

## Fruit polymorphism in ephemeral species of Namaqualand. VI. Intermorphic competition among plants cultivated from dimorphic diaspores

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Plants raised from disc and ray diaspores of *Dimorphotheca sinuata*, a polymorphic annual species from Namaqualand, were grown in replacement series. There were four plants per pot with disc to ray ratios of 4:0, 2:2 and 0:4. The plants were grown under different moisture and nutrient regimes. Disc plants were more aggressive than ray plants and thus the stronger competitors. Disc plants had a higher total dry matter in mixture than in monoculture under high moisture conditions. There was no difference in production between mixtures and monocultures of the ray plants. Ray plants were influenced more by disc plants than disc plants by ray plants. Both disc and ray plants were more successful when water and nutrients were freely available. Moisture was the main factor influencing intermorphic competition.

Plante gekweek vanaf buis- en lintdiaspore van *Dimorphotheca sinuata*, 'n polimorfiese spesie van Namakwaland, is gekweek in vervangingsreeks. Daar was vier plante per pot met buis-tot-lint-verhoudings van 4:0, 2:2 en 0:4. Die plante is gekweek onder verskillende vog- en voedingstoestande. Buisplante was aggressiewer as lintplante en dus sterker kompeteerdere. Buisplante het onder hoë vogtoestande 'n hoër totale droë massa in mengsels as in suiwer stande gehad. Daar was geen verskil in die produksie van gemengde en suiwer stande van lintplante nie. Lintplante is meer beïnvloed deur buisplante as buisplante deur lintplante. Beide die buis- en lintplante was meer suksesvol as voldoende water en voeding beskikbaar was. Vog was die hoof faktor wat intermorfiese kompetisie beïnvloed het.

**Keywords:** Arid environment, *Dimorphotheca sinuata*, moisture, Namaqualand, nutrients.

### Introduction

One of the major factors influencing growth and survival of individual plants is competition from neighbours (Firbank & Watkinson 1985). Competition is described as a purely physical process and arises from the reaction of one plant upon the physical factors about it and the effects of the modified factors upon its competitors (Clements *et al.* 1929). Two plants do not compete with each other as long as water, nutrients and light are in excess of the needs of both plants. When the immediate supply of a single necessary factor falls below the combined demands of the plants, competition starts (Hall 1974; Wilson 1988).

Species living in a mixture may have different nutrient requirements, morphologies and life histories and may modify their environment in ways that make it more suitable for another species, without a corresponding loss to themselves (Menchaca & Connolly 1990). It is generally accepted that in order to coexist more than transiently, species must differ, because the intensity of competition increases with increasing similarity between interacting plants (Aarssen 1984, 1989; Johansson & Keddy 1991). Another view, held by Goldberg and Werner (1983), is that in most communities, individuals of any one species will come into contact with plants of many different species. Therefore, it is unrealistic to expect strong selection for reduction of overlap in resource utilization between any particular pair of species because of variable and possibly opposing selection pressures depending on the array of neighbours. Aarssen (1989) interpreted coexistence at the species level as a consequence of selection resulting from interactions at the individual level within local neighbourhoods. Selection for competitive

ability is an evolutionary change as a consequence of selection from competition and depends upon within-species genotypic variation (Aarssen 1989).

Two contrasting experimental designs, additive and replacement series, have been used to study the interactive behaviour of components in mixed stands (Jolliffe *et al.* 1984). The additive design has been criticized because the effects of frequency and density are confounded (Harper 1977). In the replacement series, a constant total density of plants is used and the planting density of one species is proportionately decreased as the planting density of the second species is increased (De Wit 1960). This design has proved popular and has been widely used in mixed-population studies (*e.g.* Hall 1974; Inouye & Schaffer 1981; Fowler 1982; Jolliffe *et al.* 1984; Firbank & Watkinson 1985; Venable 1985; Connolly 1986; Wilson 1988; Aarssen 1989; Reader & Best 1989; Rejmánek *et al.* 1989; Roush *et al.* 1989; Taylor & Aarssen 1989; Connolly *et al.* 1990; Menchaca & Connolly 1990; Akey *et al.* 1991; Johansson & Keddy 1991).

Polymorphism, the production of two or more diaspore types on the same individual plant, occurs in *Dimorphotheca sinuata* DC. The differences in anatomy (Beneke 1991; Beneke *et al.* 1992a&b), germination (Beneke *et al.* 1992c) and growth (Beneke *et al.* 1992d) of the two diaspore types have already been described elsewhere. To explain the importance of polymorphism in *D. sinuata* it seemed important to know which of the two morphs was the superior competitor and whether a particular morph would have an advantage under specific environmental conditions. The objective of this paper was thus to determine (a) whether

there was any difference in production between pure stands and mixtures of plants cultivated from the different diaspore types; (b) whether biomass allocation differed between plants growing in pure stands and mixtures; (c) which of the two diaspore types developed into the stronger competitor; and (d) whether water and nutrient stress have any effect on the outcome of competition.

## Materials and Methods

Diaspores of *Dimorphotheca sinuata* DC. were collected in August 1989 in the Goegap Nature Reserve. The reserve is situated approximately 10 km south-east of Springbok. According to the classification of Acocks (1988), the reserve lies in the Namaqualand Broken Veld, an arid zone known as Namaqualand, in the north-western part of the Cape Province in the Republic of South Africa. This area has an annual rainfall of 162 mm, falling mainly in the winter, and an annual temperature of 17.7°C measured at Okiep (Weather Bureau 1988).

Plants grown from disc and ray diaspores were cultivated in replacement series (De Wit 1960) at a total density of four plants per pot. Plants grown from disc diaspores are hereafter called disc plants and those from ray diaspores, ray plants.

Since intact ray diaspores germinate very poorly owing to mechanical and chemical resistance of the pericarp (Beneke *et al.* 1992c), germination was improved by excising the embryos. These excised disc and ray diaspore embryos were sown directly into pots with a volume of 1.25 dm<sup>3</sup> which had been filled with 1.638 kg of quartz sand (particle size 0.8 – 1.6 mm). All plants were grown out of doors at the University of Pretoria. The effect of four different treatments, combinations of moisture and nutrient regimes, on competition between ray and disc plants was examined.

### (a) High-moisture – high-nutrient regime (HM–HN)

Plants were watered daily with the amount of water needed to bring the moisture level to pot capacity. Plants received Arnon & Hoagland's complete nutrient solution (Hewitt 1962) on the same day as the low-moisture treatments. Enough nutrient solution was added to displace all the moisture present in the pot with fresh solution.

### (b) High-moisture – low-nutrient regime (HM–LN)

Same as (a) but a dilution of Arnon & Hoagland's complete nutrient solution, consisting of one part solution to two parts water, was used.

### (c) Low-moisture – high-nutrient regime (LM–HN)

Pots were left to dry to one-third of field capacity whereafter the amount of water was added to bring the moisture level to pot capacity. Every second watering enough Arnon & Hoagland's complete nutrient solution was added to displace all the moisture present in the pot.

### (d) Low-moisture – low-nutrient regime (LM–LN)

Same as (c) but a third strength nutrient solution was used.

Five months after sowing, five replicates for each treatment were harvested and the leaf area (cm<sup>2</sup>) and dry mass (g) values were determined on a per plant and per pot basis for each respective plant morph.

A LiCor LI 3100 leaf area meter was used to determine the leaf area. Plant parts were dried at 60°C, for one week, to a constant mass to determine the dry mass. Only the

above-ground parts were harvested since the roots of the plants were intertwined.

From the above-mentioned values the following values were calculated: (a) Cb, competitive balance index (Wilson 1988); (b) RYP, relative yield per plant (Fowler 1982); (c) RYT, relative yield total (Fowler 1982); (d) A, aggressivity (Mc Gilchrist & Trenbath 1971); (e) *k*, relative crowding coefficient (Hall 1974); (f) species monoculture response (Jolliffe *et al.* 1984); (g) species mixture response (Jolliffe *et al.* 1984); (h) relative monoculture response (Jolliffe *et al.* 1984); (i) relative mixture response (Jolliffe *et al.* 1984); (j) SA, biomass allocation to stems; (k) LA, biomass allocation to leaves; (l) RA, biomass allocation to inflorescences.

A one-way analysis of variance, ANOVA, was used to test for statistical significant differences at  $p = 0.05$ . For paired comparisons among species and treatments, the Scheffé test was used (Steyn *et al.* 1987). Statistically homogeneous groups are shown under the figures. Asterisks in graphs indicate statistically significant differences between plants of the different diaspore types.

## Results and Discussion

### Dry-matter production

Disc plants of *D. sinuata* in a mixture with ray plants produced significantly ( $p = 0.05$ ) more total above-ground dry matter per plant than in monoculture in the high-moisture treatments (Figures 1a & 1b). However, in the moisture stress treatments there were no significant differences (Figures 1c & 1d). There were no significant differences ( $p = 0.05$ ) in total dry-matter production per plant between monocultures and mixtures of ray plants in any of the treatments (Figures 1a – 1d). Total dry-matter production in monocultures of the plants cultivated from the two diaspore types did not differ significantly ( $p = 0.05$ ) in any of the treatments (Figures 1a – 1d). Menchaca and Connolly (1990) found that *Lolium perenne* L. cv. S32 performance was enhanced in mixture by comparison with a pure stand of *Lolium perenne*, but in *Trifolium repens* L. cv. N.Z. Huia the total yield was greatest in a pure stand.

Disc plants of *D. sinuata* cultivated in a mixture produced significantly ( $p = 0.05$ ) more total dry mass than ray plants in a mixture in the high-moisture treatments (Figures 1a & 1b). Disc plants in a mixture produced significantly ( $p = 0.05$ ) more total dry mass per plant in the HM–HN treatment than disc plants in any of the other treatments (Figures 1a – 1d). Ray plants in a mixture in the HM–HN treatment produced significantly ( $p = 0.05$ ) more dry mass per plant than other ray plants cultivated in the nutrient stress treatments (Figures 1a, 1b & 1d). According to Venable (1985), disc plants of *Heterotheca latifolia* Buckl. produced more total dry matter in a mixture than in a pure stand whereas ray plants produced less. When the watering regime is favourable and competition is intense, disc plants of *Heterotheca latifolia* are favoured, but under dry conditions the ray plants are superior, though they never attain the total dry-matter production that disc plants do in favourable conditions (Venable 1985).

Plants cultivated in a mixture can be suppressed by their neighbours. The degree of suppression depends on several factors such as (a) the effectiveness of each species in competing for limiting sources; (b) the responsiveness of

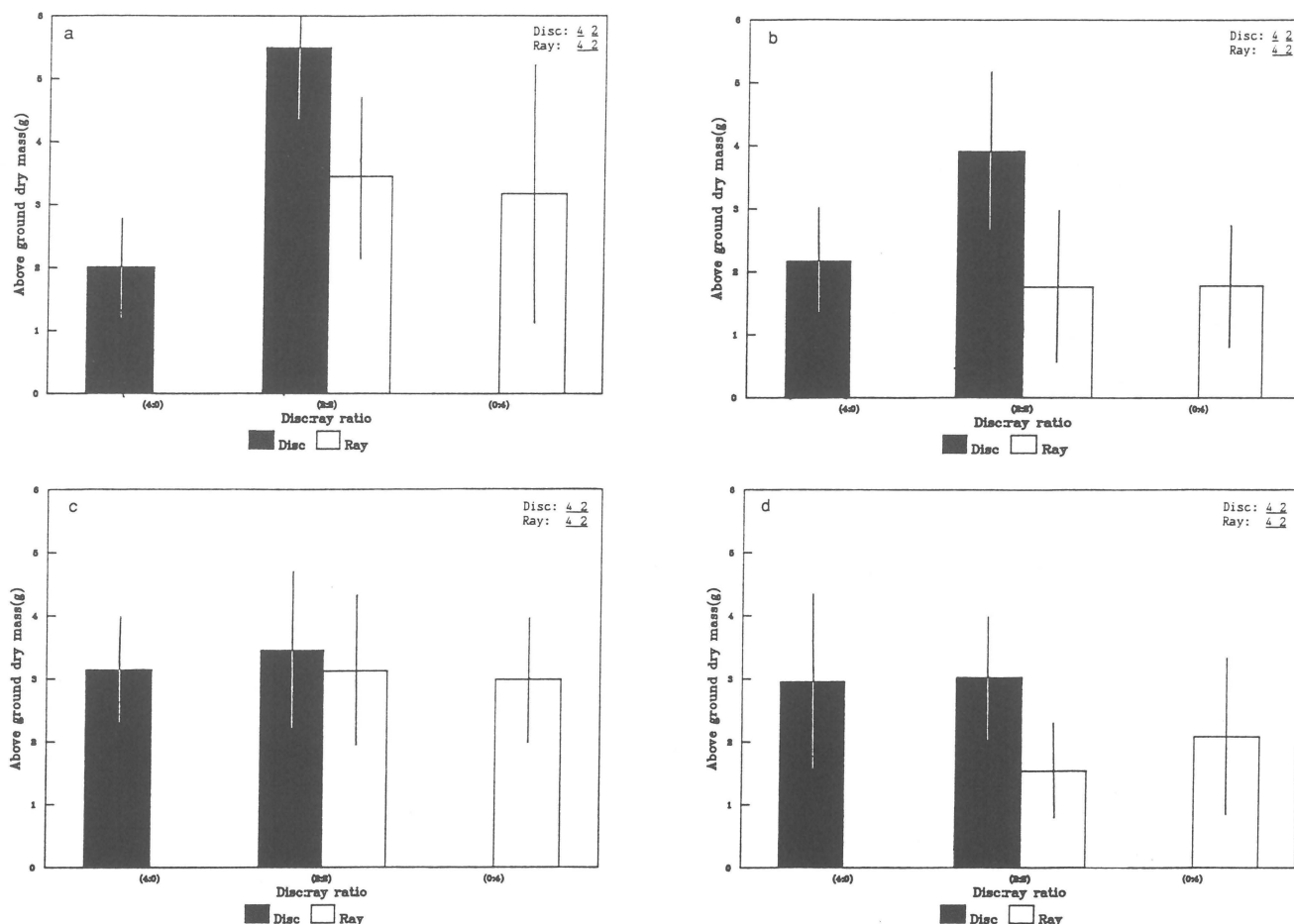


Figure 1 The total above-ground dry-matter production per plant of disc and ray plants of *Dimorphotheca sinuata* in (a) a high-moisture – high-nutrient regime (HM–HN); (b) a high-moisture – low-nutrient regime (HM–LN); (c) a low-moisture – high-nutrient regime (LM–HN); and (d) a low-moisture – low-nutrient regime (LM–LN). Bars represent the standard deviations. Statistically homogenous groups are indicated under the figures.

each species to resource supply; and (c) the effect of different species proportions in the mixture on the preceding factors. Wilson (1988) stated that an increase in yield in a mixed stand can indicate niche separation, which is of potential agricultural significance as a means of obtaining higher yields than with monocultures.

Replacement model

The model illustrated in Figure 2 is a schematic representation applicable to most of the series in this study. According to this model the influence of species A on species B is stronger than the influence of species B on species B. Therefore, the interspecific competition between A and B is stronger than the intraspecific competition between individuals of species B. The influence of species B on species A is less than the influence of species A on species A. Therefore, the intraspecific competition between individuals of species A is stronger than the interspecific competition between A and B. If there had been a linear relationship, the growth of the individual would not be affected by the identity of the neighbour and there would be no inter- or intraspecific competition effect on the species (De Wit 1960).

Since it is a basic assumption for conventional replacement series experiments and their analysis, that the plant populations must be grown at a density beyond the point of

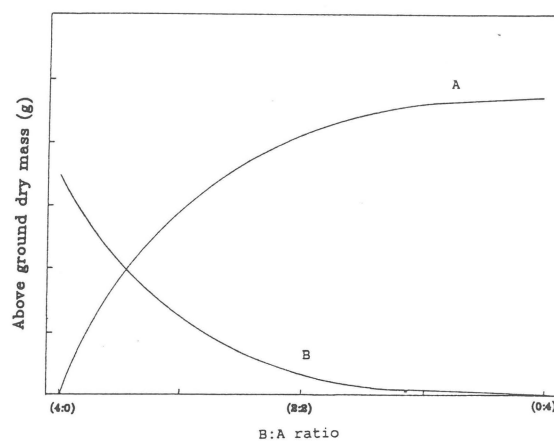
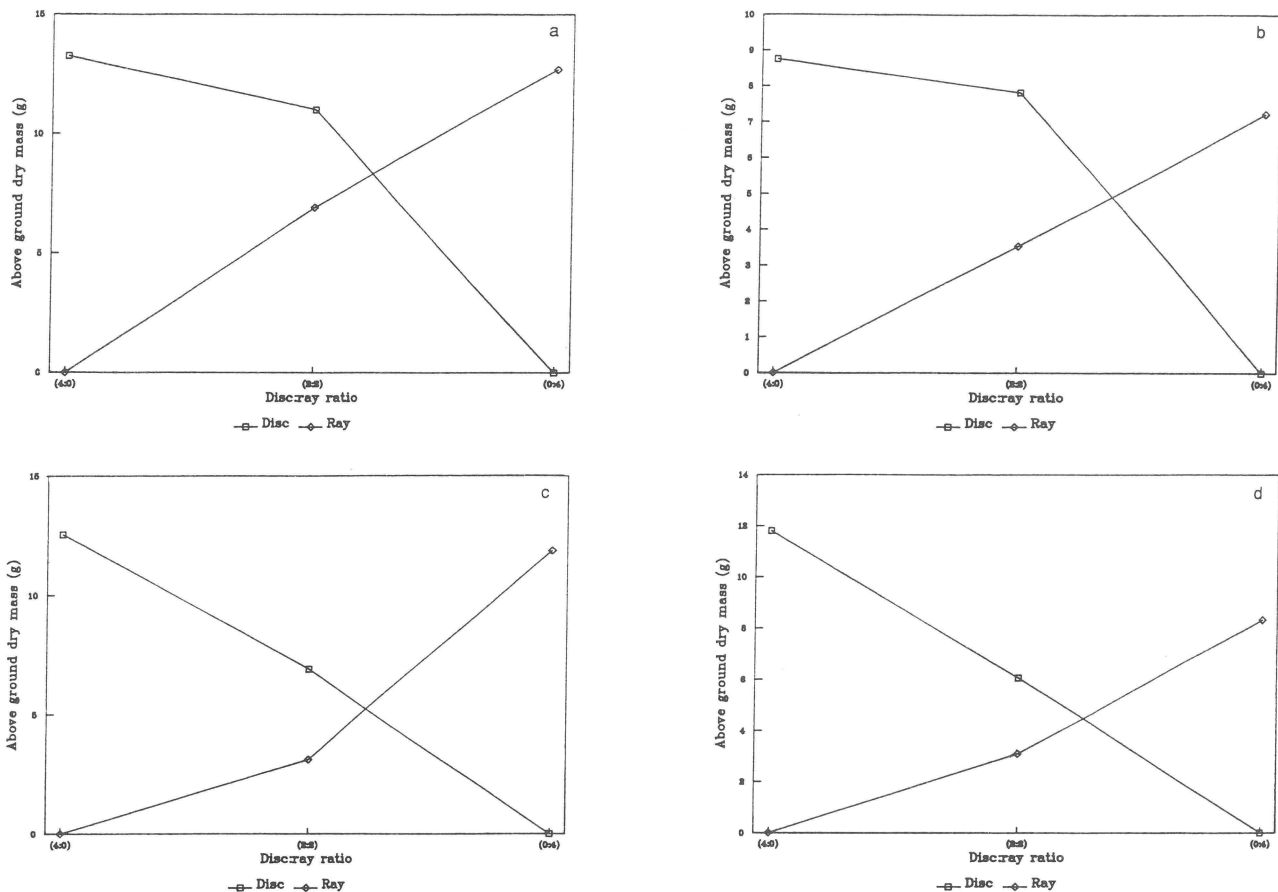


Figure 2 A schematic representation of the replacement model (De Wit 1960) applicable to most of the series.

constant final yield (Roush *et al.* 1989; Taylor & Aarssen 1989), the experiments were conducted at a density of four plants per pot, at which density the constant final yield was already reached in both the disc and ray plants (Beneke *et al.* 1992e).

Figures 3a – 3d illustrate the influence of inter- and intra-morphic competition on plants cultivated from the disc and ray diaspore types in combinations of different moisture and



**Figure 3** The influence of inter- and intramorphic competition on disc and ray plants of *Dimorphotheca sinuata* in (a) a high-moisture – high-nutrient regime (HM–HN); (b) a high-moisture – low-nutrient regime (HM–LN); (c) a low-moisture – high-nutrient regime (LM–HN); and (d) a low-moisture – low-nutrient regime (LM–LN).

nutrient treatments. The intramorphic competition between individuals of disc plants was stronger than the intermorphic competition with individuals of ray plants in the high-moisture treatments (Figures 3a & 3b). Ray plants were not influenced by the identity of neighbouring plants. In the moisture stress treatments (Figures 3c & 3d), disc plants were not influenced by the identity of their neighbours, but the intermorphic competition between ray and disc plants was stronger than intramorphic competition between individuals of the ray plants.

It seems as if nutrients do not influence intra- or intermorphic competition between plants cultivated from the different diaspore types. However, in the literature (Fowler 1982; Connolly 1986; Reader & Best 1989) there is evidence that adding nutrient resources intensifies competition so that the yield per plant of the weaker competitor is even more reduced.

#### Competitive balance

The relative competitive ability of the components in a mixture is expressed by the competitive balance index (Cb) (Wilson 1988). A Cb value of zero indicates no competition or equal competitive abilities. Any other value indicates that one species has a higher competitive ability than the other.

The values of the Cb index of both the disc and ray plants of *D. sinuata* are shown in Table 1. The competitive ability of the disc plants was greater than that of the ray plants in all the moisture and nutrient treatments.

**Table 1** The Competitive Balance Index (Cb) of disc and ray plants of *Dimorphotheca sinuata*

Treatments	Disc plants	Ray plants
HM–HN	0.41	–0.41
HM–LN	0.60	–0.60
LM–HN	0.05	–0.05
LM–LN	0.33	–0.33

Relative yield per plant (RYP) and the relative yield total (RYT)

The relative yield per plant (RYP) is the average performance of an individual of the same species in a pure stand of the same total density (Fowler 1982). The relative yield total (RYT) is the weighted average of the relative yields of the mixture components.

If the growth of an individual is not affected by the identity of the neighbouring individuals, then RYP is equal to 1. A RYP greater than 1 implies that intraspecific competition with its own species is stronger than interspecific competition with the other species. A RYP smaller than 1 implies that intraspecific competition is less than interspecific competition (Fowler 1982).

Table 2 shows RYP and RYT values for plants cultivated from different diaspore types in various combinations of moisture and nutrient treatments.



**Table 2** The relative yield per plant (RYP) and relative yield total (RYT) of disc and ray plants of *Dimorphoteca sinuata* in a replacement series under different moisture and nutrient regimes

Series	RYP, competitive plant types		RYT
	Disc	Ray	
HM-HN			
4D:0R	1.00	0.00	1.00
2D:2R	1.66	1.09	1.38
0D:4R	0.00	1.00	1.00
HM-LN			
4D:0R	1.00	0.00	1.00
2D:2R	1.79	0.98	1.39
0D:4R	0.00	1.00	1.00
LM-HN			
4D:0R	1.00	0.00	1.00
2D:2R	1.10	0.53	0.81
0D:4R	0.00	1.00	1.00
LM-LN			
4D:0R	1.00	0.00	1.00
2D:2R	1.03	0.74	0.88
0D:4R	0.00	1.00	1.00

The results obtained with the RYP values confirmed those found in the previous models. Relative yield per plant was greater than 1 for the disc plants in the HM treatments (Table 2). The intramorphic competition between individuals of disc plants was stronger than the intermorphic competition with individuals of ray plants. The RYP values of ray plants in the HM treatments were approximately 1, and the plants were not affected by the identity of the neighbouring plants. In the water stress treatments the RYP values of the disc plants equaled 1, and the plants were thus not affected by the identity of the neighbours (Table 2). In contrast, RYP values of ray plants were smaller than 1, indicating that intramorphic competition between individuals of ray plants was less than intermorphic competition with disc plants. Water seemed to be the main factor which the two plant types competed for in the pots.

The RYT is a measure of resource use and reflects the sum of the proportional changes in yield in a mixture, and, if the species compete for the same resources, will be equal to 1. If two species use somewhat different resources, the proportional gain to individuals of one species from growing in a mixture will be greater than the loss to the other, and the RYT will be greater than 1 (Fowler 1982). In such a situation both species may have a RYP greater than 1. A RYT greater than 1 implies some degree of niche differentiation, and the possibility of coexistence of the species involved (Fowler 1982). According to Trenbath (1974), a RYT greater than 1 is rare in agricultural experiments, except when fixation of nitrogen by legumes is involved. It is more common in mixtures of coexisting species from natural communities, since such species may have coevolved niche differentiation. A RYT smaller than 1 implies mutual antagonism (Harper 1977).

The RYT values of mixtures cultivated in the HM treatments (Figures 4a & 4b) were greater than 1, implying that the morphs utilized somewhat different resources. It seems

as if nutrients did not have any effect on the RYT of the species in the mixture. In the moisture stress treatments (Figures 4c & 4d), RYT values were smaller than 1. The species competed for water, the limiting factor, and nutrients did not seem to play a role.

### Aggressivity

The relative competitive ability of a species is expressed as the aggressiveness ( $A$ ) of species B relative to species A (Martin & Snaydon 1982). Aggressivity has been used in several competition studies (Mitchley & Grubb 1986; Wilson & Keddy 1986; Goldberg 1987; Goldberg & Fleetwood 1987).

The competitive ability of the plants cultivated from the disc diaspores was greater than that of the plants cultivated from the ray diaspores (Table 3), in all four treatments.

### Relative crowding coefficient

The relative crowding coefficient ( $k$ ) is frequently used as a measure of competitive power (Hall 1974). If two species compete for the same space the products of their relative crowding coefficients for yield should equal 1, and the two species are mutually exclusive. If the product of their relative crowding coefficients for yield is greater than 1, although they may still be competing for the same resource(s), they are also competing for different space, *i.e.* non-competitive interference is taking place in addition to competition.

The values of the relative crowding coefficient as well as the products of the crowding coefficients are given in Table 4. The products of the crowding coefficients were greater than 1 in all the moisture and nutrient treatments. This indicates that the plants of the different diaspore types were competing with each other, as well as for different space niches in a non-competitive way.

### Species monoculture response and species mixture response

Jolliffe *et al.* (1984) proposed that the interpretation of data from replacement series experiments should involve comparisons among projected monoculture yields, actual monoculture yields and actual mixture yields.

Monoculture and mixture responses separate the effects of intraspecific and interspecific competition. It has the advantage that it can be used for all species, proportions and densities, whereas the relative crowding coefficient (De Wit 1960) which serves as the index of competition in the conventional approach, is only valid where the two species are mixed in equal proportions (Jolliffe *et al.* 1984).

Species monoculture response, the difference between the projected yield ( $Y_p$ ) and the monoculture yield ( $Y_m$ ) at any given planting density of a species, is a measure of intraspecific competition. The species monoculture responses increased with increasing density of each morph. Thus, the higher the density the greater was the influence of intramorphic competition. The relative monoculture response is the relative effect of intraspecific competition on the yield of an individual species in monoculture. The higher the density the higher the relative monoculture response became. Intramorphic competition in plant stands of disc plants was stronger than in ray plant stands under HM-HN

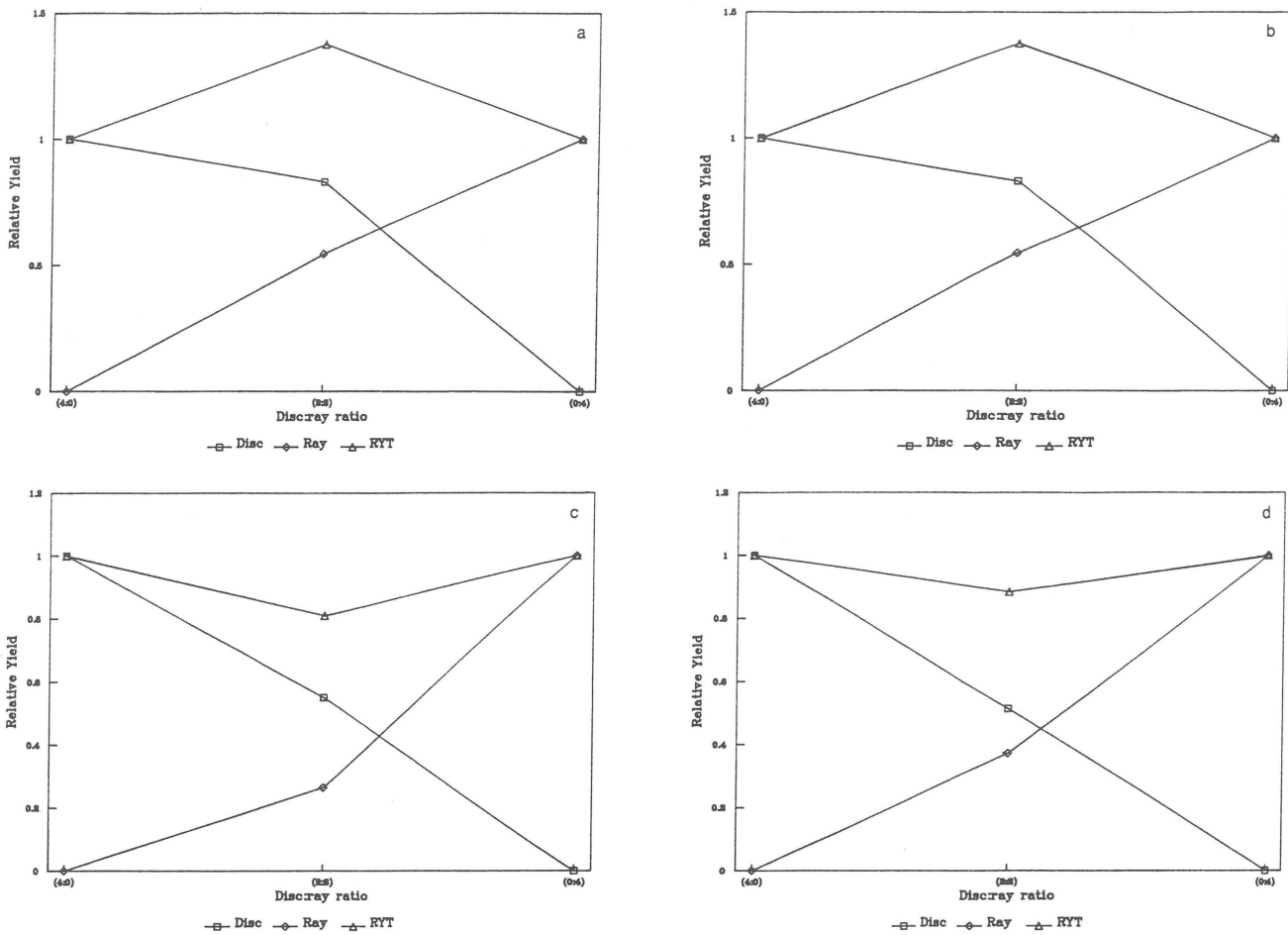


Figure 4 Relative yield total (RYT) of disc and ray plants of *Dimorphotheca sinuata* in (a) a high-moisture – high-nutrient regime (HM-HN); (b) a high-moisture – low-nutrient regime (HM-LN); (c) a low-moisture – high-nutrient regime (LM-HN); and (d) a low-moisture – low-nutrient regime (LM-LN).

Table 3 Agressivity of disc and ray plants under different moisture and nutrient regimes

	Agressivity	
	Disc plants	Ray plants
HM-HN		
Disc	—	-0.143
Ray	0.143	—
HM-LN		
Disc	—	-0.200
Ray	0.200	—
LM-HN		
Disc	—	-0.144
Ray	0.144	—
LM-LN		
Disc	—	-0.071
Ray	0.071	—

Table 4 The relative crowding coefficients (k) of disc and ray plants of *Dimorphotheca sinuata* under different moisture and nutrient regimes

	k		
	Disc plants	Ray plants	k × k
HM-HN	4.88	1.20	5.86
HM-LN	8.41	0.95	7.99
LM-HN	1.22	0.36	0.44
LM-LN	1.05	0.59	0.62

competition caused by the presence of the other species in the mixture. The relative effect of interspecific competition on the yield of a species in a mixture is termed relative mixture response. The species mixture response and the relative mixture response increased with increasing densities of the other species in the mixture. The higher these values of the responses, the greater the influence of interspecific competition.

The species mixture and relative mixture responses are given in Table 5. By comparing the values of the different responses of plants cultivated from the two diaspore types, the influence of the one type on the other can be deduced. The species mixture and relative mixture responses of the disc plants were smaller than those of the ray plants in all

treatments (Table 5), since the species monoculture and relative monoculture response of disc plants were higher than of ray plants (Table 5).

The difference between the monoculture ( $Y_m$ ) and the mixture yield ( $Y_x$ ) is called the species mixture response. This difference arises from the occurrence of intraspecific

**Table 5** The species monoculture response under a high moisture and nutrient (HM–HN) treatment and the species mixture response under different moisture and nutrient regimes

	Disc plants	Ray plants
HM–HN		
Species monoculture response	4.63	3.63
Relative monoculture response	0.58	0.53
Species mixture response	-2.17	-0.28
Relative mixture response	-0.65	-0.09
HM–LN		
Species mixture response	-1.74	0.02
Relative mixture response	-0.80	0.01
LM–HN		
Species mixture response	-0.31	-0.14
Relative mixture response	-0.10	-0.05
LM–LN		
Species mixture response	-0.06	0.54
Relative mixture response	-0.02	0.26

the treatments conducted. Therefore, the ray plants were influenced more by disc plants than disc plants were influenced by ray plants in all treatments.

#### Biomass allocation

There was no significant difference ( $p = 0.05$ ) in biomass allocation to the stems and inflorescences between the disc and ray plants of *D. sinuata* (Figures 5a – 5h) in any of the different treatments.

Disc plants in HM monoculture and ray plants in HM–HN monoculture allocated significantly ( $p = 0.05$ ) more biomass to their stems than disc and ray plants in a mixture (Figures 5a, 5b & 5e).

Monocultures of disc plants that received HM–HN as well as LM–LN allocated significantly ( $p = 0.05$ ) more biomass to their leaves than disc plants in mixtures (Figures 5a & 5d). Since disc plants are stronger competitors than ray plants, plants in a disc plant monoculture need to expand their leaves more than disc plants in a mixture because competition in a mixture with ray plants seems to be less severe than competition in a pure stand of disc plants.

Reproductive allocation of disc plants in a mixture was significantly ( $p = 0.05$ ) higher than that of disc plants in monoculture, in all the treatments (Figures 5a – 5d). Ray plants which received HM–HN as well as those which experienced LM–LN allocated significantly ( $p = 0.05$ ) more biomass to reproduction in a mixture than in a pure stand (Figures 5e & 5f).

#### Conclusions

Disc plants produced more total above-ground dry matter in mixtures than in monocultures in the HM treatments, but there were no differences in the moisture stress treatments. There were no differences in production between monocultures and mixtures of ray plants. Both the disc and ray plants were the most successful in the HM–HN treatment.

Under HM conditions intramorphic competition among disc plants was stronger than intermorphic competition with ray plants, whereas ray plants were not influenced by the

identity of the neighbour. Under moisture stress disc plants were not influenced by the identity of the neighbour, however, the effect of intermorphic competition on ray plants was greater than intramorphic competition among ray plants. Ray plants were, thus, more influenced by disc plants and the supply of moisture. The nutrient supply was not an important factor in determining the outcome of competition. Intramorphic competition was stronger in disc monocultures than in ray monocultures.

The aggressivity of the disc plants was greater than that of the ray plants. Disc plants proved to be the stronger competitor in all the calculations made.

Ray diaspores exhibit delayed germination if the embryos are not excised. To ensure the presence of ray plants in the replacement series, the embryos of diaspores therefore had to be excised. However, under natural conditions those seedlings which germinate first (generally disc plants) will capture a disproportionate amount of environmental resources and deprive seedlings which germinate later (generally ray plants) of part of their share. Once a size hierarchy has been established between two individuals in a population, it will be progressively exaggerated, especially under density stress.

Disc plants are the superior competitors, and are responsible for the dispersal and abundance of the species. The ray diaspores, which germinate very poorly (Beneke *et al.* 1992c), produce less competitive plants. Their function is to escape unexpected dry periods in time. Polymorphism is an adaptation to arid, unpredictable environments, to assure the species expansion under favourable conditions and survival under unfavourable conditions.

#### Acknowledgements

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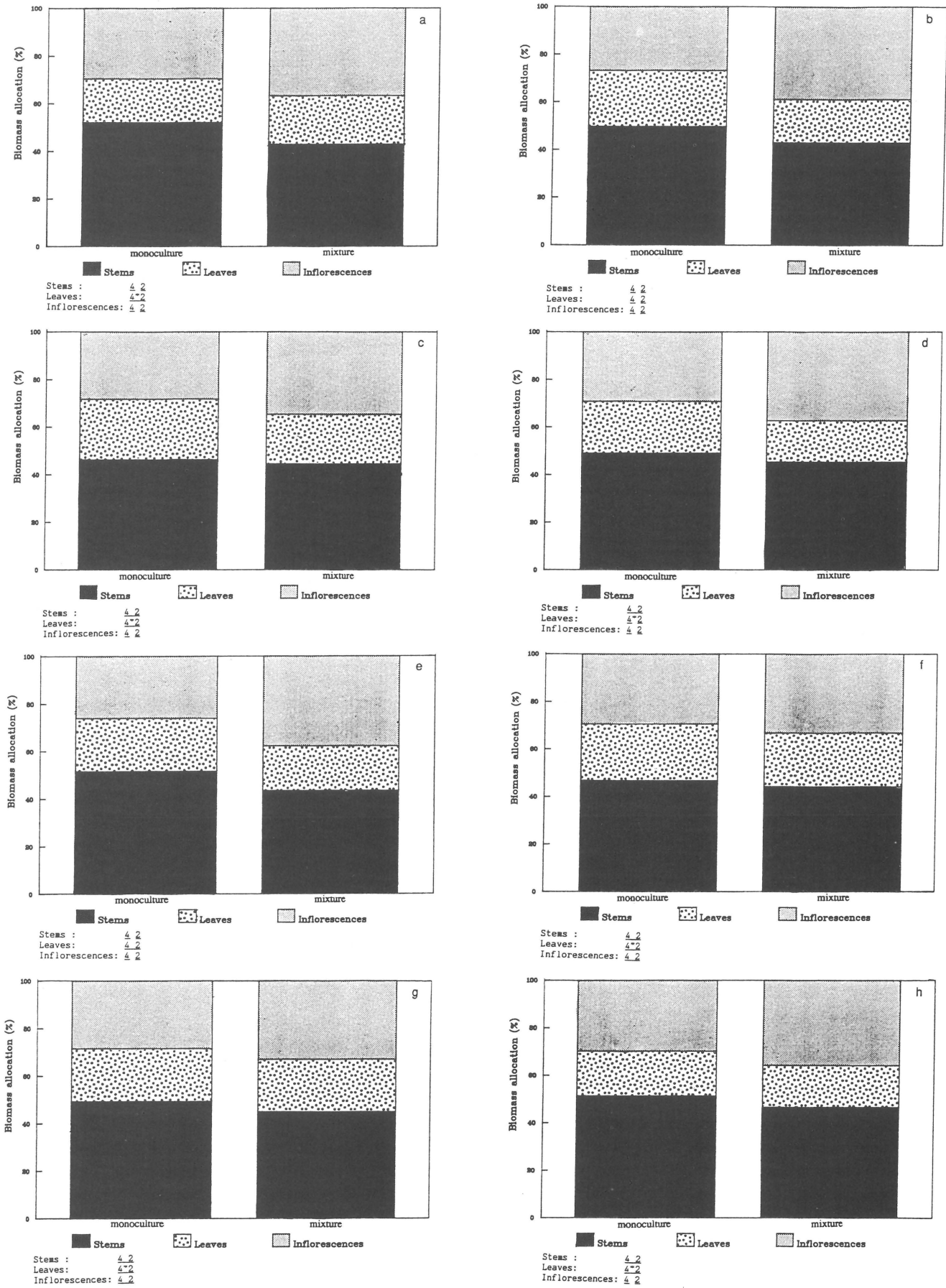


Figure 5 Biomass allocation in *Dimorphotheca sinuata* plants: Disc plants cultivated in (a) a high-moisture – high-nutrient regime (HM-HN); (b) a high-moisture – low-nutrient regime (HM-LN); (c) a low-moisture – high-nutrient regime (LM-HN); and (d) a low-moisture – low-nutrient regime (LM-LN); and ray plants cultivated in (e) a high-moisture – high-nutrient regime (HM-HN); (f) a high-moisture – low-nutrient regime (HM-LN); (g) a low-moisture – high-nutrient regime (LM-HN); and (h) a low-moisture – low-nutrient regime (LM-LN). Statistically homogenous groups are indicated under the figures. Asterisks denote statistically significant differences between plants of the different diaspore types.

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