Community-level competition between five Namaqualand pioneer plant species

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Namaqualand is renowned for its floral displays of many annual and some perennial species, with many tourists visiting the area during the flowering season. Various species grow in high densities on abandoned fields and other disturbed areas. Does competition between species affect the relative abundance of the different species and consequently the floral display? Five annual species were chosen and cultivated in monocultures and in mixtures of all five species. At the densities examined no significant difference between expected relative abundance and actual relative abundance was found, interspecific competition was therefore not large enough to cause significant changes in species abundance. Relative yield per plant (RYP) values indicated an interspecific competition hierarchy: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia cakilefolia* with *S. arenarius* being least affected by interspecific competition and *U. cakilefolia* the most. *Senecio arenarius, D. sinuata* and *O. grandiflorum* have similar competitive abilities while *H. variabilis* and *U. cakilefolia* also have similar, but weaker competitive abilities.

Keywords: Community-level competition, competitive ability, competitive hierarchy, relative yield per plant.

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Introduction

Ecologists have long been interested in competitive interactions, coexistence and coevolution, because of their great potential for shaping patterns of distribution and abundance of competing plant species (Gaudet & Keddy 1988; Lüscher & Jacquard 1991; Silvertown & Dale 1991; Goldberg & Barton 1992; Lüscher *et al.* 1992; Duralia & Reader 1993; Shipley & Keddy 1994; Huston & DeAngelis 1994).

However, most of the experimental work on species interactions has been conducted at the level of the individual, and the community-level consequences of species interactions have seldom been tested directly. To determine the importance of competition in the community, it has to be demonstrated that some community-level parameter, e.g. species composition, in the absence of competition would differ from the observed species composition.

One of the reasons for the rarity of experimental tests of community-level effects of competition is the lack of appropriate analytical approaches. Goldberg (1994) suggested a new approach to quantify the effect of competition on community-level parameters. She uses monocultures to calculate what the species composition of a community would be in the absence of interspecific competition and then quantifies the difference between this null community and the observed community which is obtained by an additive mixture of all the species grown together. The null community is characterized by combining the abundances of all the species in monocultures to generate an expected species composition in the mixture under the null hypothesis that interspecific competition has no effect on relative abundances (Goldberg 1994). The method quantifies only effects of interspecific competition, because in an additive design the initial density of each species, and therefore initial levels of intraspecific competition are the same in the monoculture and the mixture (Goldberg 1994).

The vegetation of Namaqualand, situated in the north-western corner of South Africa, is particularly rich in ephemeral species (van Rooyen *et al.* 1990). The area is unique in being the only desert in the world to have such an extravagant and diverse spring flower display (Lovegrove 1993).

These displays which attract many tourists each year are created by annual species growing in high densities on abandoned fields and other disturbed areas. Species composition of these ephemeral populations varies considerably between localities and also from year to year (van Rooyen 1988). Temperatures at the time of the first rainfall event determine which species will germinate optimally and the unpredictability in the timing of the first rain therefore results in annual variation in species composition (van Rooyen & Grobbelaar 1982; van Rooyen *et al.* 1992a). The question now arises whether competition between these species affects the relative abundance of the species and consequently the flower display.

The aim of the study was to investigate community-level competition between five Namaqualand pioneer plant species and to determine whether interspecific competition affected the relative abundance of the different species. The five species chosen for this study all occur abundantly in Namaqualand and create mass floral displays. Although they occur in mixed stands they often produce patches where one species dominates.

Materials and Methods

Diaspores of *Dimorphotheca sinuata* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo and *Senecio arenarius* Thunb. were collected at Goegap Nature Reserve near Springbok, and *Heliophila variabilis* Burch. ex DC. and *Ursinia cakilefolia* DC. at Skilpad Wildflower Reserve near Kamieskroon.

Diaspores of all species were sown in May in quartz sand-filled pots (particle size 0.8–1.6 mm), with a volume of 0.125 m^3. The plants were grown out of doors at the University of Pretoria. Each species was sown in a monoculture and in a mixture with all the other species. The monocultures were thinned out to a density of 10 individuals per pot (per 0.25 m^2) after a four-week period. The mixtures were also thinned out from the time of germination to a final density of 10 individuals per species per pot (per 0.25 m^2) after four weeks. The plants were watered daily with tap water and from the fourth week received 4 l Arnon and Hoagland's complete nutrient solution (Hewitt 1952) per pot weekly.

The above-ground parts of each plant were harvested 105 days (± 15 weeks) after sowing and the dry mass per plant was determined after being dried for one week at 60°C to a constant mass.

The following indices were calculated:

(a) RYP, relative yield per plant:

$$RYP_{im} = Y_{im}/(Y_{ii})$$

with RYP_{im} = RYP of species i in a mixture, Y_{im} = yield of species i in a mixture and Y_{ii} = yield of species i in a monoculture.

(b) RY_{im}, expected relative abundance of species i (Goldberg 1994):

$$RY_{im} = Y_{im}/\Sigma Y_{im}$$

with Y_{im} = the final abundance of species i in monoculture and ΣY_{im} = the sum of abundances of all the separate monocultures.

(c) RY_{ix}, actual relative abundance in mixture (Goldberg 1994):

$$RY_{ix} = Y_{ix}/\Sigma Y_{ix}$$

with Y_{ix} = final abundance of species i in mixture and ΣY_{ix} = the sum of abundances of all the species in the mixtures.

A one-way analysis of variance (Bonferroni) was used to test for statistically significant differences ($\alpha = 0.05$). The chi-square goodness-of-fit test was used to test for differences between observed and expected relative abundance values (Steyn *et al.* 1987). Statistical analyses were done with the aid of the STATGRAPHICS computer program (STATGRAPHICS 6.0 1992, Inc, USA.).

Results and Discussion

A very highly significant difference ($P < 0.001$) in the biomass per plant of a species was found between individuals of a species grown in monocultures and in mixtures. In all cases the mass was larger in the monoculture than in the mixture (Table 1) which can be ascribed to the higher density in the mixture. Plots with small populations impose few demands on resources, while plots with larger populations impose higher demands, resulting in more intense competition (Wilson & Tilman 1995).

The RYP values indicated a hierarchy: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia cakilefolia* (Table 1). *Senecio arenarius* is therefore least affected by interspecific competition from the four other species, whereas *U. cakilefolia* is most affected. These RYP values also show that *S. arenarius, D. sinuata* and *O. grandiflorum* are almost equal competitors, and *H. variabilis* and *U. cakilefolia* are similar, but weaker competitors (Table 1). The three species in the first group (*S. arenarius, D. sinuata* and *O. grandiflorum*) are taller and more robust than the two species (*H. variabilis* and *U. cakilefolia*) in the second group. When the effect of neighbours on each other is proportional to their relative sizes, competition is said to be symmetric (Silvertown & Lovett Doust 1993), when the effect is disproportionate to their relative sizes, competition is asymmetric (Weiner 1990). Competition among the species within each of these to groups is likely to be symmetric, whereas competition between species of different groups is probably asymmetric. Oosthuizen *et al.* (1996) investigated three of these species in a replacement series. In two-species mixtures they found that intraspecific competition between individuals of *D. sinuata* or *S. arenarius* was stronger than interspecific competition from individuals of *U. cakilefolia.* The RYP values of *D. sinuata* as well as *S. arenarius* were approximately equal to one when these species were cultivated in a replacement series, indicating that these species utilized the same resources and competition between them was symmetric (Oosthuizen *et al.* 1996). On the other hand, competition between *U. cakilefolia* and either *D. sinuata* or *S. arenarius* was asymmetric (Oosthuizen *et al.* 1996).

Hara (1993) put forward an hypothesis relating community stability and species diversity to the mode of competition. In distinctly multi-layered communities, e.g. forests, the species in the same vertical layer undergo symmetric competition, while competition between the species of different layers is asymmetric. A plant population undergoing strongly asymmetric competition is a stable system, little affected by spatial and temporal variations in environmental conditions. On the other hand, a plant population undergoing symmetric competition (e.g. a mono-layered grassland) is an unstable system highly sensitive to temporal and spatial environmental fluctuations. Although symmetric competition cannot act as a structuring force in plant communities, it brings about variation and hence diversity. The ephemeral populations in Namaqualand lie between these two extreme types of competition. Although the layered nature of the community is not as apparent as in forests, the five species chosen in this study belonged to different height groups. The asymmetric competition between the layers brings about structural stability, but species in each layer compete symmetrically, bringing about species diversity.

In Goldberg's (1994) approach, the effect of interspecific competition is measured by comparing the expected relative abundance to the final (actual) relative abundance (Table 2). A chi-square value of 0.0552 with four degrees of freedom and a significance level of 0.9996 showed that there was no significant difference between the observed and expected values (Table 2). Therefore the overall effect of interspecific competition was not large enough to cause a significant change in the relative abundances of the species in the mixtures. In monocultures, Namaqualand ephemeral species do not show a high degree of density-dependent mortality but are able to counteract the effects of density by exhibiting large fluctuations in the size of the individual (van Rooyen *et al.* 1992b; Oosthuizen 1994). Van Rooyen *et al.* (1992b) found that for *D. sinuata*, total yield per unit area increased with increasing density until a level was reached where yield remained fairly constant at a further increase in density. *Senecio arenarius* seemed to be dependent on optimum densities for optimum performance and densities in excess of the optimum do not produce a larger floral display (Oosthuizen 1994). When pure stands of a species occur in Namaqualand it is probably

Table 1 Above-ground dry mass and relative yield per plant (RYP) for five Namaqualand pioneer plant species

Species	Above-ground dry mass (g) per plant in: Monoculture	Mixture	Relative yield per plant (RYP)
Dimorphotheca sinuata	7.432	3.152	0.424
Heliophila variabilis	3.106	0.822	0.265
Oncosiphon grandiflorum	8.886	3.688	0.415
Senecio arenarius	9.913	4.629	0.467
Ursinia cakilefolia	5.460	1.200	0.220

Table 2 The actual and expected relative abundance values of five Namaqualand pioneer plant species grown in mixtures and monocultures

Species	Actual relative abundance (observed)	Expected relative abundance (expected)
Dimorphotheca sinuata	0.244	0.216
Heliophila variabilis	0.062	0.090
Oncosiphon grandiflorum	0.252	0.248
Senecio arenarius	0.351	0.288
Ursinia cakilefolia	0.091	0.159

because of the local distribution of seed and/or conditions for germination, rather than competition.

Since competition involves two or more organisms utilizing the same resources, it is obvious that competing organisms must have, to some extent, overlapping niches (Barbour *et al.* 1987). If the members of a community compete and their competitive abilities are transitive, the species with the highest competitive rank must eventually exclude all others. If, as in real communities, species actually coexist, then this must be in spite of competition, and not because of it (Silvertown & Dale 1991). Similar species could coexist because interspecific competition is approximately equal to intraspecific competition, thereby weakening interspecific interactions that might otherwise lead to exclusion (Aarssen 1983). Nearly equivalent species may persist indefinitely with minor environmental fluctuations (Keddy 1989; Silvertown & Lovett Doust 1993). This may be the case in Namaqualand which has an unpredictable climate in which the competitive milieu of the species changes each season (van Rooyen 1988). These constantly changing conditions promote coexistence, as no species is able to retain a competitive advantage long enough to exclude the others.

Although interspecific competition is not strong enough to change the species composition or even the relative abundance of the species, competition does affect the performance, in particular, of the inferior competitors (Beneke *et al.* 1992a, b; Oosthuizen *et al.* 1996; Rösch *et al.* 1996a, b). As a consequence, the stronger competitors could dominate the flower display where the species grow in mixtures.

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