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Predicting competitive interactions between pioneer plant species by using plant traits

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Abstract. A competitive effect hierarchy for 15 Namaqualand pioneer plant species was established by using the mean mass of the phytometer (*Dimorphotheca sinuata*) when grown in combination with itself and 14 other species. There were no clear groupings of species in the hierarchy. This competitive hierarchy (gradient) indicated which species are strong competitors (resulting in a low phytometer mass) with *D. sinuata* and which species are weak competitors (resulting in a high phytometer mass).

Each plant species has a certain combination of plant traits which determines its life history strategy and competitive ability. Regressions of various plant traits (measured on plants grown singly) against phytometer biomass indicated which traits were significantly correlated. The traits, most being size-related, were: maximum shoot mass, total mass, stem mass, reproductive mass, leaf area, stem allocation, specific leaf area (SLA), vegetative height \times diameter, leaf area ratio (LAR); and mean number of days to flower initiation. A forward stepwise multiple regression of the significant traits was used to determine an equation to predict competitive effect.

Keywords: Competitive effect hierarchy; *Dimorphotheca sinuata*; Life history strategy; Namaqualand; Phytometer.

Nomenclature: Arnold & De Wet (1993).

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 (Lüscher & Jacquard 1991; Silvertown & Dale 1991; Goldberg & Barton 1992; Lüscher et al. 1992; Duralia & Reader 1993; van der Maarel & Sykes 1993; Huston & DeAngelis 1994; Shipley & Keddy 1994). Variation in relative competitive ability between environments has been proposed to control the species composition of plant communities (Gaudet & Keddy 1988; Wilson & Tilman 1995).

The importance, and even existence, of competition in arid ecosystems has often been questioned (Fowler 1986). Noy-Meir (1979) predicted that the dynamics of populations in deserts would be determined mainly by

the direct responses of individuals to changes in the abiotic environment and that competitive interactions between and within species should be rare. Shmida et al. (1986) reasoned that, under the harsh and unpredictable conditions characterizing desert environments, it would be improbable that densities would increase to levels at which competition would become important. Results obtained in other studies (Klikoff 1966; Friedman & Orshan 1974; Inouye et al. 1980; Kadmon & Shmida 1990a, b) contradict these predictions and suggest that competitive effects may play a major role in determining the dynamics of desert annual plant populations. In a review on the available evidence of competition in arid communities, Fowler (1986) demonstrated that competition certainly does occur in arid and semi-arid regions.

Namaqualand is situated in the arid Northern Cape Province of South Africa. The study area lies within the winter rainfall area and the climate can be described as a warm, dry desert climate, characterised by sparse, irregular winter rainfall and large daily and seasonal temperature fluctuations (Schulze 1965).

Arid and semi-arid regions characteristically support an abundant flora of annual plants which complete their life-cycles in short periods following substantial rainfall (Bowers 1987). Namaqualand is renowned for its many annual and some perennial species, with many tourists visiting the area during the flowering period. The variability of the climate in Namaqualand affects the time of germination, length of the growing season, timing of reproduction and reproductive success (Van Rooyen et al. 1992a; Steyn et al. 1996), as well as the relative abundance of species from year to year.

'Competitive ability' includes both competitive effect, the ability to depress growth and reproduction of neighbours and competitive response – the ability to withstand the negative effects of neighbours (Goldberg 1990). These can both be estimated by growing species in additive mixtures and measuring the reduction in performance of species in mixtures relative to controls (Keddy et al. 1994; Wilson & Gitay 1995). In this study, only competitive effect among a group of 'neighbour' species on a single 'target' species (phytometer) was measured.

Plant traits have been found to be important in determining and predicting a plant's competitive ability (Grime 1979; Gaudet & Keddy 1988; Tilman 1988; Keddy 1989; Grace 1990; Goldberg & Landa 1991; Goldberg & Barton 1992). However, different opinions have been expressed as to what particular plant trait confers a competitive advantage to a species. Gaudet & Keddy (1988) found a strong relationship between competitive ability and plant biomass of, mostly perennial, wetland species. We studied a very different set of species: mostly annual desert species and use a much expanded set of plant traits.

Previous studies on Namaqualand ephemeral plant species have indicated the importance of intra- as well as interspecific competition among a limited number of species (van Rooyen et al. 1992b; Beneke et al. 1992a, b; Oosthuizen 1994; Rösch et al. 1997). The aim of the study was firstly to determine a competitive effect hierarchy of 15 pioneer plant species using *Dimorphotheca sinuata* as phytometer and secondly, to test whether the competitive effect of a species could be predicted from any of 26 plant traits determined for each species grown singly. All the species chosen are abundant in old fields or disturbed veld and contribute toward the production of the mass floral displays in Namaqualand. The phytometer, *D. sinuata*, is one of the most abundant species in Namaqualand and occurs singly or in mixtures in very dense stands.

Material and Methods

The 15 pioneer plant species used in this study are listed in Table 1 (below). Voucher specimens of all species are stored in the H.G.W.J. Schweickerdt Herbarium (PRU) at the University of Pretoria. Identifications were made at the National Herbarium (PRE).

Each of the species was grown singly and four individuals of each species were grown in combination with the phytometer *Dimorphotheca sinuata*. In early April 1994 seeds were sown on quartz sand (particle size 0.8 -1.6 mm) in 1000 cm³ pots, kept outdoors at the University of Pretoria. All plants were watered daily and once a week received Arnon and Hoagland's complete nutrient solution (Hewitt 1952), at full strength, until field capacity was reached.

In the single-plant pots the seedlings were thinned to a density of one per pot, two weeks after sowing. In the mixtures the seedlings were thinned out after four weeks to the desired density of one phytometer, *Dimorphotheca sinuata*, (in the centre) and four individuals of the other species (symmetrically around the centre phytometer).

In September (161 days after sowing) the phytometer

plants were harvested and the dry mass of the leaves, stems and reproductive organs determined. Five replicates were used for each species combination. The mean dry mass of *Dimorphotheca sinuata* in each species combination was used to determine a competition gradient between the species.

Traits

The following phenological attributes were determined for each species grown singly:

- Mean number of days to emergence was calculated by noting when the first seedling in each of 10 pre-selected pots emerged.
- Similarly, the days to bud formation, days to anthesis, days to first ripe fruit and death were determined using five pre-selected pots.
- The collective mass of 100 diaspores of each species was determined and a mean mass per diaspore calculated.

To determine the maximum values for each trait in the first 25 weeks of the plant's life, five replicates of each species were harvested every four weeks, for five harvests, commencing in May. The plant attributes which were measured or calculated – based on the formulae of Květ et al. (1971), Causton & Venus (1981), Hunt (1982), Coombs et al. (1986) and Causton (1991) – at each harvest are given in Table 2. Leaf area was determined with a LiCor LI 3100 leaf area meter and the dry mass of the plant was determined after being dried for one week at 60 °C to a constant mass. The above-ground parts and roots were separated at soil level.

Data collected from the species grown singly was used to determine the maximum value over the harvests for each plant trait for each species. Due to the large variation in life history strategies of the species examined the timing of the peak phase occurred at different harvests. To compare the species at an equivalent stage of phenological development the maximum value of each plant attribute was used. A simple linear regression (Sokal & Rohlf 1982) between these maximum values and the phytometer's mass when grown with the different species indicated a relationship or lack thereof between each plant trait and *D. sinuata*'s total above-ground mass. The traits, indicating significant relationships, were then used in a forward stepwise multiple regression to determine an equation for predicting competitive ability. All statistics were computed using STATGRAPHICS 6.0, 1992, Inc. USA.

Table 1. Namaqualand pioneer plant species used in this study with their maximum shoot biomass (MSB) and the above-ground phytometer dry mass (PDM).

	MSB	PDM
<i>Hypertelis salsoloides</i>	0.037	13.31
<i>Lessertia diffusa</i>	0.163	12.84
<i>Spergula arvensis</i>	0.343	12.75
<i>Conicosia elongata</i>	1.037	12.54
<i>Manulea altissima</i>	0.092	11.74
<i>Grielum humifusum</i>	0.073	11.28
<i>Leysera tenella</i>	0.533	9.22
<i>Gazania lichtensteinii</i>	1.074	8.88
<i>Heliophila rigidiuscula</i>	0.729	7.37
<i>Osteospermum pinnatum</i>	1.891	6.99
<i>Ursinia calenduliflora</i>	1.923	6.76
<i>Foveolina albida</i>	1.216	6.46
<i>Oncosiphon grandiflorum</i>	2.362	5.52
<i>Senecio arenarius</i>	2.242	5.10
<i>Dimorphotheca sinuata</i>	3.333	3.33

Results and Discussion

Basic data for maximum shoot mass (y) and above-ground phytometer dry mass (x), as presented in Table 1, are negatively related to each other (linear regression $y = -0.473x + 13.444$; $r^2 = 0.66$). A competitive effect hierarchy (Fig. 1) was established by using the mean phytometer mass when it was grown in combination with itself and 14 other species. *Dimorphotheca sinuata*'s mass (phytometer) was least when in competition with itself (Fig. 1). Other strong competitors were *S. arenarius*, *Oncosiphon grandiflorum*, *F. albida*, *U. calenduliflora* and *Osteospermum pinnatum* (Fig. 1). The weaker competitors were *Hypertelis salsoloides*, *Lessertia diffusa*, *Spergula arvensis*, *C. elongata*, *M. altissima* and *G. humifusum* (Fig. 1). The weaker competitors are all perennial or facultative perennial species (except *Senecio arvensis*), while the stronger competitors are the annual species. In competition experiments using four other target species at two nutrient levels it was also found that the perennial and facultative perennial species were weaker competitors and that this could be as a result of a delay in their phenological development compared with annuals (Rösch et al. in press). It should, however, be stressed that these results were obtained when both the annuals and perennials were grown from seeds sown at the same time and are not applicable to situations where the perennials have established a year or more previously.

Table 3 shows the correlation coefficients of plant traits, measured when the plant was grown singly, against phytometer biomass. Maximum shoot mass and maximum total mass were highly significantly ($P < 0.001$) negatively related to phytometer biomass (Table 3). Other traits with highly significant ($P < 0.01$), correlations were those of maximum stem mass, maximum reproductive mass and maximum leaf area (Ta-

Table 2. Attributes measured or calculated at each harvest.

Attribute (dimensions)	Symbol or formula
Leaf area (cm ²)	A
Leaf mass (g)	W_l
Stem mass (g)	W_s
Reproductive mass (g)	W_r
Root mass (g)	W_r
Plant height (mm)	
Plant crown diameter (mm)	
Shoot mass (g)	$W_{sh} = W_l + W_s + W_r$
Total plant mass (g)	$W = W_{sh} + W_r$
Relative growth rate (g g ⁻¹ day ⁻¹)	$= (\ln W_2 - \ln W_1) / (t_2 - t_1)$
Leaf allocation (%)	$= W_l / W \times 100$
Stem allocation (%)	$= W_s / W \times 100$
Reproductive allocation (%)	$= W_r / W \times 100$
Root allocation (%)	$= W_r / W \times 100$
Root : Shoot ratio	$= W_r / W_{sh}$
Leaf area ratio (LAR)	$= A / W$
Specific leaf area (SLA)	$= A / W_l$

ble 3). Significant correlations ($P < 0.05$) were obtained with maximum stem allocation, SLA, vegetative height \times diameter, LAR and mean number of days to flower initiation. All significant traits (with the exception of the mean number of days to flower initiation) have a negative correlation coefficient and are related to plant size. Although the traits that were significantly correlated with competitive effect were almost all size related, attributes such as plant height and diameter which also

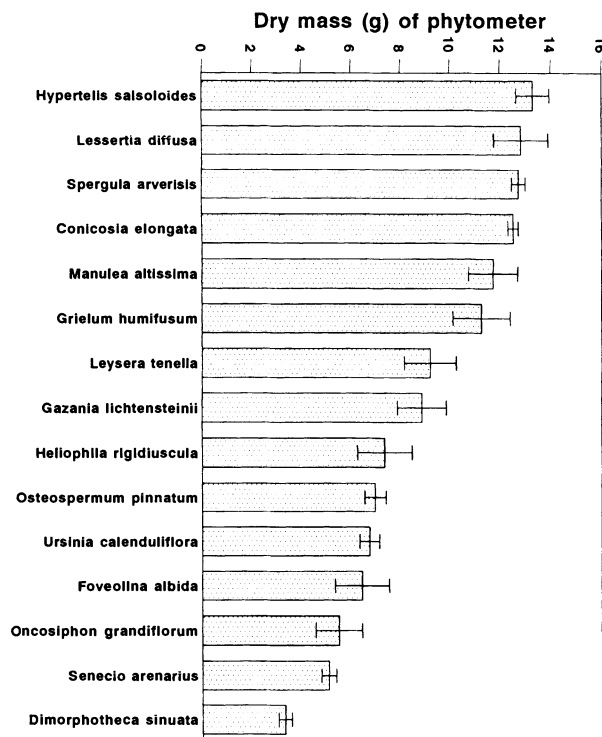


Fig. 1. Competitive effect hierarchy determined by using the above-ground dry mass of the phytometer (*Dimorphotheca sinuata*) when grown in combination with the other species.

Table 3. Linear regressions between plant traits of 15 Namaqualand species and phytometer (*Dimorphotheca sinuata*) above-ground mass

Plant trait	Correlation coefficient (<i>r</i>)
Maximum shoot mass	-0.812 ***
Maximum total mass	-0.800 ***
Maximum stem mass	-0.737 **
Maximum reproductive mass	-0.675 **
Maximum leaf area	-0.661 **
Maximum stem allocation	-0.614 *
Maximum specific leaf area (SLA)	-0.598 *
Maximum vegetative height × maximum diameter	-0.561 *
Maximum leaf area ratio (LAR)	-0.528 *
Mean number of days to flower initiation	0.517 *
Maximum root mass	-0.490 n.s.
Maximum plant height	-0.485 n.s.
Maximum relative growth rate	-0.447 n.s.
Maximum plant diameter	-0.437 n.s.
Maximum leaf mass	-0.431 n.s.
Maximum reproductive allocation	-0.411 n.s.
Maximum height × maximum diameter	-0.324 n.s.
Total number of inflorescences	-0.176 n.s.
Maximum root allocation	0.172 n.s.
Maximum leaf allocation	0.189 n.s.
Number of days to anthesis	0.191 n.s.
Maximum root : shoot ratio	0.200 n.s.
Number of days to death	0.202 n.s.
Seed mass	0.226 n.s.
Number of days to first ripe fruit	0.403 n.s.
Number of days to emergence	0.423 n.s.

P* < 0.05, *P* < 0.01, ****P* < 0.001, n.s. = not significant. Regressions are simple linear regressions with phytometer biomass.

indicate plant size, yielded no significant relationships. Below-ground size, as reflected in root mass and root allocation, seemed less important than above-ground size. While leaf area and the traits relating to leaf area (SLA and LAR) were significantly correlated to competitive effect, leaf mass and leaf allocation yielded no significant correlations.

That size related traits (Table 3) are well correlated with competitive ability is supported by the findings of Gaudet & Keddy (1988) and Keddy (1989). Goldberg & Werner (1983) reasoned that because a large component of depletion ability (competitive ability) is simply total biomass or surface area of resource-acquiring organs, per-plant effects should be strongly related to plant size and species should be much more similar in competitive effect on a per-unit size basis than on a per-individual basis. However, in some studies involving old-field annual species it was found that neighbour identity and not just neighbour biomass, determined target plant performance (McConnaughay & Bazzaz 1990; Tremmel & Bazzaz 1993).

With the exception of mean number of days to flower initiation, all other phenological attributes were not significantly correlated (Table 3). Because plants must accumulate enough resources before they are able to reproduce, this time taken before flower initiation

could be an indication of the plants' ability to accumulate resources faster than its neighbour, thus giving it an advantage and increasing competitive ability.

Maximum vegetative height × maximum diameter was a better indicator of competitive effect than maximum total height × maximum diameter. Many species, for example *Manulea altissima*, produce inflorescences at the tip of long slender stems and thus a more accurate indication of plant size/volume is obtained with vegetative height.

According to Grime, one of the key characteristics of plants that is positively correlated with competitive ability is maximum growth rate (Grime 1979; Grace 1991), yet in this experiment the relationship was not significant (Table 3). Grime's contention was not confirmed in the studies by Roush & Radosevich (1985) and Mynhardt et al. (1994), which showed that LAR showed a strong relationship with relative competitive ability while relative growth rate did not. The latter findings are supported by this study, which indicate a significant relationship between competitive effect and LAR but not with relative growth rate (*r* = -0.528, Table 3).

A forward stepwise multiple regression using maximum shoot mass, maximum leaf area, number of days to flower initiation, maximum stem allocation, LAR, SLA and maximum vegetative height × maximum diameter was used to determine an equation to predict competitive effect. An equation,

$$y = 17.1265 - 0.4183(\text{shoot mass}) - 0.0163(\text{SLA}) \quad (1)$$

was obtained with a *r*² value of 0.83, i.e. 82.77% of plants competitive effect can be accounted for by the use of the equation.

The phytometer chosen in this study proved to be the strongest competitor in the hierarchy. Nielsen (1993, in Keddy et al. 1994) warned that "it is probably best to avoid both strong and weak competitors, since this tends to produce many species with similar competitive performances". They suggest that species of intermediate competitive performance may be the best choice as it will produce the best spread of relative performances, enhancing resolution for the next stages of analysis (Keddy et al. 1994).

Only a single phytometer species was used in this study, so to generalize about the competitive effect hierarchy that was obtained it has to be assumed that neighbour hierarchies are consistent among phytometer species. This was indeed found in a subsequent study (Rösch in press) with four target species, chosen over the whole spectrum of the hierarchy. Concordant competitive effect hierarchies were also reported by Goldberg & Landa (1991), however Keddy et al. (1994) found no such consistency.

If generalizations are to be made on the validity of the results of this experiment, it also has to be shown that the hierarchy obtained does not change over environments. This is a controversial point, which has not been resolved (Tilman 1988; Grime 1988; Mehrhoff & Turkington 1990; Campbell & Grime 1992; Goldberg & Barton 1992; Goldberg & Scheiner 1993; Grace 1993; Goldberg 1994; Keddy et al. 1994; Silvertown et al. 1994). A subsequent study (Rösch in press) to investigate competitive effect and response of 10 Namaqualand pioneer plant species at two nutrient levels, demonstrated that the competitive effect hierarchy of these arid land species was concordant over nutrient levels. The status of the species was, therefore, not affected by the nutrient level and the strong competitors at a high nutrient level were also strong competitors at a low nutrient level (Rösch in press).

Gaudet & Keddy (1988) determined the plant traits of 44 species growing in competition with a phytometer and correlated these traits with the biomass of the phytometer. Using multiple linear regressions they showed that there was a strong relationship between certain plant traits (such as plant biomass, plant height, canopy diameter, canopy area and leaf shape) and competitive ability ($r^2 = 0.74$).

The conclusions reached in this study on desert annuals, incorporating many more plant traits largely confirms those reached by Gaudet & Keddy (1988) on an entirely different set of species, i.e. wetland plants. In spite of the limitations of this study, in which only one phytometer species was used in a single environment, useful results were obtained. The position of a species in a competitive effect hierarchy can be predicted fairly accurately from values obtained on plants grown in a productive environment in the absence of the phytometer.

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