flowering or non-flowering) and the ratios of diameter/number of flowers were compared for the nearest *G. diffusa* individual (within 1 m) to a randomly chosen *G. diffusa* and for the neighbouring individuals of *G. diffusa* to a central *L. constricta* to examine the impact of intra- and interspecific interactions upon the establishment and reproductive potential of the annual. The sizes of *G. diffusa*, establishing next to a conspecific or *L. constricta*, were compared by means of a *t*-test (Steel & Torrie 1960). The effect of distance on establishment was determined by arbitrarily grouping data into those individuals found within 50 cm of the randomly chosen individual and those found from 50 cm to 1 m. A Chi-square test for 2 × 2 contingency tables (Zar 1974) was employed to determine differences in the numbers of individuals successfully establishing in each zone for the intra- and interspecific cases. *T*-tests were used to distinguish the differences in average diameters for the intra- and interspecific cases between these zones and for differences between the intra- and interspecific cases within each zone. A Chi-square test for 2 × 2 contingency tables was also used to determine the effect that distance of establishment has on flowering status. Finally, a Median test was used to compare the ratios of diameter/number of flowers for the intra- and interspecific situations to determine if differences occur in the number of flowers produced per individual (Zar 1974).

Results

The average lengths covered by *Leipoldtia constricta, Gorteria diffusa* and other species along a 5-m line

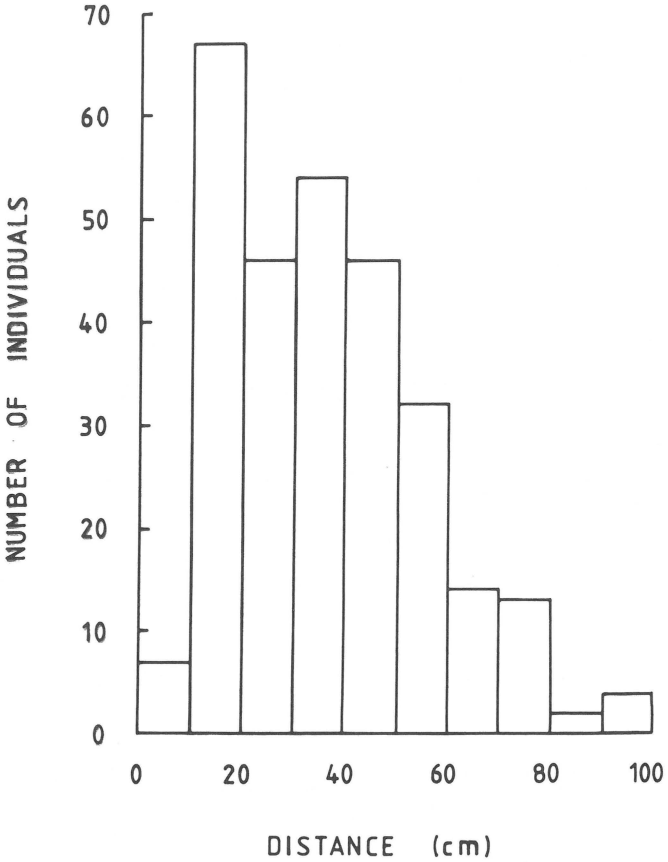

Figure 1 The number of individuals of *Gorteria diffusa* establishing at 10-cm intervals from the centre of the canopy of *Leipoldtia diffusa*.

transect were 1.37 (± 0.16) m, 0.24 (± 0.08) m and 0.33 (± 0.22) m respectively. The cover of this vegetation stand was 39% and the relative abundances of the dominant species were 71% for *L. constricta* and 12% for *G. diffusa*. A significant positive linear correlation was found between the nearest-neighbour distances (X) and the sums of sizes (Y) for pairs of *L. constricta* individuals. As the distance between nearest-neighbour individuals decreased, their sum of sizes decreased ($Y = 0.58X + 38.28$ cm, $n = 90$, $r = 0.72$, $P < 0.001$). A similar result was obtained for intraspecific pairs of *G. diffusa* ($Y = 0.52X + 59.29$ mm, $n = 150$, $r = 0.42$, $P < 0.001$). The relationship between nearest-neighbour distances (X) and the sum of flower numbers (Y) produced for pairs of *G. diffusa* also showed a positive correlation suggesting a negative interaction between the distance apart that two individuals established and their reproductive potentials ($Y = 0.12X + 4.53$ flowers, $n = 150$, $r = 0.33$, $P < 0.001$).

Negative interactions also occurred between the perennial succulent, *L. constricta*, and the annual, *G. diffusa*. Nearest-neighbour analyses revealed positive correlations between average distance of *G. diffusa* individuals found within 1-m radius from *L. constricta* (X) and the sum of their averaged sizes in mm with that of *L. constricta* in cm (Y_1) or the average numbers of flowers produced by the annual (Y_2). Therefore, proximity to the perennial shrub reduced the size that the annual could attain ($Y_1 = 0.66X + 40.13$, $n = 50$, $r = 0.59$, $P < 0.001$) as well as the number of flowers produced ($Y_2 = 0.05X + 0.31$, $n = 50$, $r = 0.42$, $P < 0.01$).

Table 1 The flowering status of individuals of *Gorteria diffusa* when their nearest neighbour was either a conspecific or the perennial, *Leipoldtia constricta*

Nearest-neighbour pair	Flowering	Not flowering
Intraspecific	131	2
Interspecific	187	89

The correlation coefficients for the intraspecific regression lines are significantly different for the annual and perennial plants ($P < 0.001$) but no significant differences are present for the comparison of the interspecific regression line with the intraspecific ones.

The magnitudes of the above effects can be determined by examining directly the diameters and reproductive status of the annual in the intra- and interspecific cases and at different distances from the randomly chosen, nearest neighbour. *Gorteria diffusa* was significantly smaller in diameter when established next to *L. constricta* than when its nearest-neighbour was another *G. diffusa* ($X \pm S.E.$ is 24.46 ± 1.34 mm versus 48.50 ± 2.35 mm, $t = 9.48$, $d.f. = 407$, $P < 0.001$). Significantly more individuals of *G. diffusa* established within 50 cm of *L. constricta* than they did next to *G. diffusa* (Figure 1, $X^2 = 27.55$, $P < 0.001$). Furthermore, the average diameters of the annual, in both the intra- and interspecific cases, were significantly smaller close to the randomly chosen individual than in the 50-cm to 1-m zone ($X \pm S.E.$ is for intraspecific, 40.50 ± 3.03 mm versus 57.38 ± 3.30 mm, $d.f. = 131$, $t = 3.75$, $P < 0.001$; for interspecific, 20.79 ± 1.21 mm versus 36.14 ± 3.74, $d.f. = 274$, $P < 0.001$). Finally, the average diameters of *G. diffusa* within each arbitrarily delineated zone were significantly smaller in the interspecific case than in the intraspecific one (less than 50 cm, $d.f. = 280$, $t = 7.18$; $P < 0.001$; 50-cm to 1-m zone, $d.f. = 126$, $t = 4.22$, $P < 0.001$).

The reproductive potential of *G. diffusa* is affected by the identity of its nearest neighbour. Practically all individuals, paired intraspecifically, were flowering while 36% of those, paired interspecifically, failed to flower (Table 1). Also in the interspecific situation, where sample size is sufficient for such analysis, *G. diffusa* flowering is significantly reduced in the zone closest to *L. constricta* (Figure 2, Table 2; $X = 10.6l$, $P < 0.005$). Finally, the numbers of flowers, when they are produced, are significantly fewer in the interspecific case than in the intraspecific one (Median test, $P < 0.05$). There was no distance effect on the numbers of flowers produced for the intra- and interspecific comparisons.

Discussion

There are negative interactions occurring between intra-

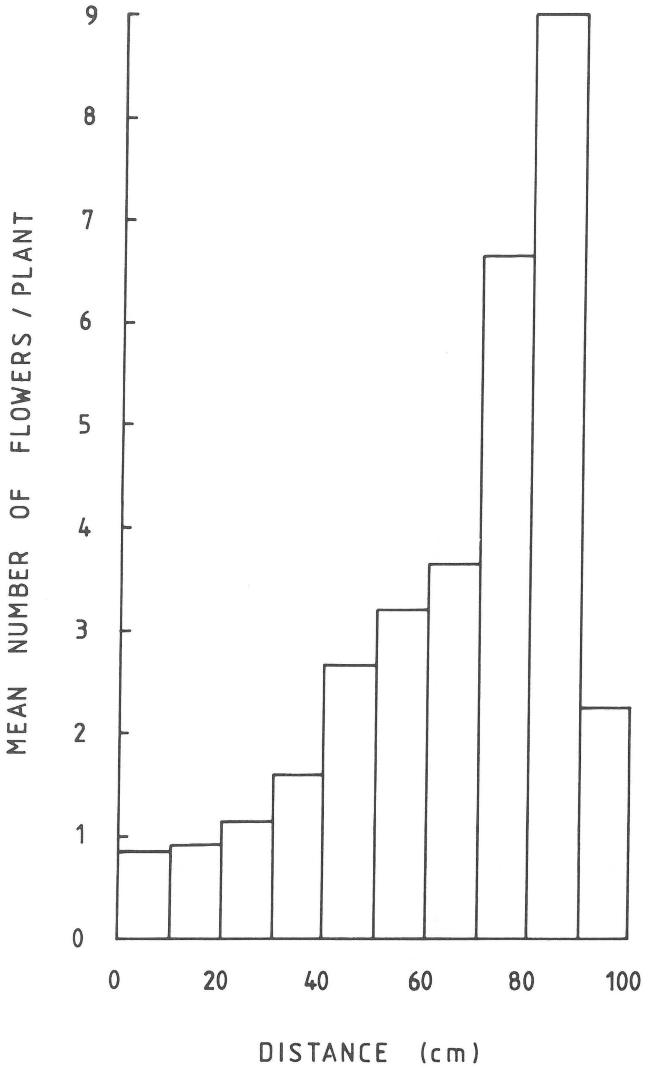

Figure 2 The mean number of flowers produced per individual of *Gorteria diffusa* at 10-cm intervals from the centre of the canopy of *Leipoldtia constricta*.

specific nearest-neighbour pairs of *Leipoldtia constricta* and *Gorteria diffusa*. The intensity of competition as measured by the correlation coefficients (Yeaton *et al.* 1985) is greater between individuals of the perennial succulent than between annual individuals. Here, the assumption is that a higher correlation coefficient indicates stronger competitive interactions which limit more effectively the size attained by a smaller individual as a function of its distance from its nearest neighbour. Because the intensity of competition is greater for the perennial species, we suggest that *L. constricta* forms the spatial pattern that leads to the organization and observed structure of this association, much as *Larrea tridentata* (D.C.) Coville and other perennials do for other plant species in the Mojave and Sonoran Deserts of North America (Went 1942; Muller 1953; Yeaton *et al.* 1977).

There are also negative interactions occurring between the perennial succulent and the annual forb. This competitive effect results in a reduction in the size of *G. diffusa* and in its reproductive potential. The latter

Table 2 The effect of distance of establishment from *Leipoidtia constricta* on the flowering status of *Gorteria diffusa*

Distance	Flowering	Not flowering
< 50 cm	131	79
> 50 cm	56	10

is best illustrated by the increased percentage of the annual forbs failing to produce flowers close to *L. constricta* (36% versus 15%). The interspecific effect of *L. constricta* on *G. diffusa* appears to be greater than that of *G. diffusa* upon itself as well, due to the increased failure of the annual to flower when it establishes within a 1-m radius of the perennial succulent. However, the intensity of competition, as measured by the correlation coefficient for the regression of the distance apart and the sum of the nearest-neighbour sizes, is intermediate to those of the intraspecific cases. Furthermore, many more individuals of the annual forb establish 'successfully' closer to the perennial than they do to each other. Therefore, there is an area adjacent to the succulent which is favourable for the establishment of *G. diffusa*. The growth form of the succulent with its multiple stems may serve to trap soil and organic materials around its base, providing a more favourable microsite for establishment of the annual (Muller 1953). Also, seeds of *G. diffusa* may be trapped at the base of the perennial resulting in increased establishment of this species in these microsites. Therefore, establishment too close to the perennial succulent results in reduced size and reproductive potential while establishment further away from the perennial results in increased competition from intraspecific neighbours later in the season. Although there is the appearance that the interspecific effect is greater in this study, self-thinning of the annual forb may have occurred early in the establishment of this species. We could detect no evidence that self-thinning had occurred in the form of dead or dying individuals of *G. diffusa* but the study was conducted towards the end of the annual's flowering period and the small, unsuccessful seedlings may have died, dried and been blown away.

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