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Competitive effect and response of ten Namaqualand ephemeral plant species at two nutrient levels

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Competitive effect and response hierarchies between Namaqualand pioneer plant species, across two nutrient levels, were constructed. The ten species investigated were: *Arctotheca calendula*, *Dimorphotheca sinuata*, *Foveolina albida*, *Gazania lichtensteinii*, *Heliophila variabilis*, *Leysera tenella*, *Oncosiphon grandiflorum*, *Osteospermum hyoseroides*, *Senecio arenarius* and *Ursinia cakilefolia*. The target species used to construct the rankings were *Dimorphotheca sinuata*, *Gazania lichtensteinii*, *Heliophila variabilis* and *Ursinia cakilefolia*. Competitive effect as well as response rankings were found to be concordant between the two nutrient levels, i.e. soil fertility did not have a significant effect on the competitive effect or response hierarchy, as well as between the target species. Competitive effect and response were significantly negatively correlated only at the low nutrient level. Competition intensity for each pairwise interaction showed no significant difference between target species however, differences were found between neighbour species and nutrient levels, competition intensity being higher at low nutrient levels.

Keywords: Arid, competition intensity, competitive effect, competitive response, nutrient level, pioneer plant species.

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Introduction

The arid Namaqualand covers an area of approximately 55 000 km^2 and is situated in the North-western corner of the Republic of South Africa. The climate is characterised by a hot, dry summer and a sparse and erratic rainfall, falling mainly in winter (Schulze 1965). Namaqualand owes its fame mainly to the display of annual wild flowers, which transforms the normally barren landscape into a land of colour in the spring following a good rainy season (Van Rooyen *et al.* 1992).

Ephemeral plant populations in Namaqualand vary considerably in species composition and abundance from year to year. This variation is primarily due to the unpredictability of the timing of the first rains. In high rainfall years, Namaqualand ephemeral plant species form dense stands and probably compete intensely for limited resources (Van Rooyen 1988; Van Rooyen *et al.* 1992; Oosthuizen *et al.* 1996a, 1996b).

Massive floral displays of ephemerals in Namaqualand are visited by many tourists each year. Competition between these species influences their performance and display (Oosthuizen *et al.* 1996a). Understanding the factors that influence competition are necessary for optimal utilization and management of the ephemeral vegetation as a tourist attraction. Any factor that can give one species a competitive advantage over another has the potential of changing the floral display.

The importance, and even existence, of competition among plants in arid ecosystems has often been questioned (Fowler 1986). Shmida *et al.* (1986) argued that, under the harsh and unpredictable conditions characterising desert environnnents, the probability is very low that densities increase up to levels in which competition becomes important. Other studies (Klikoff 1966; Friedman & Orshan 1974; Inouye *et al.* 1980; Kadmon & Shmida 1990a, 1990b) suggest that competition may play a major role in determining the dynamics of desert annual plant populations.

'Competitive ability' has two components (Goldberg 1990): competitive effect (the ability to depress the growth or reproduction of neighbours) and competitive response (the ability to withstand the negative effects of neighbours). 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).

In this study a phytometer or indicator approach based on a modified additive design was applied in which the relative competitive performance of a species is evaluated by measuring its relative ability to suppress the growth of a common indicator species (the phytometer) (Gaudet & Keddy 1995).

The question as to whether the intensity of competition varies as a function of habitat productivity has not been resolved (Tilman 1988; Grime 1988; Mehrhoff & Turkington 1990; Goldberg & Barton 1992; Campbell & Grime 1992; Grace 1991, 1993; Goldberg & Scheiner 1993; Goldberg 1994; Silvertown *et al.* 1994; Keddy *et al.* 1994; Huston & DeAngelis 1994). Grime (1977, 1979, 1988) and Campbell and Grime (1992), have argued that the traits that determine competitive ability are constant across productivity gradients, whereas Tilman (1977, 1985, 1988) has argued that trade-offs in competitive ability for different resources result in changes in the traits that determine competitive success across productivity gradients (Goldberg & Barton 1992).

The aim of this study was to determine the competitive effects and responses of ten prominently displaying plant species that occur in dense stands in Namaqualand at two fertility levels. The questions to be answered were: Are the competitive effect and response hierarchies consistent a) among target species and b) across nutrient levels?

Material and Methods

Arctotheca calendula (L.) Levyns, *Dimorphotheca sinuata* DC., *Foveolina albida* (DC.) T. Norl., *Gazania lichtensteinii* Less., *Heliophila variabilis* Burch. ex DC., *Leysera tenella* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo, *Osteospermum hyoseroides* (DC.) T. Norl., *Senecio arenarius* Thunb. and *Ursinia cakilefolia* DC. diaspores were collected in Namaqualand. Voucher specimens of all species are kept in the H.G.W.J. Schweickerdt Herbarium (PRU) at the University of Pretoria. Identifications were made by the National Herbarium (PRE) and nomenclature follows Arnold & De Wet (1993).

Diaspores of the ten species were sown, out of doors, in sand filled pots with a volume of 1000 cm^3 in April 1995 at the University of

Table 1 Effect and response relative yield per plant (RYP) values of four target species grown with ten neighbour species at two nutrient levels

Species	*D. sinuata*		*G. lichtensteinii*		*H. variabilis*		*U. cakilefolia*		Mean	
	Response	Effect	Response	Effect	Response	Effect	Response	Effect	Response	Effect
High nutrient level										
Arctotheca calendula	0.569	0.619	0.785	0.322	0.842	0.340	0.715	0.549	0.728	0.458
Dimorphotheca sinuata	0.634	0.667	0.987	0.373	0.917	0.166	0.741	0.501	0.820	0.427
Foveolina albida	0.139	1.240	0.000	0.000	1.085	0.202	0.606	0.784	0.458	0.556
Gazania lichtensteinii	0.085	1.122	0.792	0.561	0.762	0.757	0.778	0.839	0.604	0.820
Heliophila variabilis	0.166	0.917	0.757	0.762	0.487	0.724	0.661	0.631	0.518	0.758
Leysera tenella	0.329	0.871	0.780	0.504	0.622	0.573	0.785	0.965	0.629	0.728
Oncosiphon grandiflorum	1.032	0.645	1.049	0.354	1.181	0.348	0.887	0.554	1.037	0.475
Osteospermum hyoseroides	0.706	0.467	1.183	0.130	0.841	0.382	0.755	0.371	0.871	0.338
Senecio arenarius	0.518	0.627	0.793	0.400	0.850	0.267	0.850	0.363	0.753	0.414
Ursinia cakilefolia	0.863	0.634	0.798	0.676	0.631	0.661	0.577	0.746	0.717	0.679
Mean	0.504	0.781	0.792	0.408	0.822	0.442	0.736	0.630		
Low nutrient level										
Arctotheca calendula	0.405	0.548	0.756	0.325	0.560	0.543	0.590	0.650	0.578	0.516
Dimorphotheca sinuata	0.473	0.507	0.737	0.311	0.637	0.386	0.623	0.468	0.618	0.418
Foveolina albida	0.233	0.807	0.526	0.714	0.518	0.782	0.425	0.680	0.425	0.746
Gazania lichtensteinii	0.311	0.737	0.781	0.720	0.842	0.438	0.569	0.702	0.626	0.649
Heliophila variabilis	0.386	0.637	0.433	0.842	0.423	0.670	0.586	0.620	0.457	0.692
Leysera tenella	0.285	0.602	0.497	0.920	0.637	0.640	0.418	0.807	0.459	0.742
Oncosiphon grandiflorum	0.401	0.740	0.889	0.360	0.673	0.698	0.737	0.595	0.675	0 598
Osteospermum hyoseroides	0.734	0.392	0.988	0.232	0.868	0.186	0.640	0.447	0.807	0.314
Senecio arenarius	0.548	0.485	0.844	0.317	0.808	0.436	0.865	0.481	0.766	0.430
Ursinia cakilefolia	0.468	0.623	0.702	0.569	0.620	0.586	0.561	0.661	0.588	0.609
Mean	0.424	0.608	0.715	0.531	0.659	0.536	0.601	0.611		

Pretoria in pairwise combinations using target and neighbour species. The four target species were *Dimorphotheca sinuata*, *Gazania lichtensteinii*, *Heliophila variabilis* and *Ursinia cakilefolia* Seedlings were thinned out to one individual of one target and one neighbour species per pot. All plants were watered daily with tap water and after the fourth week received, 120 ml Arnon and Hoagland's complete nutrient solution (Hewitt 1952) once a week. Competitive effects and responses of the species were investigated at two nutrient levels i.e. plants of the high nutrient level received 120 ml full-strength nutrient solution and those of the low nutrient level, half-strength.

The above-ground parts of the plants were harvested 119 days (17 weeks) after sowing and the dry mass of each plant was determined after being dried for one week at 60°C to a constant mass. Five repetitions of all treatments were harvested.

The following indices were calculated:

a) RYP, relative yield per plant (Harper 1977):

$$RYP_{ij} = Y_{ij}/(Y_i)$$

where

RYP_{ij} is the RYP of species i in interaction with plant species j.

Y_{ij} is the yield of an individual of species i grown with an individual of species j and,

Y_i is the yield of an individual of species i grown alone.

It should be noted that these measures of relative yield are based on an additive design and not a replacement series design (Keddy *et al.* 1994).

b) I, competition intensity (Keddy *et al.* 1994):

$$I = (1 - RYP_{ij}) + (1 - RYP_{ij})$$

where

I is the intensity of the interaction between species i and j.

A one way analysis of variance (Bonferroni) as well as a multifactor ANOVA were used to test for significant differences at $\alpha = 0.05$ (Sokal & Rohlf 1982). Target species RYP values were used to determine differences between nutrient levels for competitive effect ability while neighbour species RYP values were used for competitive response ability. Differences in competition intensity between nutrient levels, target and neighbour species were also determined using Bonferroni.

Kendall's rank correlations (Steyn *et al.* 1987) were used to test for concordance of ranking of competitive effect and response between nutrient levels and among target species within a nutrient level. Mean RYP values were used to establish one effect and one response matrix for each treatment. The effect matrices include the mean effect of each neighbour species on each target species, mean effect of each neighbour species on all target species (row means of

Table 2 Analysis of variance for relative yield per plant values

Effect	Significance level	Response	Significance level
Main effects		Main effects	
A: Nutrient level	0.7433	A: Nutrient level	0.0026**
B: Target species	0.0000***	B: Target species	0.0000***
C: Neighbour species	0.0000***	C: Neighbour species	0.0000***
Interactions		Interactions	
AB	0.0220*	AB	0.3426
AC	0.7043	AC	0.2986
BC	0.6244	BC	0.0871

* P< 0.05, **P< 0.01, *** P< 0.001 for significant difference

matrix) and the mean effect of all neighbour species on each target species (column means of matrix). Similarly the response matrices include mean response of each neighbour species to each target species, mean response of each neighbour species to all target species (row means of matrix) and the mean response of all neighbour species to each target species (column means of matrix) (Keddy *et al.* 1994). Species within each effect and response matrix are ranked with one corresponding to the species with the highest competitive performance (i.e. a neighbour species with a low mean competitive effect value or high mean competitive response value).

Statistical results were obtained with the aid of the STATGRAPHICS computer program (STATGRAPHICS 6.0 1992, Inc. USA.)

Results and Discussion

Relative yield per plant values for competitive effect and response

The RYP values for all the pairwise combinations were used to establish one effect and one response matrix for each nutrient level (Table 1). A multifactor analysis of variance showed no significant difference in effect RYP values between the two nutrient levels, however, a very highly significant difference ($P < 0.001$) between target species and between neighbours was found (Table 2). Effect RYP values between target species differed significantly between *D. sinuata* and *G. lichtensteinii*, between *D. sinuata* and *H. variabilis*, and between *U. cakilefolia* and *G. lichtensteinii*. No significant difference in competitive effect or response could be demonstrated between *Dimorphotheca sinuata* and *Ursinia cakilefolia* within a nutrient level. Local farmers maintain that at high nutrient levels *D. sinuata* is favoured whereas *U. cakilefolia* has an advantage at low nutrient levels. Although not significant, results in Table 1 lend support to this theory by indicating that *D. sinuata* was the stronger effect competitor at the high nutrient level while *U. cakilefolia* was the stronger competitor at the low nutrient level.

In the case of the response RYP values, a multifactor ANOVA showed a highly significant difference ($P < 0.001$) between target species and between neighbour species and a significant difference ($P < 0.05$) between the different nutrient levels (Table 2). Between the target species, competitive response of *D. sinuata* differed significantly from the three other target species. At the low nutrient level the measured response (RYP) of all four target species was less than at the high nutrient level.

Competitive effects of the ten species were significantly correlated ($P < 0.05$) among the two nutrient levels (Figure 1).

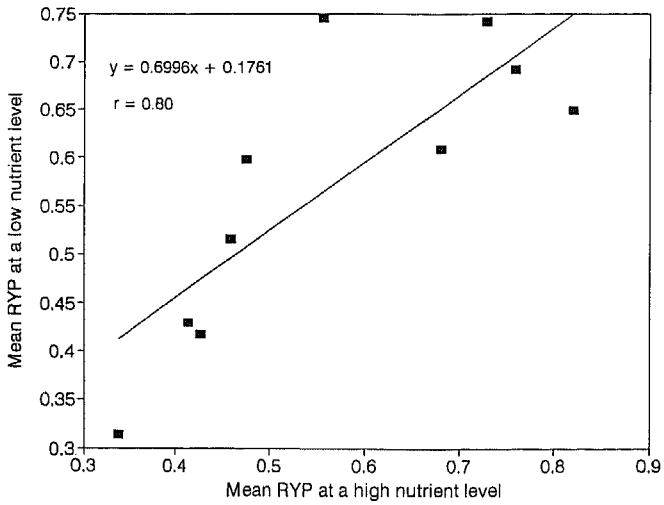

Figure 1 Correlation between relative competitive effect for ten Namaqualand pioneer plant species at two nutrient levels.

Similarly, there was a significant correlation between the competitive responses at the two nutrient levels ($P < 0.05$, Figure 2). Thus nutrient level does not affect the status of the species i.e. the strong competitors at the low nutrient level were also the strong competitors at the high nutrient level and the same applies for the weaker competitors. In their study on wetland plants, Keddy *et al.* (1994) found competitive effect to be significantly correlated wheras competitive response was not.

At the high nutrient level competitive effect and response were not significantly ($P > 0.05$) negatively correlated (Figure 3), whereas the negative correlation was significant ($P < 0.05$) at the lower nutrient level (Figure 4). Therefore, at a low nutrient level a strong effect competitor is a weak response competitor and vice versa although this is not the case at the high nutrient level. Non-significant correlations between competitive effect and response were reported by Keddy *et al.* (1994) and Goldberg and Landa (1991), although other experiments have revealed different results: a positive relationship was found by Goldberg and Fleetwood (1987) and a negative relationship was found by Miller and Werner (1987).

Competitive hierarchy

Kendall's rank correlation coefficient indicated that the mean competitive effect and response rankings of each target species

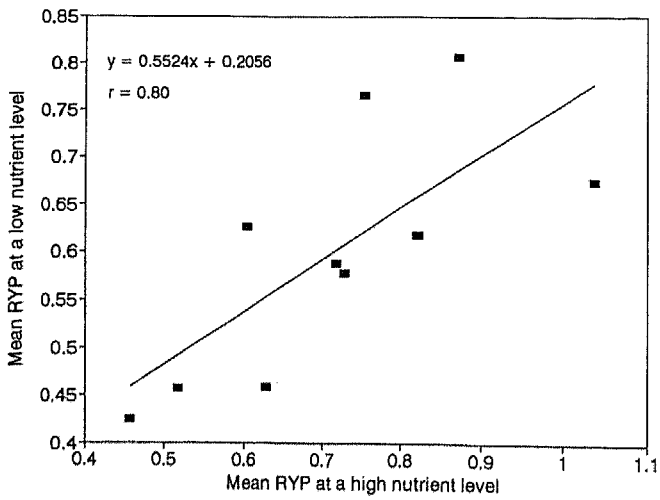

Figure 2 Correlation between relative competitive response for ten Namaqualand pioneer plant species at two nutrient levels.

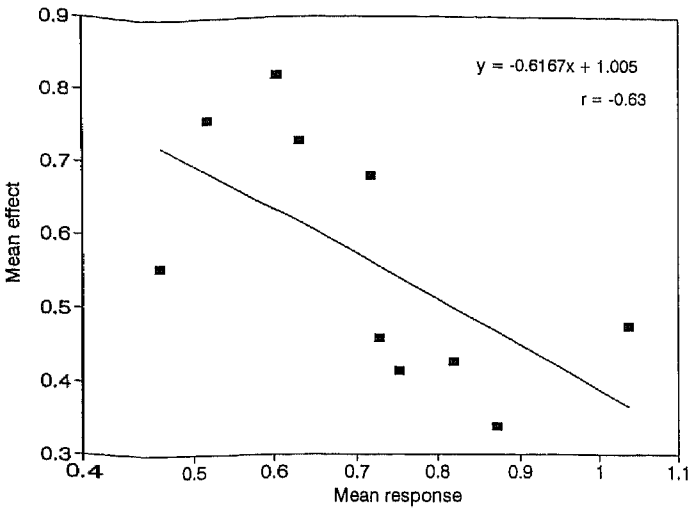

Figure 3 Correlations between mean effect and response in the high nutrient treatment.

between the two nutrient levels were concordant ($P < 0.001$, Table 3). The mean effect and response of all neighbours on each target species, across the two treatments were also concordant ($P < 0.05$, Table 3). When separated into target species, the rankings were concordant among four targets across the two nutrient levels ($P < 0.05$, Table 3).

As was the case in this study, Goldberg and Landa (1991) found hierarchies of competitive effect to be highly concordant among neighbour species, suggesting that rankings of competitive effects are independent of the target species. The hierarchy found in this study agrees with the hierarchies produced in other studies on Namaqualand pioneer plant species (Oosthuizen 1996a, 1996b; Rösch 1997a; Rösch 1997b). Harper (1977) states that competitive hierarchies are consistent and Keddy *et al.* (1994) have also shown that competitive effect hierarchies are unaffected by soil fertility. Because of the consistency of competitive effect hierarchies Keddy *et al.* (1994) have suggested concentrating on determining which traits enable some plants to compete better than others. This was done in a study of fifteen Namaqualand pioneer plant species by Rösch *et al.* (1997b). It was found that the traits best related to competitive effect ability were all size related indicating that the larger the plant the stronger it acts as a competitor (Rösch *et al.* 1997b).

However, several studies have shown that competitive hierarchies change over time and within the same environment (Connolly *et al.* 1990; Menchaca & Connolly 1990), and therefore which traits determine competitive ability must depend on factors such as relative sizes or stages of the life cycle in the competing plants (Goldberg & Landa 1991). Because a large component of depletion ability (competitive ability) is total biomass or surface area of resource acquiring organs, per plant effects should be strongly related to plant size and species should be more similar in competitive effect on a per-unit size basis than on a per-individual basis (Goldberg & Werner 1983).

Competitive response in this study showed the same pattern as competitive effect i.e. perfect agreement between treatments. Goldberg and Landa (1991) found that hierarchies in competitive response among target species were similar regardless of neighbour species. Positions in competitive response hierarchies should depend on either relative abilities to tolerate depleted resource levels due to the presence of neighbours or relative abilities to avoid experiencing depleted resource levels because of pre-emption of resources from neighbours (Goldberg & Landa 1991). Which of these is more important should be related to relative sizes of targets and neighbours (Goldberg 1990).

In contrast, Keddy *et al.* (1994) found that response rankings were not concordant across environments when the rankings were based on all three indicator species and there was no concordance across the environments for any of the species analyzed separately.

According to the Kendall's rank correlation values competitive effect and response rankings (using mean effect and response on all target species) for both nutrient levels are in perfect disagreement (not concordant) with one another ($P < 0.001$, Table 3). That is, if a species is a good effect competitor it is also a weak response competitor. Across targets, competitive effect and response (in both treatments) are also in perfect disagreement ($P < 0.05$, Table 3). Results by Keddy *et al.* (1994), however, indicate that one cannot generalize from competitive effect to competitive response.

In some studies it has been found that the choice of indicator species had no effect on the results (Gaudet & Keddy 1988). Others have found that the choice of indicator species affects the magnitude of competition (Wilson & Keddy 1986; DiTommasio & Aarssen 1989; Wilson 1993), the relative importance of below and above ground competition (Putz & Canham 1992), and the importance of competition (Reader & Bonser 1993). Keddy *et al.* (1994) suggest that when choosing target species it is probably best to avoid both strong and weak competitors, since this tends to produce many species with similar competitive performances. A species of intermediate competitive performance may be the best choice as it will produce the best spread of relative competitive performances (Keddy *et al.* 1994). In this case the use of

Table 3 Kendall's competitive effect and response rankings (coefficients and significance levels)

Target species	Effect coefficient	Effect significance level	Response coefficient	Response significance level
**Dimorphotheca sinuata*	1.0000	0.0001	1.0000	0.0001
**Gazania lichtensteinii*	1 .0000	0.0002	0.7222	0.0067
**Heliophila variabilis*	1.0000	0.0001	0.9888	0.0001
**Ursinia cakilefolia*	0.9556	0.0001	1.0000	0.0001
*Mean	1.0000	0.0001	1.0000	0.0001
**Mean across targets	1.0000	0.0415	1.0000	0.0415

*Competitive effect and response tested for concordance between two nutrient levels

**Competitive effect and response tested for concordance between two nutrient levels across four targets

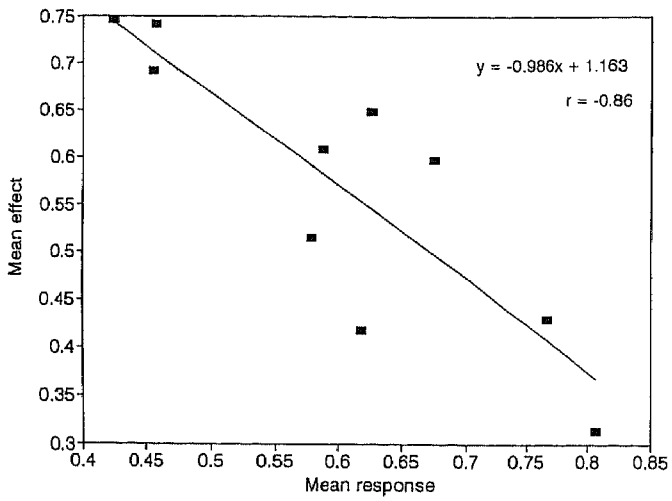

Figure 4 Correlations between mean effect and response in the low nutrient treatment.

species with a range of competitive abilities produced effect and response hierarchies that were consistent among the four species and the two treatments thus the choice of target species did not affect the resulting hierarchies.

Competition intensity

Mean competition intensity for each pairwise interaction showed no significant difference between target species (Table 4). However, between nutrient levels and neighbours there was a significant difference in competition intensity ($P < 0.05$, Table 4). Competition intensity was greater at the low nutrient level than at the high nutrient level. However, it was found by other authors (Campbell & Grime 1992; Wilson & Tilman 1993) that competition intensity does not vary with nitrogen addition.

Conclusion

Individual competitive ability can be compared between species in two distinct ways: in their competitive effect or ability to suppress other individuals and in their competitive response or ability to avoid being suppressed (Goldberg & Landa 1991). Relative yield per plant (RYP) values for competitive effect differed significantly between target species and between neighbour species but not between nutrient levels. In contrast RYP values for competitive response differed significantly between target species and neighbour species as well as between nutrient levels.

Table 4 Analysis of variance for competition intensity

Competition intensity	Significance level
Main effects	
A: Nutrient level	0.0169 *
B: Target species	0.2128
C: Neighbour species	0.0452*
Interactions	
AB	0.1053
AC	0.6090
BC	0.3945

* $P < 0.05$ for significant difference

Competitive response therefore seemed more sensitive to nutrient levels than competitive effect. This study concluded that competitive effect hierarchies as well as competitive response hierarchies across two nutrient levels and between targets within a nutrient treatment are concordant. Competitive effect and response hierarchies within nutrient levels were found to be in perfect disagreement. Competition between Namaqualand ephemeral plant species is such that the hierarchy is unaffected by the choice of target species and unaffected by nutrient level i.e. soil fertility will not change a species' ranking.

Competitive intensity for each pairwise interaction showed no significant difference within target species, however differences were found between nutrient levels and neighbour species.

Extrapolating from experimental results to field conditions should always be done with caution, since there are many more factors interacting in the field. It can however, be assumed that the status of these Namaqualand ephemeral plant species is not affected by nutrient level and a strong competitor at a low soil fertility should remain a strong competitor at a high soil fertility. At a low soil fertility a strong effect competitor also acts as a weak response competitor, while this is not the case at a high soil fertility. Competition intensity is stronger at the low nutrient level and species show less competitive response than at the high nutrient level i.e. their ability to be suppressed by neighbours is reduced.

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