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LIFE HISTORY STRATEGIES OF NAMAQUALAND PIONEER PLANT SPECIES

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LIFE HISTORY STRATEGIES OF NAMAQUALAND PIONEER PLANT SPECIES

by

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Namaqualand, the place to get out of your car and walk in the veld and, more often than not, get down on your knees!

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Abstract

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Namaqualand presents tourists with massive floral displays of species at high densities in disturbed areas. Understanding the interactions and functioning of these species is necessary for optimal utilization and management.

Multivariate analysis of plant traits were used to place species into guilds. Perennial, facultative perennial and annual species were distinguished. Plant traits, measured on species grown singly, were used to determine a competitive effect hierarchy and an equation to predict the position of a species in the hierarchy. Competitive effect and response hierarchies were determined at two nutrient levels. Interspecific competition was not large enough to significantly change the relative species abundance in multispecies mixtures compared to the expected abundance.

Namaqualand's changing environmental conditions promote coexistence between species as no species is able to retain a competitive advantage long enough to exclude the others.

Chapter 1

INTRODUCTION

Namaqualand is famous for its mass floral displays of many annual and some perennial species. In spring, after a good rainy season, this arid region is transformed into a land of colour. The flowering plants occur in the natural vegetation but are especially spectacular on the old fields or other disturbed areas. In these large stands of individuals only one or two species dominate, whereas the species diversity is much higher in less disturbed vegetation. Interactions between all these species determines the end result - a spectacular carpet of flowering plants. What these interactions are and the outcome of the interactions must be understood in order to preserve this natural asset.

Temporal variability in arid environments is a strong selective force shaping the demographic characteristics of individual species in terms of their life history patterns and population dynamics (Fox 1992). 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.* 1992, Steyn *et al.* 1996), as well as the relative abundance of species from year to year. These different life history patterns which have evolved, determine the competitive success of a plant species and its continued existence in its environment.

Grime's theory of life history strategies (Grime 1977, 1979) has evoked the processes of disturbance, stress and competition as opposing forces selecting for contrasting syndromes of characteristics (Grace 1991). Tilman's (1977) resource based theory of competition has been extended (Tilman 1985, 1988) to explain the suites of traits associated with old-field succession and gradients in soil fertility and disturbance (Grace 1991). The relative abundance of species with different attributes varies with the level of stress (water and nutrient availability) and disturbance (grazing and ploughing) (Fernándes Alés *et al.* 1993). In effect the many variations in life history patterns of species enable them to exist in different parts of a mosaic of disturbed environments (Fernándes Alés *et al.* 1993, Iwasa & Levin 1995).

Plant traits are also important in determining and predicting a plant's competitive ability (Grime 1979, Gaudet & Keddy 1988, Tilman 1988, Keddy 1989, Grace 1990, Goldberg & Landa 1991, Keddy *et al.* 1994) and understanding community data (Dodd *et al.* 1995, Kindscher & Wells 1995).

The importance, and even existence of competition in arid ecosystems has often been questioned (Fowler 1986). Shmida *et al.* (1986) stated that, under the harsh and unpredictable conditions characterising desert environments, the probability is very low that densities increase up to levels in which competition becomes very important. Also, Noy-Meir (1979) argued that the dynamics of populations in deserts are determined mainly by the direct responses of the individuals to changes in the abiotic environment, and competitive interactions between and within species are rare. However, results obtained in other studies (Klikhoff 1966, Friedman & Orshan 1974, Inouye *et al.* 1980, Kadmon & Shmida 1990a, 1990b) contradict these predictions, and suggest that competitive effect may play a major role in determining the dynamics of the desert annual plant populations. In a review on the available evidence for competition in arid plant communities, Fowler (1986) demonstrated that competition certainly does occur in arid and semi-arid regions and it may involve many different species.

Definitions of competition fall into two types: those which describe it as a mechanism (Grime 1977); and those which emphasise the outcome of the interaction (Keddy 1989, Silvertown 1987). There are two classes of mechanisms of competition. In exploitative competition the individuals, by using resources, deprive others of benefits to be gained from these resources (Schoener 1983). Whereas interference competition is when individuals harm one another by fighting, such as producing toxins (Schoener 1983).

"Competitive ability" has two components (Goldberg 1990): competitive effect (the ability to depress growth or reproduction of neighbours) and competitive response (the ability to withstand the negative effects of neighbours). These can both be estimated by growing the species in additive mixtures and measuring the reduction in performance of species in mixtures relative to controls (Keddy *et al.* 1994).

A hotly debated issue is whether the intensity of competition varies as a function of habitat productivity (Grace 1993, Goldberg 1994). Two "opposing" theories have been developed. Grime (1977, 1988) and Campbell & Grime (1992), have argued that the traits that determine competitive ability are constant across productivity gradients, whereas Tilman (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). Variation in competitive ability among environments has also been found by Mehrhoff & Turkington (1990), Silvertown *et al.* (1994) and Keddy *et al.* (1994). In recent years it has become clear that differences among studies in both predicted and observed patterns are often simply a consequence of differences in methods of quantifying the influence of competition (Goldberg & Scheiner 1993, Grace 1993).

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, Goldberg & Barton 1992, Lüscher *et al.* 1992). Variation in relative competitive ability has been proposed to control the species composition of plant communities (Gaudet & Keddy 1988, Wilson & Tilman 1995).

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).

In general, competitive hierarchies are consistent (Harper 1977) and recent work has shown that competitive effect hierarchies are unaffected by soil fertility (Keddy *et al.* 1994), and estimates of relative competitive effect are a good predictor of field distribution (Keddy *et al.* 1994). 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 of the competing plants (Goldberg & Landa 1991). Because a large component of depletion 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 more similar in competitive effect on a per-unit size basis than on a per-individual basis (Goldberg & Werner 1983).

In addition to the effects of proportion, density, and the specific identity of neighbouring individuals, the direction and intensity of competition may also be affected by the physical environment in which it occurs. If the direction of competitive dominance (i.e. which member of a pair of species outcompetes the other) is reversed between patches or sites, or between seasons, both species may be able to coexist (Fowler 1982).

Aim

In order to understand the functioning and interactions of Namaqualand plant species the aim of the study was a) to determine several life history traits of 30 Namaqualand pioneer plant species; b) to construct an equation to predict competitive effect by using plant traits; c) to use life history data to arrange 30 species into guilds; d) to investigate the competitive effect and response of ten prominently displaying plant species; and e) to determine community level competition between five Namaqualand pioneer plant species.

The thesis is presented in the form of papers. These papers are to be submitted for publication in various scientific journals. Except for the papers, an introduction, an overview of methods, general conclusions and comprehensive list of references are included.

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Chapter 2

MATERIAL AND METHODS

This chapter summarises the material and methods used in this study. The chapters that follow contain more detailed descriptions of the methods. Diaspores of all species used in the study were collected either in the Goegap Nature Reserve approximately 12 km east of Springbok (29°41'S, 17°55'E) or in the Skilpad Wildflower Reserve near Kamieskroon (30°9'S, 17°47'E). The species used were *Anchusa capensis* Thunb.; *Arctotheca calendula* (L.) Levyns, (HR 22); *Arctotis diffusa* Thunb., (HR 26); *Cotula thunbergii* Harv., (HR 9); *Diascia tanyceras* E. Mey. ex Benth., (HR 19); *Felicia merxmuelleri* Grau., (HR 6); *Heliophila variabilis* Burch. ex DC., (HR 14); *Manulea altissima* L.f. subsp. *glaricaulis* (Hiern) Hilliard, (HR 8); *Spergula arvensis* L. (HR 18) and *Ursinia cakilefolia* DC. (HR 23) collected at Skilpad Wildflower Reserve, and *Arctotis fastuosa* Jacq.; *Conicosia elongata* (Haw.) N.E. Br., (HR 27); *Dimorphotheca polyptera* DC., (HR 5); *Dimorphotheca sinuata* DC., (HR 25); *Felicia australis* (Alston) Phill., (HR 12); *Foveolina albida* (DC.) T. Norl., (HR 11); *Gazania lichtensteinii* Less., (HR 1); *Grielum humifusum* Thunb. var. *humifusum*, (HR 10); *Heliophila rigidiuscula* Sond., (HR 21); *Hypertelis salsoloides* (Burch.) Adamson, (HR 28); *Lessertia diffusa* R. Br., (HR 4); *Leysera tenella* DC., (HR 7); *Oncosiphon grandiflorum* (Thunb.) Kallersjo, (HR 2); *Oncosiphon suffruticosum* (L.) Kallersjo, (HR 3); *Osteospermum amplectens* (Harv.) T. Norl., (HR 17); *Osteospermum hyoseroides* (DC.) T. Norl., (HR 20); *Osteospermum pinnatum* (Thunb.) T. Norl. var. *pinnatum*, (HR 13); *Senecio arenarius* Thunb., (HR 16); *Senecio piptocoma* O. Hoffm. (HR 15) and *Ursinia calenduliflora* (DC.) N.E. Br. (HR 24) collected at Goegap Nature Reserve (Figure 1).

Voucher specimens of all the species are kept in the H.G.W.J. Schweickerdt Herbarium at the University of Pretoria. Identification was made by the National Herbarium (PRE) and nomenclature is according to Arnold & De Wet (1993). All the plants for the various experiments were grown out of doors at the University of Pretoria. All plants, unless otherwise specified, were watered with tap water daily

Anchusa capensis *Arctotheca calendula* *Arctotis diffusa*

Arctotis fastuosa *Conicosia elongata* *Cotula thunbergii*

Diascia tanyceras *Dimorphotheca polyptera* *Dimorphotheca sinuata*

Figure 1. Namaqualand plant species used in this study (excluding *Oncosiphon grandiflorum*, *O. suffruticosum* and *Spergula arvensis*).


Felicia australis

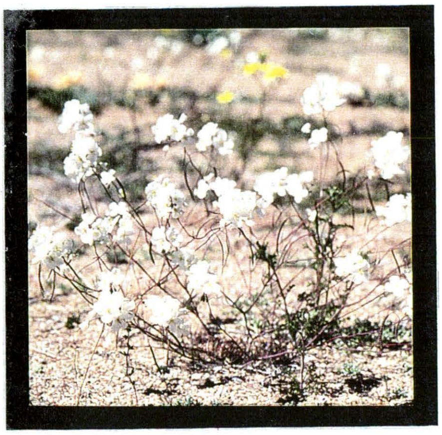

Felicia merxmuelleri

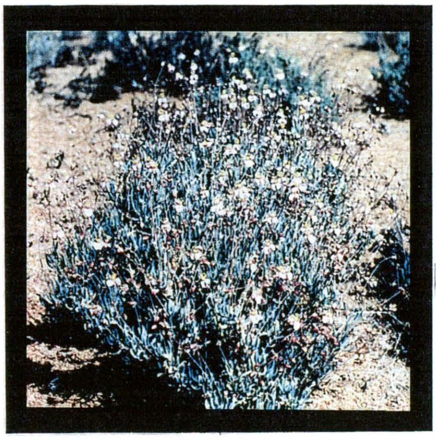

Foveolina albida


Gazania lichtensteinii


Grielum humifusum


Heliophila rigidiuscula


Heliophila variabilis


Hypertelis salsoloides

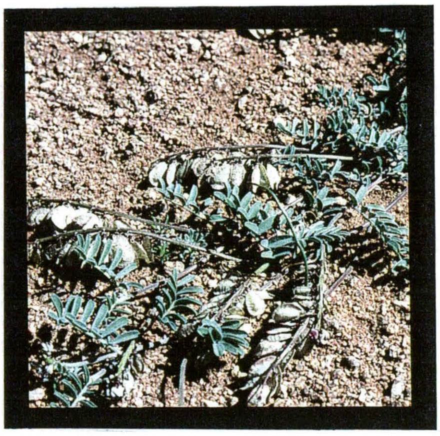
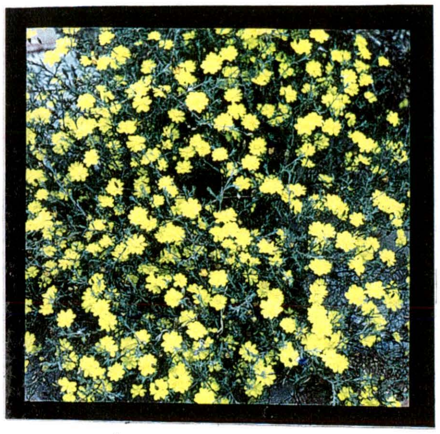

Lessertia diffusa

Figure 1. (Continued)



Leysera tenella

Manulea altissima

Osteospermum amplectens

Osteospermum hyoseroides

Osteospermum pinnatum

Senecio arenarius

Senecio piptocoma

Ursinia cakilefolia

Ursinia calenduliflora

Figure 1. (Continued)

until field capacity was reached and received Arnon and Hoagland's complete nutrient solution (Hewitt 1952) at full-strength weekly.

Study area

Namaqualand is situated in the arid north-western corner of the Northern Cape Province in the Republic of South Africa and covers approximately 55 000km^2. Geographically, the area can roughly be divided into four distinct regions (Le Roux & Schelpe 1988): the Sandveld, Richtersveld, Namaqualand "Hardeveld", and the Knersvlakte. The species used in this study typically occurs in the "Hardeveld" which according to Acocks' veld types lies predominantly within the Namaqualand Broken Veld (Acocks 1988).

The 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). The average annual rainfall at Okiep is 162mm and the average annual temperature is 17.7°C (Weather Bureau 1988).

Namaqualand owes its fame mainly to the display of wild flowers, which transforms the normally barren landscape into a land of colour in the spring following a good rainy season (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992) and many tourists visit the area during the flowering period. The life cycles of the annual plant species are synchronised with the climate in such a way that they are able to escape unfavourable conditions of drought and high temperatures in the form of seeds, and are in an actively growing state only when temperatures and moisture regimes offer comparatively favourable conditions (Van Rooyen, Theron & Van Rooyen 1992). Each species has its own specific temperature at which germination takes place optimally (Beneke *et al.* 1992, Visser 1993). Because the first rains may fall from April to July, germination of different species are favoured from year to year depending on when the first rains fall (Le Roux & Schelpe 1988).

Methods

1) Life history traits

Diaspores of each of thirty species were sown in quartz sand filled pots, with a volume of 1000cm^3, at the University of Pretoria in 1994. The plants were thinned out to one individual per pot. Pre-selected pots were used to determine average number of days to emergence, bud formation (flower initiation), anthesis, first ripe fruit and death for each species. Seed mass and dispersal type were established for each species (Chapter 3).

Five replicates of each species were harvested every four weeks, for five harvests. Leaf area, leaf mass, stem mass, reproductive mass, root mass, plant height, plant diameter, number of infloresences, shoot mass, total mass, relative growth rate, leaf allocation, stem allocation, reproductive allocation, root allocation, root : shoot ratio and leaf area ratio were determined. All values measured and calculated are described in Chapter 3.

2) Predicting competitive ability

Phytometer (*Dimorphotheca sinuata*) diaspores were sown in the centre of each pot (volume 1000cm^3) with diaspores of itself or one of fourteen other species around it. After emergence, the seedlings were thinned out to one phytometer (in the centre) and four individuals of another species (symmetrically around the centre phytometer). Plants were harvested 18 weeks after sowing. Data from the species grown singly (life history traits experiment - Chapter 3) were used to determine the maximum value, over all the harvests, of the various plant traits.

Simple linear regressions between these values indicated a relationship or lack thereof between the different plant traits and the phytometer's above-ground mass when grown with the different species. Significant relationships were used in a forward stepwise multiple regression (Statgraphics 6.0 1992) to determine an equation for predicting competitive ability.

3) Multivariate analysis using plant traits

Results of the life history traits experiment (Chapter 3) were used in the multivariate analysis (Chapter 5). The species maximum value for each attribute, over all the harvests, was used to place each species into one of three classes for each attribute. An ordination, using all the plant traits, was done and this ordination enabled the exclusion of perennials and facultative perennials from the next ordination. The ordination of species was conducted by using Principal Component Analysis (PCA) (Gauch 1981), in the computer program CANOCO (Ter Braak 1987). The traits best correlated with the x- and y-axes were determined using Pearson's product moment (Kindscher & Wells 1995).

4) Pairwise interactions

Four target (*Dimorphotheca sinuata*, *Gazania lichtensteinii*, *Heliophila variabilis* and *Ursinia cakilefolia*) species were grown in pairwise combination with six neighbour (*Arctotheca calendula*, *Foveolina albida*, *Leysera tenella*, *Oncosiphon grandiflorum*, *Osteospermum hyoseroides* and *Senecio arenarius*) species as well as in all combinations of the four target species (Chapter 6).

The target species were sown in one half of the pot (volume 1000cm^3) and the neighbour species in the other half of the pot. After emergence, seedlings were thinned out to one target and one neighbour individual per pot. Pots containing single species were thinned out to one individual per pot. The plants were watered daily with tap water and received 120ml Arnon and Hoagland's complete nutrient solution weekly (Hewitt 1952). Competitive effect and response of all the species were determined at two nutrient levels by the addition of nutrient solution at full strength (Treatment 1) or at half-strength (Treatment 2).

Above-ground parts of the plants were harvested 17 weeks after sowing. Indices (Relative yield per plant, RYP (Harper 1977) and Competitive intensity, I (Keddy *et al.* 1994)) calculated are described in Chapter 6. Relative yield per plant for each species in all combinations was used to determine competitive effect and response rankings of the species and Kendall's rank correlations used to test for concordance of rankings (Keddy *et al.* 1994).

5) Monocultures versus mixtures

In 1995, plants of five species (*Dimorphotheca sinuata*, *Heliophila variabilis*, *Oncosiphon grandiflorum*, *Senecio arenarius* and *Ursinia cakilefolia*) were grown in monocultures of ten individuals per pot (volume 0.125m^3) and in mixtures of ten individuals per species per pot (volume 0.125m^3). Above-ground parts of the plants were harvested 15 weeks after sowing and dry mass determined. Relative yield per plant, expected and actual relative abundance of species in mixtures were calculated. Differences between observed and expected values were investigated. Indices calculated are explained in Chapter 7.

Statistical analysis of data

A one way analysis of variance (ANOVA) was used to test for statistically significant differences at $\alpha = 0.05$. Bonferroni's test (Steyn *et al.* 1987) was used for paired comparisons between treatments and to test for differences between monocultures and mixtures. Regressions were used to determine relationships or lack thereof between various variables. The chi-square goodness-of-fit test was used to test for differences between observed and expected values. All statistics including Pearson's product moment (Kindscher & Wells 1995) and Kendall's rank correlations (Keddy *et al.* 1994) were computed using STATGRAPHICS 6.0, 1992, Inc. U.S.A..

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Chapter 3

LIFE HISTORY TRAITS OF THIRTY NAMAQUALAND PIONEER PLANT SPECIES

Introduction

Namaqualand covers approximately 55 000 km^2 and is situated in the arid north-western corner of the Northern Cape Province in the Republic of South Africa. The average annual rainfall and average annual daily temperature at Okiep are 162 mm and 17.7°C respectively (Weather Bureau 1988). Namaqualand has a very low, sporadic winter rainfall which has given rise to adaptations of the plants for survival during moist winters and dry, hot summers. In winter and spring the plant cover is high with perennials and many annuals but in summer this becomes a barren scene (Le Roux & Schelpe 1988). Life in hot deserts is challenging for plants because they face severe physiological stress from heat and drought, and because even during the "rainy seasons" the availability of moisture is rather unpredictable (Fox 1992). The life cycles of the plants are synchronised with the climate in such a way that they are able to escape the unfavourable conditions of drought and high temperature in the form of seeds, and are in an actively growing state only when temperature and moisture regimes offer comparatively favourable conditions (Van Rooyen *et al.* 1992).

Life history patterns describe the patterns of growth, reproduction and longevity of plants. They are different in different habitats and change through time as succession takes place (Barbour *et al.* 1987). The distribution of energy into three processes (growth, reproduction and maintenance) determines the life history pattern of the plant but the energy distribution also depends on the biotic and abiotic environment surrounding the plant (Barbour *et al.* 1987). It is assumed that the organisms quantitative allocation of energy is an essential feature of its strategy, possessing the following aspects:

1) 'life cycle strategy' which is related to the whole complex pattern of energy allocation in time and space; and

2) 'reproductive strategy' which is related to the energy allocation associated with reproduction (Kawano & Nagai 1975).

Desert plants are subject to strong natural selection on at least three kinds of interrelated traits:

a) life history traits i.e. the timing and amount of germination, growth and flowering;
b) plastic responses of life history traits to environmental influence; and
c) physiological traits affecting growth, reproduction and survival (Fox 1992).

Plant attributes vary within and among species as well as populations. Various combinations that occur determine whether a species will grow in an area or not. The relative abundance of species with different attributes vary with the level of stress (water and nutrient availability) and disturbance (grazing and ploughing) (Fernándes Alés *et al*. 1993).

The various plant traits characteristic of a species determine a species competitive ability, thus competitive hierarchies between species can be established. If consistent hierarchies occur, the question "what traits determine position in the hierarchy?" arises (Goldberg & Landa 1991). A number of traits have been hypothesized or demonstrated to be related to competitive ability (Keddy 1989).

The aim of the study was to determine several life history traits of thirty Namaqualand species. These plant traits were later used to determine a plants competitive ability and to arrange fifteen plant species in a competitive hierarchy (Chapter 4). An ordination using all the plant traits of the 30 Namaqualand plants species was done to establish whether similar species could be grouped together into functional guilds by using plant traits (Chapter 5).

Material and Methods

Diaspores of thirty species were collected in Namaqualand. *Anchusa capensis* Thunb., *Arctotheca calendula* (L.) Levyns, *Arctotis diffusa* Thunb., *Cotula thunbergii* Harv., *Diascia tanyceras* E. Mey. ex Benth., *Felicia merxmuelleri* Grau., *Heliophila variabilis* Burch. ex DC., *Manulea altissima* L.f. subsp. *glarbicaulis* (Hiern) Hilliard, *Spergula arvensis* L. and *Ursinia cakilefolia* DC. diaspores were collected at Skilpad Wildflower Reserve near Kamieskroon at 17° 47' East and 30° 9' South. The diaspores of the other eleven species were collected near Springbok (29° 41' S, 17° 55' E). The species were: *Arctotis fastuosa* Jacq., *Conicosia elongata* (Haw.) N.E. Br., *Dimorphotheca polyptera* DC., *Dimorphotheca sinuata* DC., *Felicia australis* (Alston) Phill., *Foveolina albida* (DC.) T. Norl., *Gazania lichtensteinii* Less., *Grielum humifusum* Thunb. var. *humifusum*, *Heliophila rigidiuscula* Sond., *Hypertelis salsoloides* (Burch.) Adamson, *Lessertia diffusa* R. Br., *Leysera tenella* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo, *Oncosiphon suffruticosum* (L.) Kallersjo, *Osteospermum amplectens* (Harv.) T. Norl., *Osteospermum hyoseroides* (DC.) T. Norl., *Osteospermum pinnatum* (Thunb.) T. Norl. var. *pinnatum*, *Senecio arenarius* Thunb., *Senecio piptocoma* O. Hoffm. and *Ursinia calenduliflora* (DC.) N.E. Br.. Voucher specimens of all the 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).

The diaspores of the individual species were sown in quartz sand filled pots (particle size 0.8 - 1.6 mm), in the beginning of April 1994 at the University of Pretoria. Two weeks after sowing the seedlings were thinned out to one per pot, and maintained at one plant per pot throughout the duration of the experiment. The plants were grown out of doors, watered daily and once a week received Arnon and Hoagland's complete nutrient solution (Hewitt 1952).

The average number of days to emergence was calculated by noting when the first seedling in each of ten pre-selected pots emerged and an average was calculated.

Similarly the days to bud formation, days to anthesis, days to first ripe fruit and death were determined using five pre-selected pots. A phenological diagram was drawn for each of the species using these values.

The collective mass of 100 diaspores of each species was determined and an average mass per diaspore calculated. The dispersal mechanism, for example : telechory, atelechory, anititelechory, anemochory, of each species was determined on the basis of morphological characteristics (Van Rooyen *et al.* 1990).

Five replicates of each species were harvested every four weeks, for five harvests starting on 11 May 1994. The following plant attributes were measured at each harvest:

1) Leaf area (cm^2) - A
2) Leaf mass (g) - W_l
3) Stem mass (g) - W_s
4) Reproductive mass (g) - W_i
5) Root mass (g) - W_r
6) Plant height (mm)
7) Plant diameter (mm)
8) Number of inflorescences present in the classes: buds, anthesis, withered and fruit.

The following calculations based on the formulae of Kvet *et al.* (1971), Causton & Venus (1981), Hunt (1982), Coombs *et al.* (1986) and Causton (1991) were made :

1) Shoot mass (g) - W_{sh}

$$W_{sh} = W_l + W_s + W_i$$

2) Total plant mass (g) - W

$$W = W_{sh} + W_r$$

3) Relative growth rate

$= (\ln W_2 - \ln W_1)/t_2 - t_1$

where W_1 and W_2 represent total dry mass at times t_1 and t_2 respectively.

4) Leaf allocation

$= W_l/W \times 100$

5) Stem allocation

$= W_s/W \times 100$

6) Reproductive allocation

$= W_i/W \times 100$

7) Root allocation

$= W_r/W \times 100$

8) Root : Shoot ratio

$= W_r/W_{sh}$

9)Leaf area ratio (LAR)

$= A/W$

10) Specific leaf area (SLA)

$= A/W_l$

Leaf areas were determined with a LiCor LI 3100 leaf area meter and the dry mass of the plant organs 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.

Results and Discussion

1) Seed mass and dispersal type

Four different telechorous agents of dispersal are distinguished (Van der Pijl 1982, Van Rooyen *et al.* 1990). When these agents operate singly the plant species is classified as either anemochorous (wind), hydrochorous (water), zoochorous (animals) or autochorous (plant itself). In most instances, however, more than one agent takes part in the diaspore dispersal of the plant species, in which case the species will be classified into more than one category (Van Rooyen *et al.* 1990).

All the species except *Arctotis fastuosa, Anchusa capensis, Grielum humifusum* and *Osteospermum pinnatum* are anemochoric i.e. dispersed by wind (Table 1). Wind dispersal enables the diaspores to be dispersed over long distances and is therefore regarded as telechory (Van der Pijl 1982).

Although anemochory occurs in all vegetation types it usually characterises deserts, steppes, grasslands and dunes (Van Rooyen *et al.* 1990). In the open chamaephytic vegetation of the study area (Namaqualand) anemochory is very effective, especially since the period with the strongest winds coincide with the main period of dissemination (Rösch 1977). Van Rooyen *et al.* (1990) found that the plant species of Namaqualand are predominately anemochorous (66.3% of all species).

All 26 species in this study that are anemochorous either weigh less than 1mg or if they weigh more, all have mechanisms or appendages which aid wind dispersal (Table 2).

Three or four seeds of *Lessertia diffusa*, each weighing 7.33mg on average (Table 2), are enclosed in a thin membranous indehiscent pod which can be dispersed by wind over long distances. *Lessertia diffusa* is hardseeded and exhibits heterodiaspory in that there is a clear difference in the time of germination of the seemingly identical seeds (Rösch 1977).

In *Conicosia elongata* the dry fruits are soft, conical and have about 15 valves that break up into separate compartments when it is ready to distribute its seeds (Le Roux & Schelpe 1988). The seeds are usually shaken out of the fruit by wind.

All four species not dispersed by wind (*Arctotis fastuosa, Anchusa capensis, Grielum humifusum, Osteospermum pinnatum*) have relatively large diaspore masses (Table 2), and have no wing-like appendages or other structures which aid wind dispersal. In the case of *G. humifusum* and *O. pinnatum*, the diaspores are dispersed over long distances, however the dispersal mechanism is not anemochorous but zoochorous (Table 1). These two species' diaspores are transported externally on animals i.e. epizoochorous dispersal. *Anchusa capensis* and *Arctotis fastuosa* have no particular adaptations to aid dispersal and are classified as atelechorous (Table 1).

Table 1. Diaspore dispersal types of 30 Namaqualand plant species

Species	Dispersal type	
	Telechoric	Atelechoric / Antitelechoric
Anchusa capensis		Atelechory
Arctotheca calendula	Anemochory	
Arctotis diffusa	Anemochory	
Arctotis fastuosa		Heterodiaspory Atelechory
Conicosia elongata	Anemochory	Atelechory Synaptospermy
Cotula thunbergii	Anemochory	Myxospermy Atelechory
Diascia tanyceras	Anemoballistic	Atelechory
Dimorphotheca polyptera	Anemochory	Heterodiaspory
Dimorphotheca sinuata	Anemochory	Heterodiaspory
Felicia australis	Anemochory	Atelechory
Felicia merxmuelleri	Anemochory	
Foveolina albida	Anemochory	Myxospermy
Gazania lichtensteinii	Anemochory	Myxospermy
Grielum humifusum	Epizoochory	Synaptospermy
Heliophila rigidiuscula	Anemochory (Dust diaspores)	Atelechory Myxospermy
Heliophila variabilis	Anemochory	Myxospermy
Hypertelis salsoloides	Anemoballistic	Atelechory
Lessertia diffusa	Anemochory	Synaptospermy Heterodiaspory
Leysera tenella	Anemochory	Heterodiaspory
Manulea altissima	Anemoballistic (Dust diaspores)	Atelechory
Oncosiphon grandiflorum	Anemochory	Myxospermy
Oncosiphon suffruticosum	Anemochory	Myxospermy
Osteospermum amplectens	Anemochory	Myxospermy Heterodiaspory
Osteospermum hyoseroides	Anemochory	Myxospermy Heterodiaspory
Osteospermum pinnatum	Epizoochory	Heterodiaspory
Senecio arenarius	Anemochory	Myxospermy
Senecio piptocoma	Anemochory	Myxospermy
Spergula arvensis	Anemoballistic	
Ursinia cakilefolia	Anemochory	Myxospermy Heterodiaspory
Ursinia calenduliflora	Anemochory	Myxospermy

Table 2. Diaspore mass of 30 Namaqualand plant species

Species	Mass per seed/achene (mg)
Manulea altissima	0.05
Felicia australis	0.06
Oncosiphon suffruticosum	0.06
Hypertelis salsoloides	0.07
Diascia tanyceras	0.08
Leysera tenella	0.08
Oncosiphon grandiflorum	0.11
Foveolina albida	0.12
Cotula thunbergii	0.14
Senecio arenarius	0.17
Heliophila rigidiuscula	0.17
Spergula arvensis	0.32
Senecio piptocoma	0.44
Heliophila variabilis	0.68
Felicia merxmuelleri	0.68
Arctotis fastuosa	0.72
Dimorphotheca polyptera	0.84
Ursinia calenduliflora	1.11
Conicosia elongata	1.22
Arctotheca calendula	1.39
Dimorphotheca sinuata (disc floret achene)	1.64
Ursinia cakilefolia	1.67
Gazania lichtensteinii	1.75
Osteospermum pinnatum	2.80
Osteospermum amplectens	2.92
Anchusa capensis	5.36
Osteospermum hyoseroides	6.64
Lessertia diffusa	7.33
Arctotis diffusa	9.86
Grielum humifusum (fruit)	49.14

In contrast to telechoric dispersal mechanisms, atelechoric and antitelechoric mechanisms do not promote long range dispersal. Atelechoric species are species that do not possess any adaptations for long distance dispersal while antitelechoric species are species with structures which hamper dispersal (Van der Pijl 1982, Ellner & Shmida 1981). Van Rooyen *et al.* (1990) noted that there was a high frequency of atelechorous and antitelechorous mechanisms present in Namaqualand species. The original explanation for atelechory and antitelechory was that they were adaptive responses to the particularly high mortality of dispersed seeds in deserts and these mechanisms evolved to reclaim the mother site (Van Rooyen *et al.* 1990). Ellner and Shmida (1981) argue that atelechory in deserts is an adaptive response to the low benefit of long-range dispersal mechanisms in deserts rather than any benefit arising from limited dispersal *per se*. They believe that antitelechory is disadvantageous and regard it as a side-effect of characters whose adaptive value is not directly related to dispersal (Ellner & Shmida 1981). These phenomena presumably developed as a component of a syndrome of characteristics related to dispersal and germination control. They indicate the importance of adaptations in arid environments which spread the time of germination, provide suitable conditions for germination and maintain a reservoir of viable seeds (Van Rooyen *et al.* 1990).

Myxospermy is an antitelechoric dispersal mechanism in which the diaspores form a superficial layer of mucilage upon moistening as a mechanism of anchorage. The myxospermic species studied were *Cotula thunbergii, Foveolina albida, Gazania lichtensteinii, Heliophila rigidiuscula, H. variabilis, Oncosiphon grandiflorum, O. suffruticosum, Osteospermum amplectens, O. hyoseroides, Senecio arenarius, S. piptocoma, Ursinia cakilefolia* and *U. calenduliflora* (Table 1). Myxospermy is said to enhance water uptake due to increased seed-soil contact (Van Rooyen *et al.* 1990).

Conicosia elongata, Grielum humifusum and *Lessertia diffusa* are the only three synaptospermic species studied (Table 1). Synaptospermic species contain more than one seed in a diaspore. Synaptospermy is a seed dispersal strategy in which there is a delay in seed dispersal and two or more seeds remain together in the inflorescence which may be the dispersal unit (Gutterman 1994). According to Van

Rooyen *et al.* (1990) synaptospermy is almost always associated with arid regions. Many of these species, however, are also well-adapted to either anemochory or zoochory (Van Rooyen *et al.* 1990). *Conicosia elongata* and *L. diffusa* are both anemochoric while *G. humifusum* is epizoochoric. Synaptospermy, heterodiaspory and hydrochasy are mechanisms allowing germination to be spread over time (Van Rooyen *et al.* 1990).

Various species exhibit heterodiaspory (Table 1). Fruit polymorphism or heterodiaspory is the production of two or more morphologically distinct types of diaspores by an individual plant (Ellner & Shmida 1981) and has been described in many species found in unpredictable environments (Harper 1977), such as frequently disturbed habitats and arid and semi-arid environments (Zohary 1937, Beneke 1991, Beneke *et al.* 1993). Polymorphism greatly enhances the ability of the species to live in highly variable environments (Maun & Payne 1989), the different seed morphs usually differ in germination behaviour and competitive performance (Beneke, Van Rooyen & Theron 1992a & 1992b, Beneke *et al.* 1993). In heterogenous environments plants producing heteromorphic seeds may be evolutionarily favoured over those not doing so, if there is a negative correlation between the establishment success of the different morphs (Silvertown 1987, Silvertown & Lovett Doust 1993).

In *Arctotis fastuosa* brown as well as black coloured achenes are formed in the same capitulum whereas in *Ursinia cakilefolia* white and black coloured achenes are formed. In both species there are, however, no differences in shape or size of the two diaspore types, the differences only occur in the surface structure of the achenes (Beneke, Von Teichman, Van Rooyen & Theron 1992a & 1992b) and has no real effect on dissemination (Rösch 1977). *Leysera tenella* has two different types of achenes in that the pappus is either fully developed or reduced, thus varying in anemochoric effectiveness of dispersal.

Dimorphotheca polyptera and *D. sinuata* both have diaspores with and without wing-like appendages. Beneke, Von Teichman, Van Rooyen & Theron (1992a) found that polymorphism in these two *Dimorphotheca* species from Namaqualand is important since it provides a two-way strategy: on the one hand the disc diaspores, which show a high germination percentage under favourable conditions, are responsible for the relative abundance and the range extension of the species, on the other hand the ray diaspores, with delayed germination protect the species against unpredictable, disastrous conditions. The three diaspore types of *Dimorphotheca polyptera* also enable the species to spread germination in space and time, while some individuals are able to exploit rainfall immediately, a seed reserve is maintained in the soil to enable repopulation should the initial germination fail (Beneke *et al.* 1993). *Lessertia diffusa*'s seeds have no structural differences but differ in the rates of germination (Rösch 1977). Seed dimorphism which involves dormancy of one type may lead to the distribution of germination in time, thus reducing the chances of extinction of a complete generation (Berger 1985). In *Osteospermum* species differences occur in the shape of the achenes. In this genus the disc florets are infertile and the heterodiaspory occurs only in the ray florets (Rösch 1977).

2) Phenological data

The perennial and the facultative perennial species (*Anchusa capensis*, *Arctotis diffusa*, *Conicosia elongata*, *Hypertelis salsoloides*, *Grielum humifusum*, *Lessertia diffusa* and *Manulea altissima*) all take longer to emerge (on average eight days) than the annuals, with the exception of *Felicia australis* and *Diascia tanyceras* which took 8.7 and 13.0 days respectively to emerge (Figure 1, Table 3). All the other annual species emerged between 3.5 and 6.8 days (Table 3). This delay in germination of the perennials could be as a result of a more cautious strategy of the perennials, whereas the annuals adopted a more opportunistic strategy. Quite obviously delaying reproduction and thus germination, causes a serious decrease in fitness for a semelparous plant unless it has a substantially higher seedling survival and/or much higher seed production than an annual (Hart 1977). These differences in phenology demonstrate the different life history patterns species have evolved in order to survive.

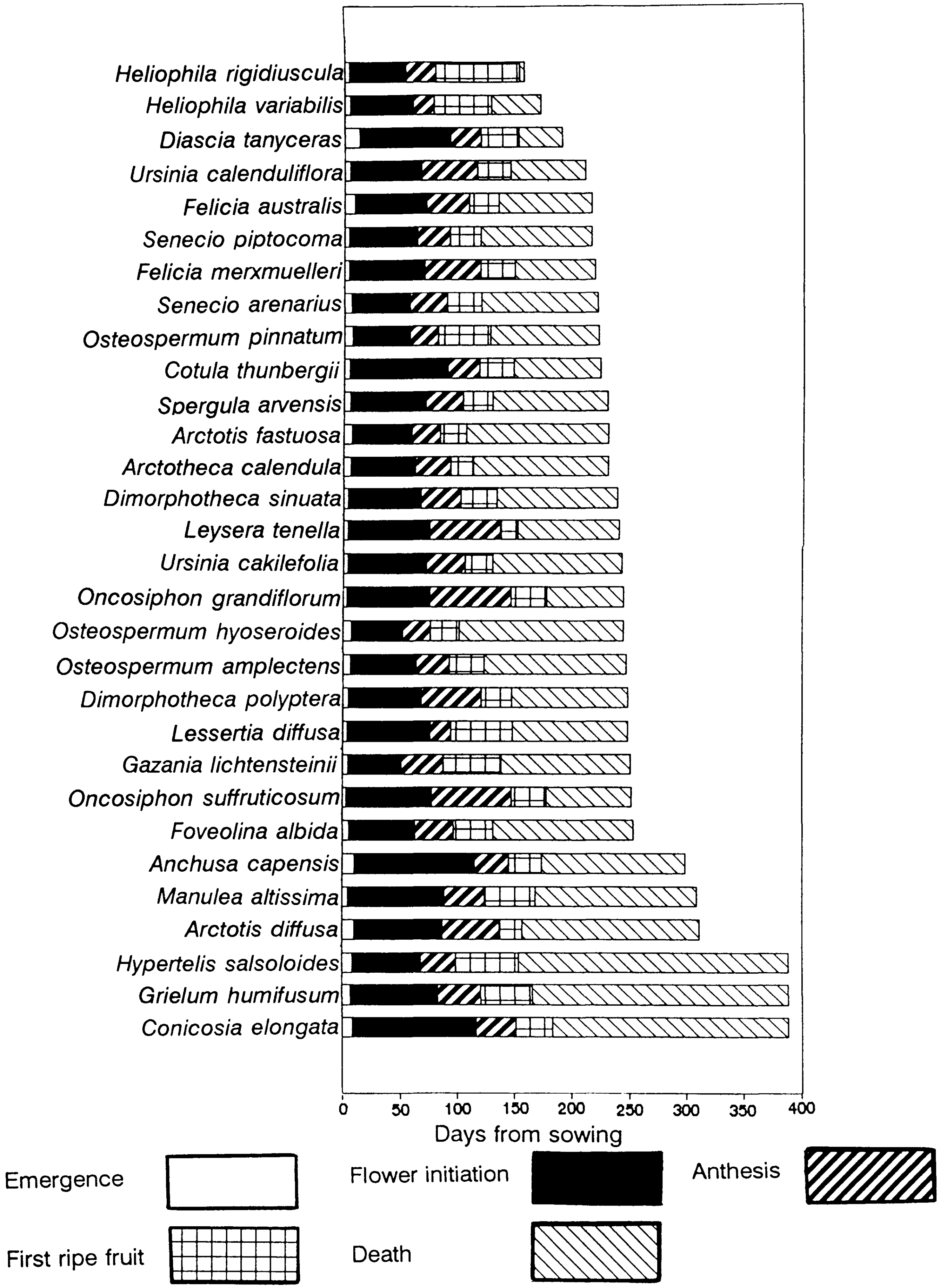


Figure 1. Phenograms of 30 Namaqualand plant species showing days to emergence, commencement of flower initiation, anthesis, first ripe fruit and death.

Table 3. Phenological data (over 13 months) of 30 Namaqualand plant species

Species	Days to emergence	Emergence to flower initiation	Flower initiation to anthesis	Anthesis to first ripe fruit	First ripe fruit to death
Anchusa capensis	10.0	106.0	30.0	28.5	125.3
Arctotheca calendula	6.2	56.0	31.6	20.4	116.6
Arctotis diffusa	10.6	76.9	50.0	19.5	155.0
Arctotis fastuosa	6.5	52.5	24.4	23.2	123.2
Conicosia elongata	8.5	108.5	35.0	32.2	204.8*
Cotula thunbergii	4.6	85.2	28.0	31.2	74.8
Diascia tanyceras	13.0	78.4	27.2	34.0	37.6
Dimorphotheca polyptera	4.8	63.4	52.8	26.5	101.5
Dimorphotheca sinuata	3.7	63.7	35.6	32.0	104.2
Felicia australis	8.7	62.3	37.6	26.4	80.4
Felicia merxmuelleri	4.3	65.5	49.2	30.8	69.8
Foveolina albida	5.1	57.1	34.4	34.8	121.8
Gazania lichtensteinii	4.7	46.5	37.4	50.4	112.8
Grielum humifusum	6.5	76.9	37.2	45.6	222.8*
Heliophila rigidiuscula	3.5	48.9	26.6	74.0	5.0
Heliophila variabilis	4.8	53.8	19.2	50.8	43.4
Hypertelis salsoloides	8.2	60.0	31.6	54.8	234.4*
Lessertia diffusa	3.6	72.6	18.4	53.6	100.8
Leysera tenella	3.2	71.8	62.0	15.2	88.1
Manulea altissima	4.7	83.9	35.6	44.0	141.0
Oncosiphon grandiflorum	3.0	72.8	71.2	30.8	67.0
Oncosiphon suffruticosum	3.0	75.6	68.8	30.1	74.6
Osteospermum amplectens	5.9	57.9	29.6	30.4	123.2
Osteospermum hyoseroides	6.4	45.4	24.8	26.0	142.2
Osteospermum pinnatum	6.8	49.4	25.2	46.8	94.2
Spergula arvensis	5.4	65.2	32.6	26.6	99.6
Senecio arenarius	6.0	50.2	32.8	30.8	101.2
Senecio piptocoma	4.1	58.5	29.2	27.6	96.7
Ursinia cakilefolia	4.0	68.6	34.8	24.0	112.0
Ursinia calenduliflora	4.7	61.5	49.2	29.6	64.8

* Still alive after 13 months

The length of the vegetative phenological phase varies greatly, some species such as *Osteospermum hyoseroides*, *Gazania lichtensteinii* and *Heliophila rigidiuscula* have very short phases, while other annual species such as *Cotula thunbergii* and *Diascia tanyceras*, facultative perennials *Manulea altissima* and *Arctotis diffusa* and perennials *Anchusa capensis* and *Conicosia elongata* have very long phases (Table 3). Annual species must accumulate enough resources in this phase in order to reproduce. In the case of perennials, the optimum reproductive effort a plant expends in a particular year will depend upon how reproductive allocation (RA) affects the lifetime balance between reproduction and survival (Silvertown 1987), i.e. RA must not decrease the chances of survival of the individual.

The transition from vegetative to reproductive growth is largely genetically controlled but is also influenced by environmental factors, such as temperature and daylength (Evans 1975). Steyn (1991) found that for *Dimorphotheca sinuata* and *Ursinia cakilefolia* the plants' response to temperature was modified by the prevailing photoperiod, although an endogenous rhythm could also play a role. In all the species flower initiation occurred later than 50 days after sowing the seeds. Most of the species took between 20 and 40 days for the flower to develop and anthesis to occur. The number of days until first ripe fruit varied greatly, some species for example *Osteospermum hyoseroides* taking 102.6 days from sowing while others such as *Conicosia elongata* took 184.2 days (Table 3).

The lifespan of the different annual species vary from 158 days in *Heliophila rigidiuscula* to 253.2 days in *Foveolina albida* (Table 3). The above-ground structures of the perennials such as *Grielum humifusum* and *Conicosia elongata* die 251.8 and 268.6 days respectively while the above-ground structures of *Hypertelis salsoloides* remain present until the next growing season.

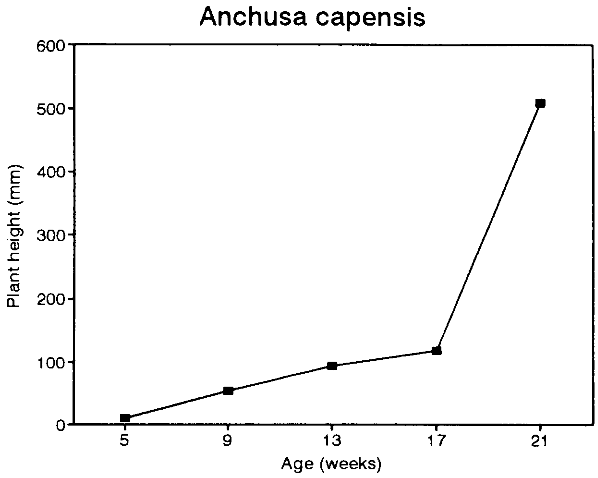
3) Plant height

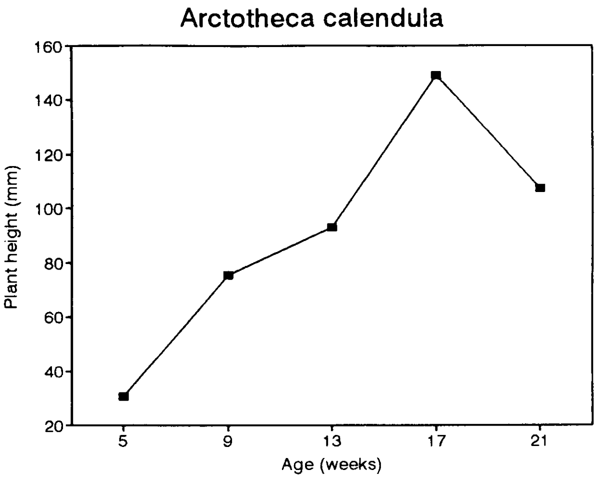
As species grow they increase in height (Figure 2), some more than others depending on their growth form. The growth form is determined by the species genotype (genetic make-up) as well as its environment. Some plant species such as *Conicosia elongata*, *Gazania lichtensteinii*, *Grielum humifusum* and *Lessertia diffusa* are shorter than 150mm, while others such as *Anchusa capensis*, *Heliophila rigidiuscula*, *H. variabilis*, *Oncosiphon suffruticosum*, *Osteospermum amplectens* and *Senecio piptocoma* are 500mm or taller (Figure 2).

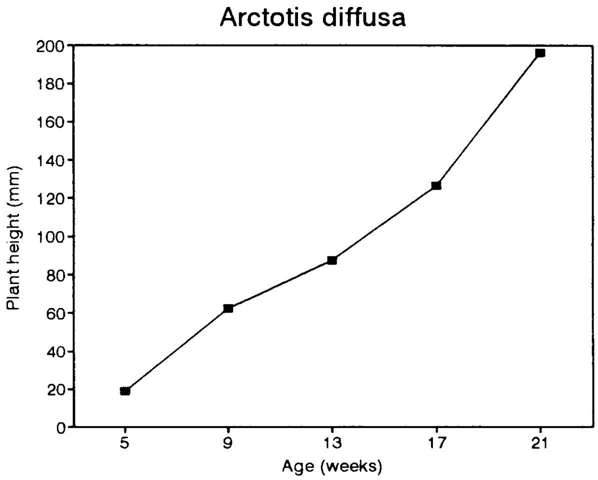
The rate of increase in plant height over time varies i.e. some species have a very pronounced lag phase such as *Anchusa capensis* and *Cotula thunbergii*, whereas others experience a gradual increase in height from the start (*Arctotheca calendula* and *Arctotis diffusa*).

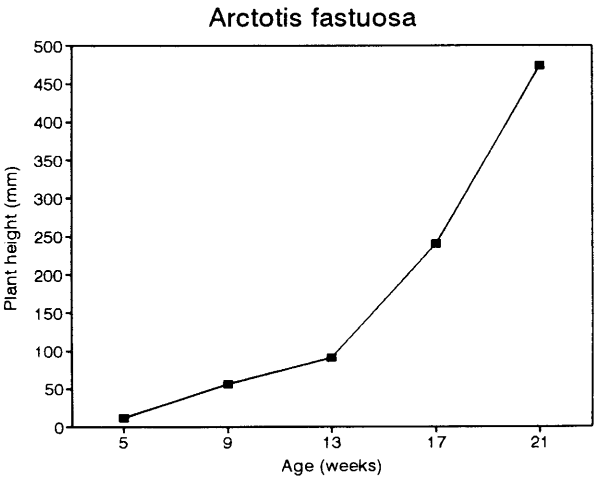
The large increase in plant height in some species after seventeen weeks is largely due to the beginning of the reproductive phase and the formation of inflorescences at the tips of long stems, for example *Anchusa capensis* in which the plant height increased from an average of 118mm to 508mm between the seventeenth and twenty-first week (Figure 2). The maximum plant height in some species such as *Anchusa capensis*, *Cotula thunbergii* and *Manulea altissima* differs markedly from the maximum vegetative plant height.

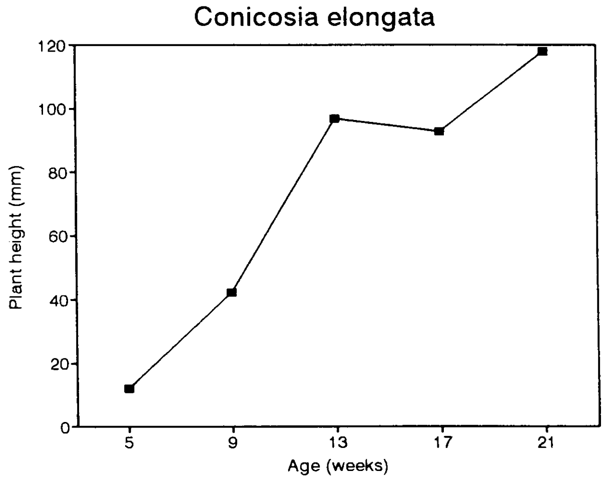
In some species the maximum plant height was already reached at an age of 17 weeks, whereafter plant height either decreased as the inflorescence died (e.g. *Arctotheca calendula*) or remained approximately constant as the species continued to flower (e.g. *Gazania lichtensteinii*).











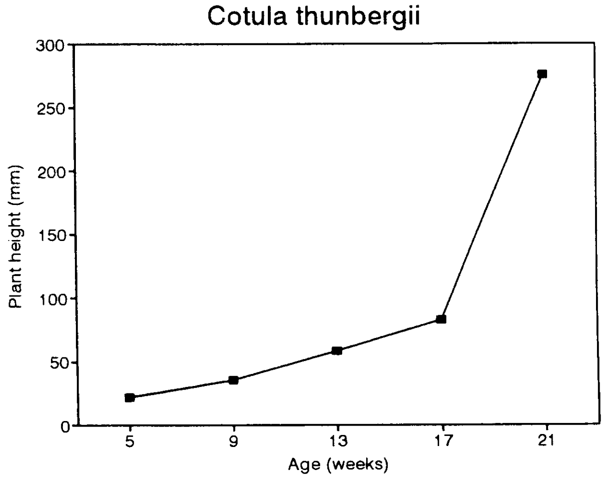
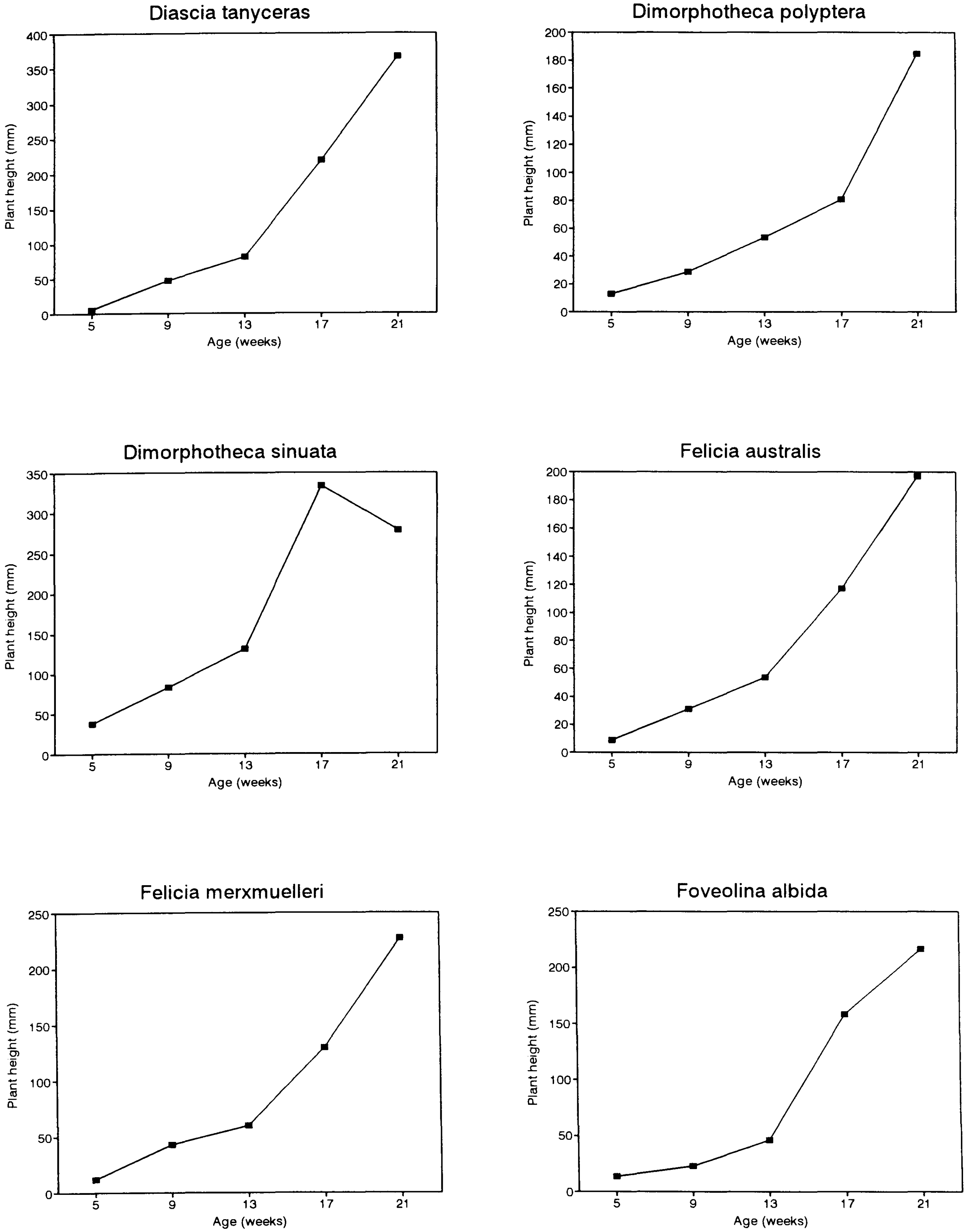


Figure 2. Average plant height plotted against time for 30 Namaqualand plant species.



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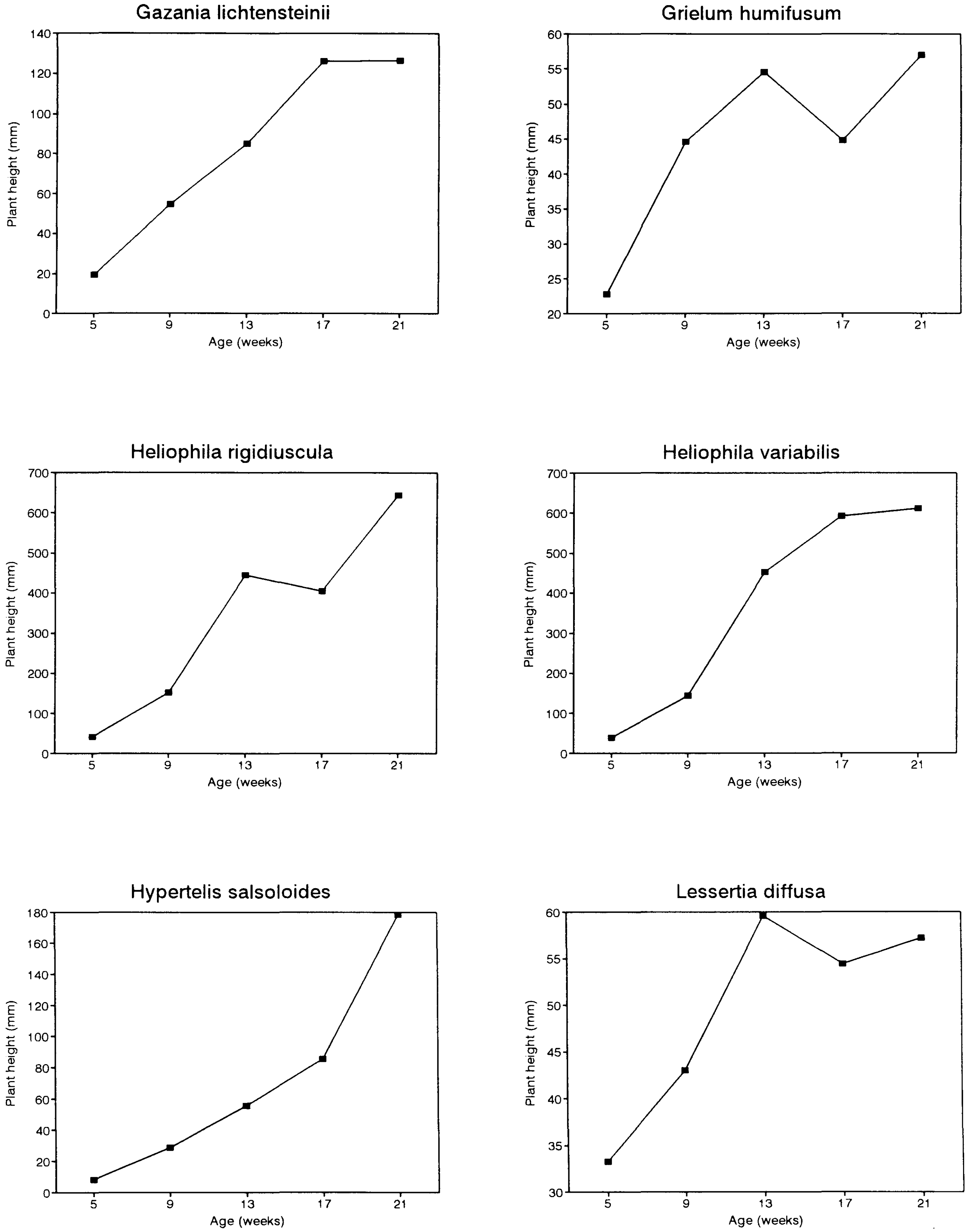

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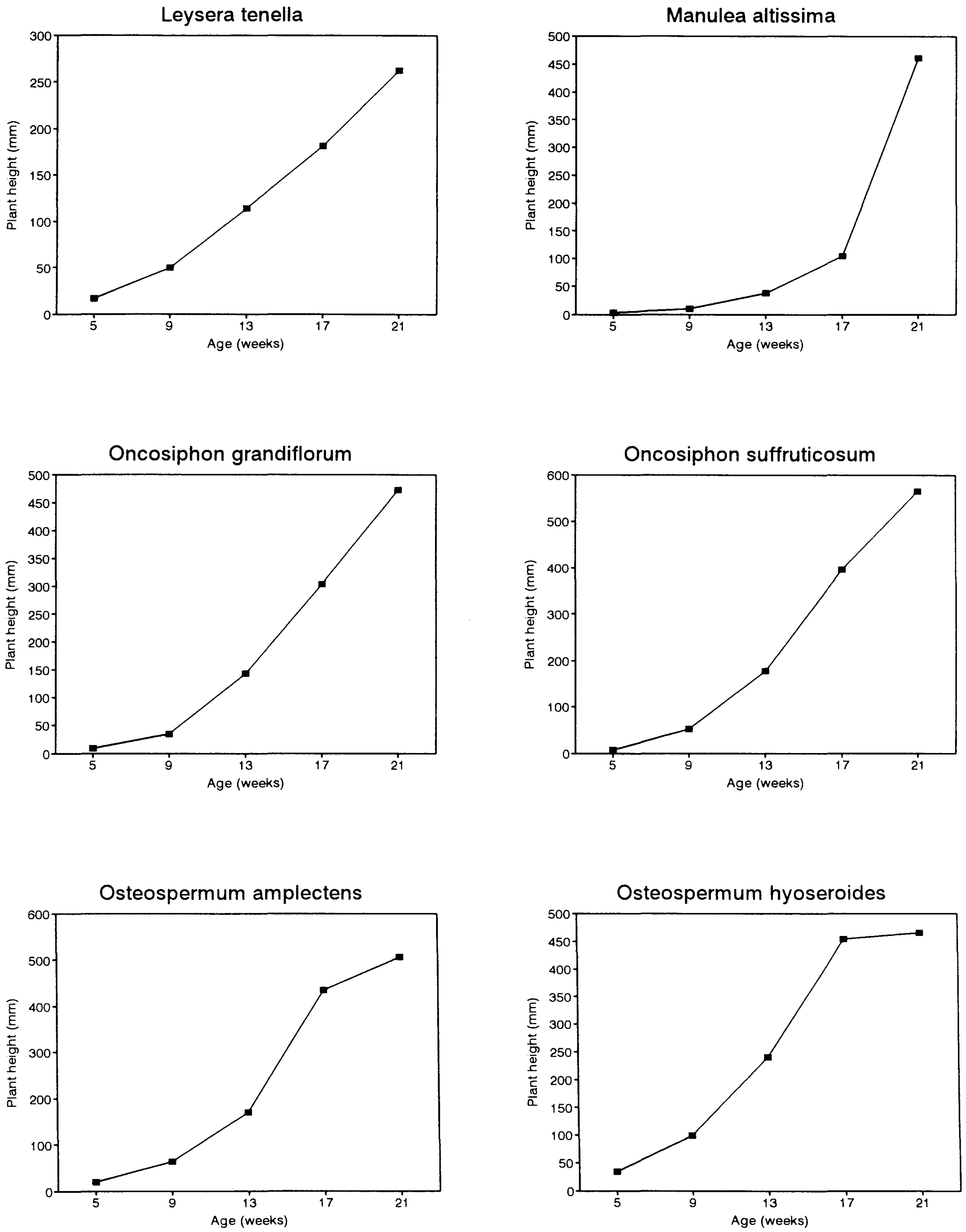

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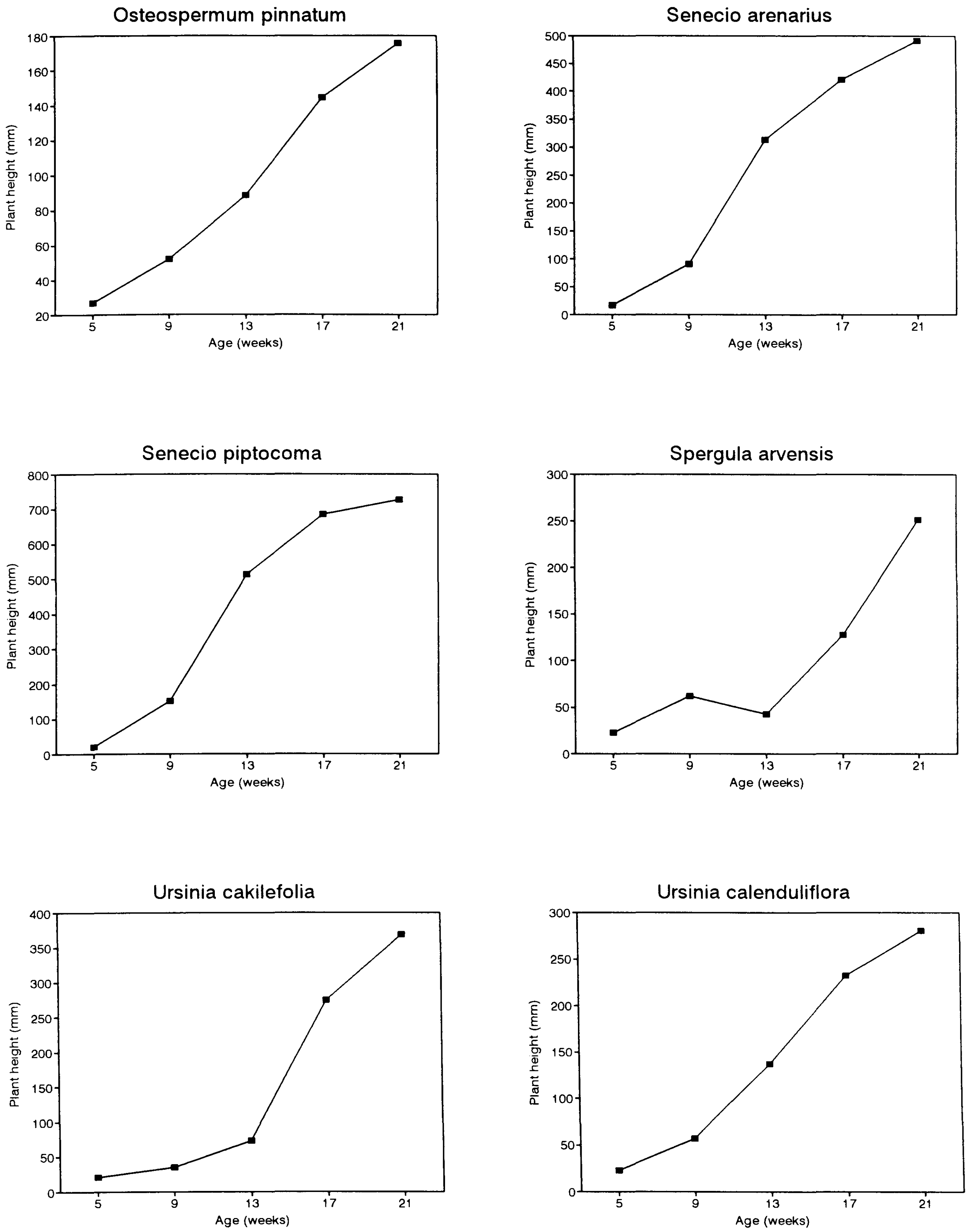


Figure 2. (Continued)

4) Dry mass

In all the species, as to be expected, the total mass of the plant increased with time. The maximum total mass of the species differs greatly. Species with low maximum total masses (*Conicosia elongata*, *Grielum humifusum*, *Hypertelis salsoloides* and *Manulea altissima*) are sharply contrasted by species with high maximum total masses (*Arctotis fastuosa*, *Oncosiphon grandiflorum*, *O. suffruticosum* and *Ursinia calenduliflora*) (Figure 3). The three perennial species (*C. elongata*, *G. humifusum* and *H. salsoloides*) were the three species with the lowest maximum total mass. Total plant mass is an indication of plant size, which is known to be an important indicator of competitive ability. Gaudet & Keddy (1988) found that plant biomass explained over 60% of the variation in competitive ability among plants.

The leaf, stem, root and reproductive masses all increased over time,the increase was slow in the lag phase and greatest after the thirteenth week after which the plant was established. Also, in all the species, except *Conicosia elongata* (Figure 3), there was a dramatic increase in reproductive mass between the seventeenth and the twenty-first week as the plants had accumulated enough resources to divert these into reproductive structures rather than vegetative structures. The phenology diagram (Figure 1) indicates that flower initiation occurred very late in *C. elongata* compared to the other species thus the reproductive mass of the species would have increased after the last harvest.

5) Biomass allocation

Life histories are, in part, the result of selection for the optimal allocation of resources or energy to life activities such as maintenance, growth and reproduction (Abrahamson 1979). The life history strategy of a plant determines its ability to survive in its habitat. In habitats that are less mature or more highly disturbed, plants tend to allocate a greater proportion of their total biomass to reproductive structures when compared to plants of more productive habitats or less disturbed areas

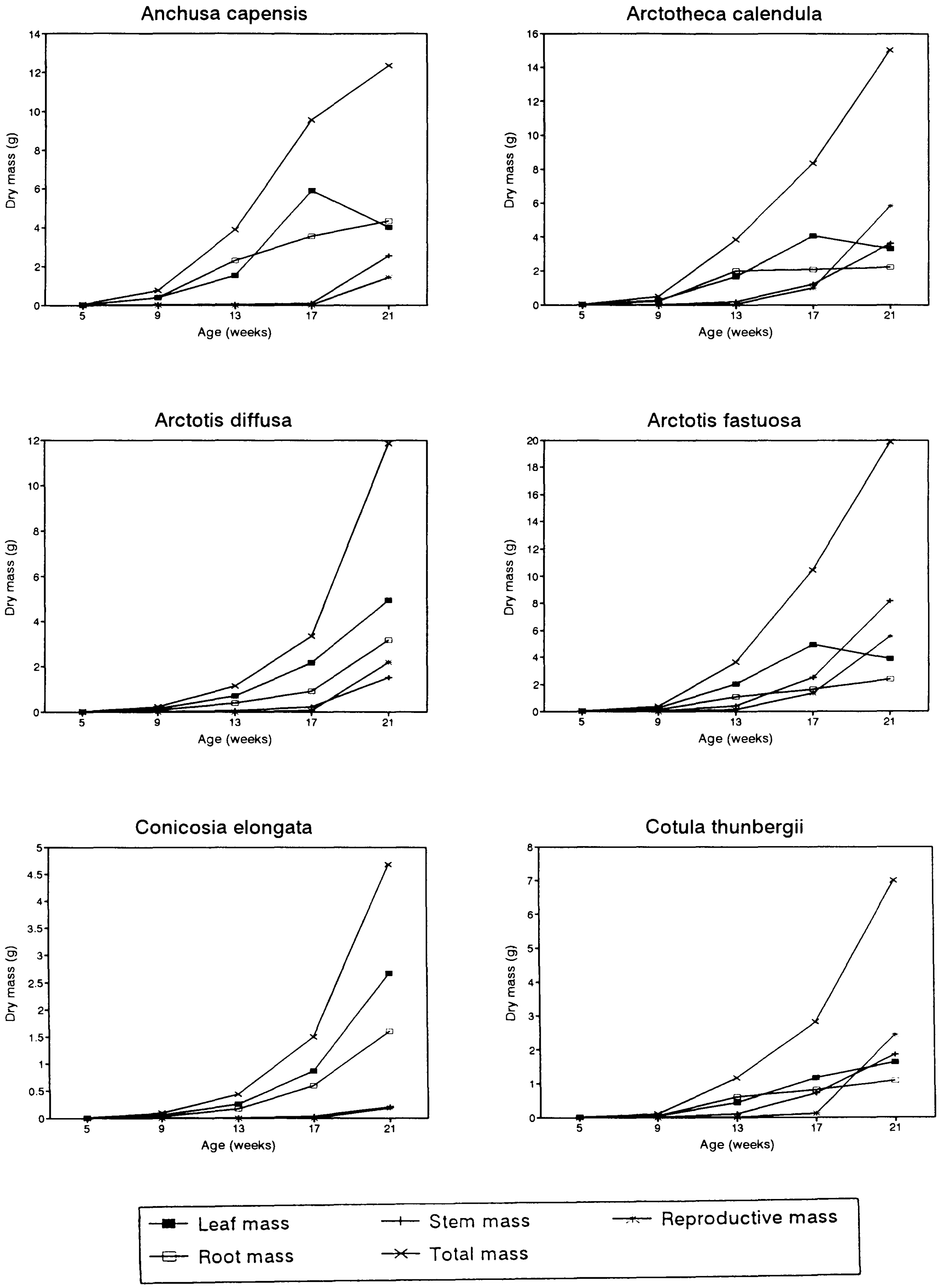
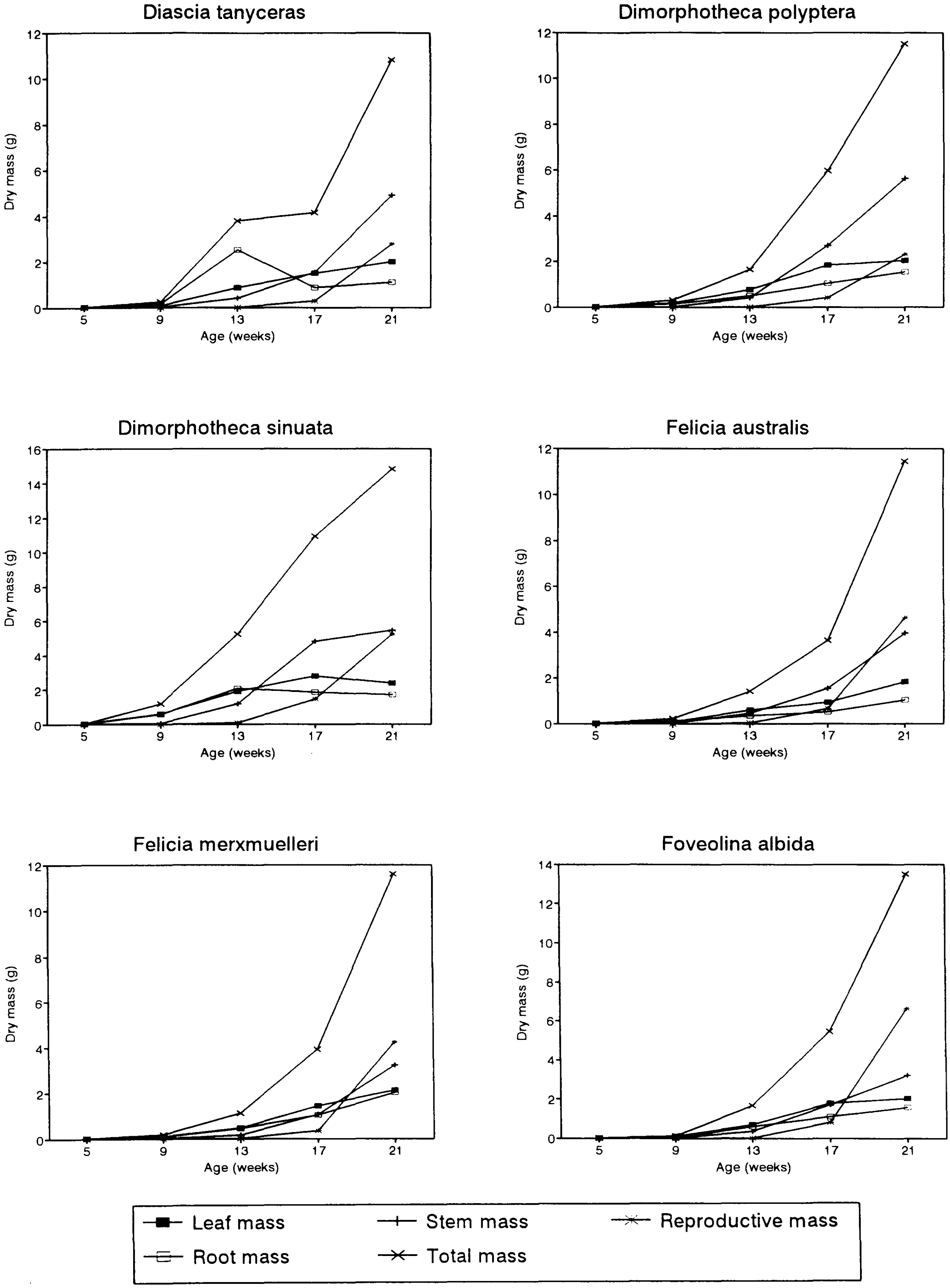


Figure 3. Total plant mass and mass of the individual organs plotted against time for 30 Namaqualand plant species.



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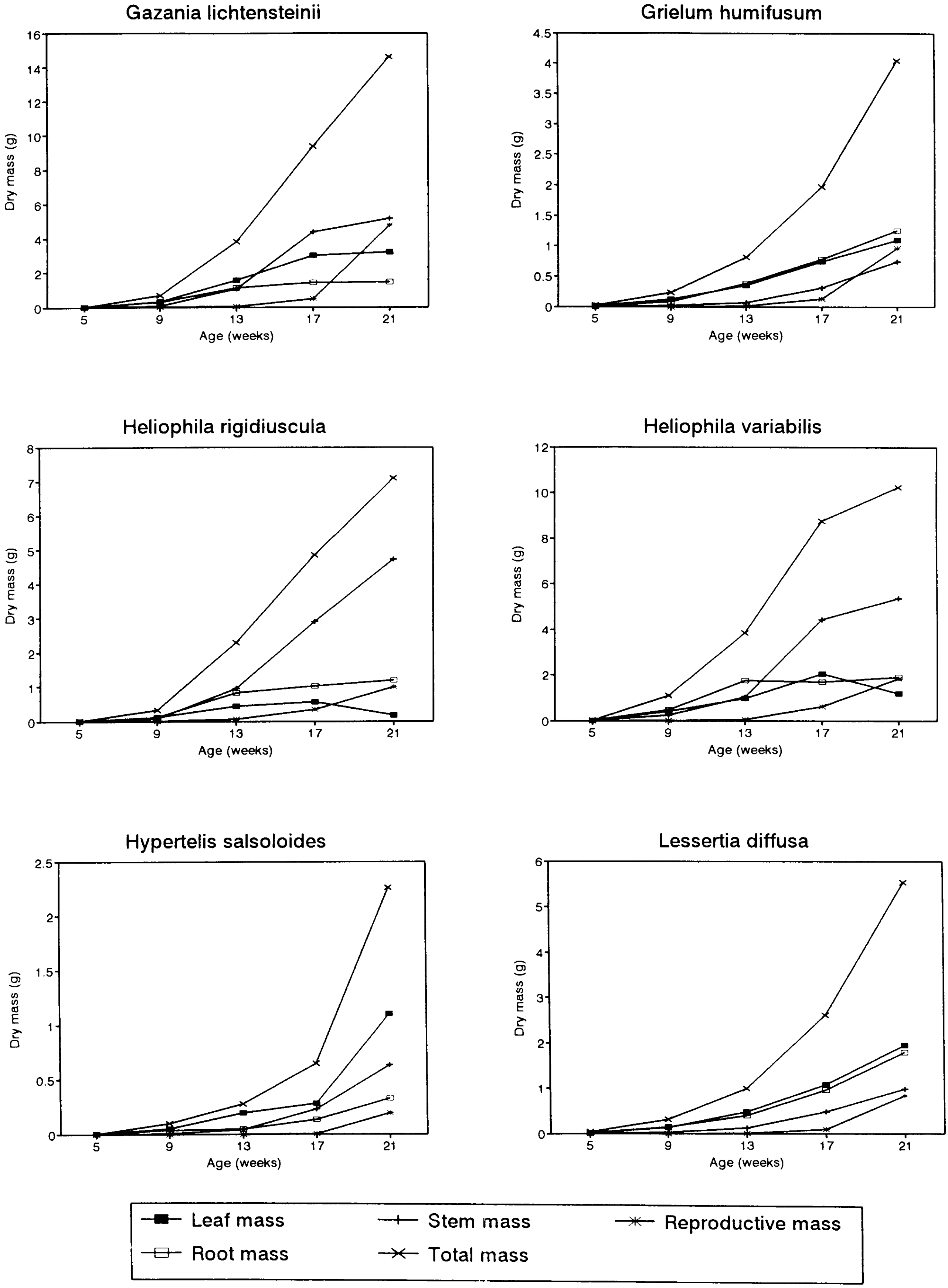

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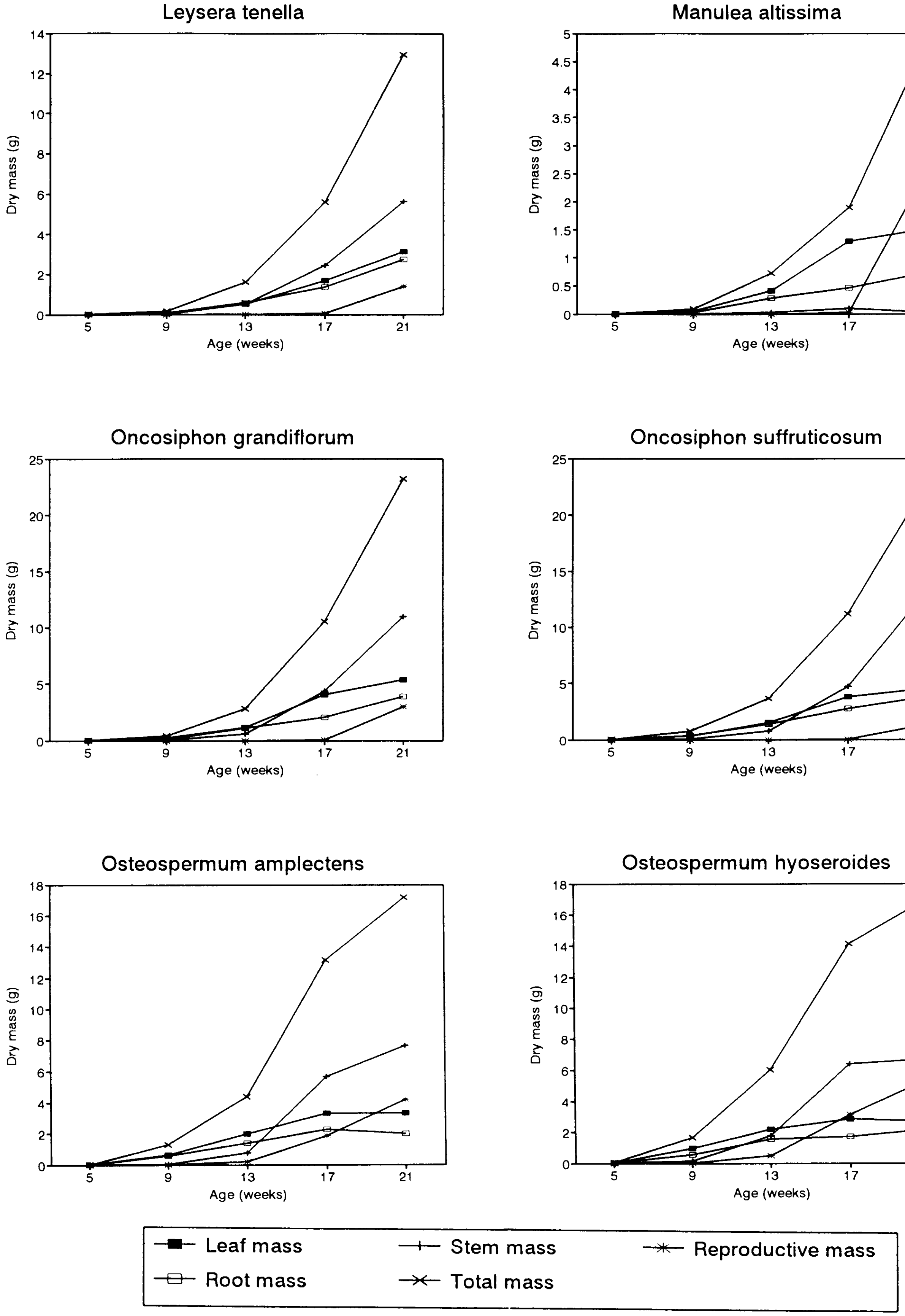

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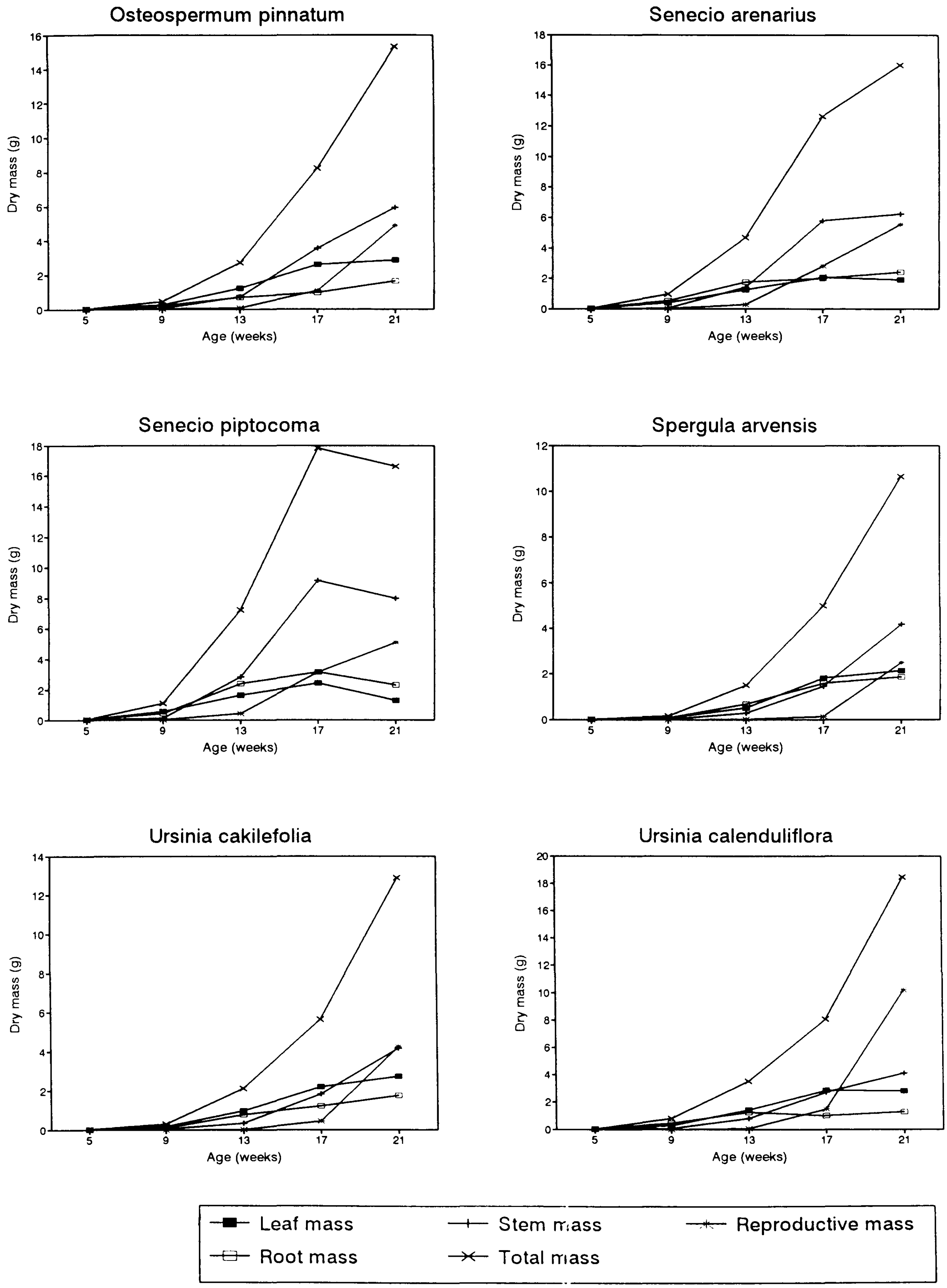


Figure 3. (Continued)

(Abrahamson 1979). As Namaqualand is considered to be a stressed environment, it is expected that reproductive allocation (RA) would be proportionately large.

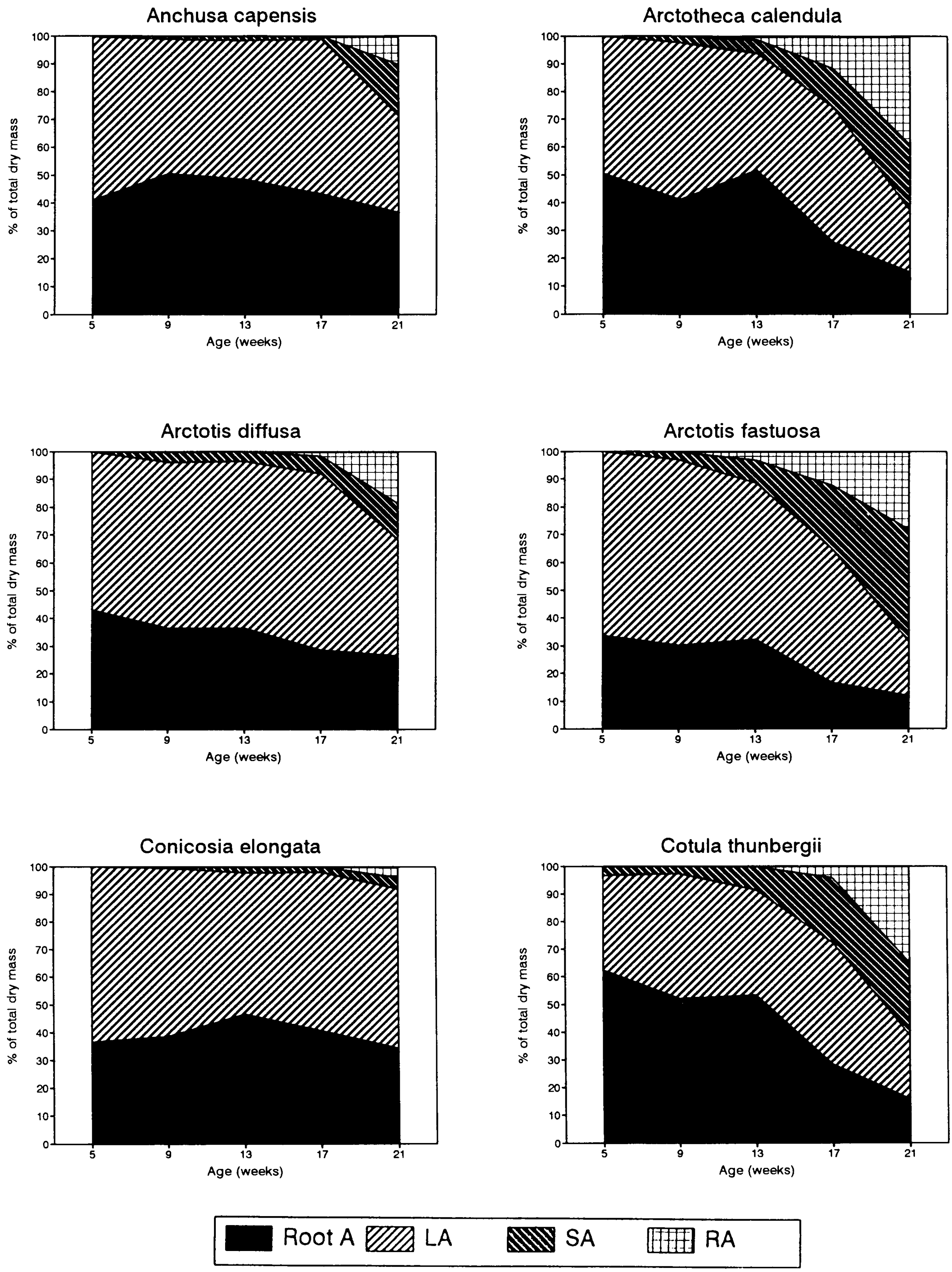
Various species invest different amounts of energy in their organs. Root allocation is initially large and declines with time in most species (Figure 4). This large initial root allocation could be as a result of the species first having to establish an effective root system for efficient water uptake. In some of the species the root allocation increased and then decreased, but the overall trend was a decline in root allocation with time. This decline in root allocation not being so prominent in perennial species.

In all the species, except *Conicosia elongata*, leaf allocation increased and then decreased with time while stem and reproductive allocation increased. *Conicosia elongata*'s (Figure 4) stem allocation remains small as it does not have a characteristic stem due to a rosette-like growth form.

The leaf allocation (LA) in all the species is much larger initially than the stem allocation (SA) as the leaves are the main photosynthetic organs in the production of assimilates needed by the plant to grow and reproduce (Figure 4).

In unpredictable habitats, such as deserts, plants which delay reproduction experience a high risk of dying before reproductive maturity (Silvertown 1987). This is a plausible explantation for the high proportion of annuals found in desert floras (Silvertown 1987). The greatest increase in RA of the perennials (*Conicosia elongata*, *Grielum humifusum* and *Hypertelis salsoloides*) and facultative perennials (*Anchusa capensis*, *Arctotis diffusa*, *Lessertia diffusa* and *Manulea altissima*) is after the seventeenth week, whereas the annuals largely increase their reproductive allocation from the ninth or thirteenth weeks.

Generally, the perennial species *C. elongata*, *G. humifusum* and *H. salsoloides* have a much smaller RA than the annuals. Their reproductive allocations are 3.7%, 24.5% and 7.2% respectively. *Anchusa capensis* and *Oncosiphon suffruticosum* have a small RA over the 21 week period because their phenological development was



Anchusa capensis

Arctotheca calendula

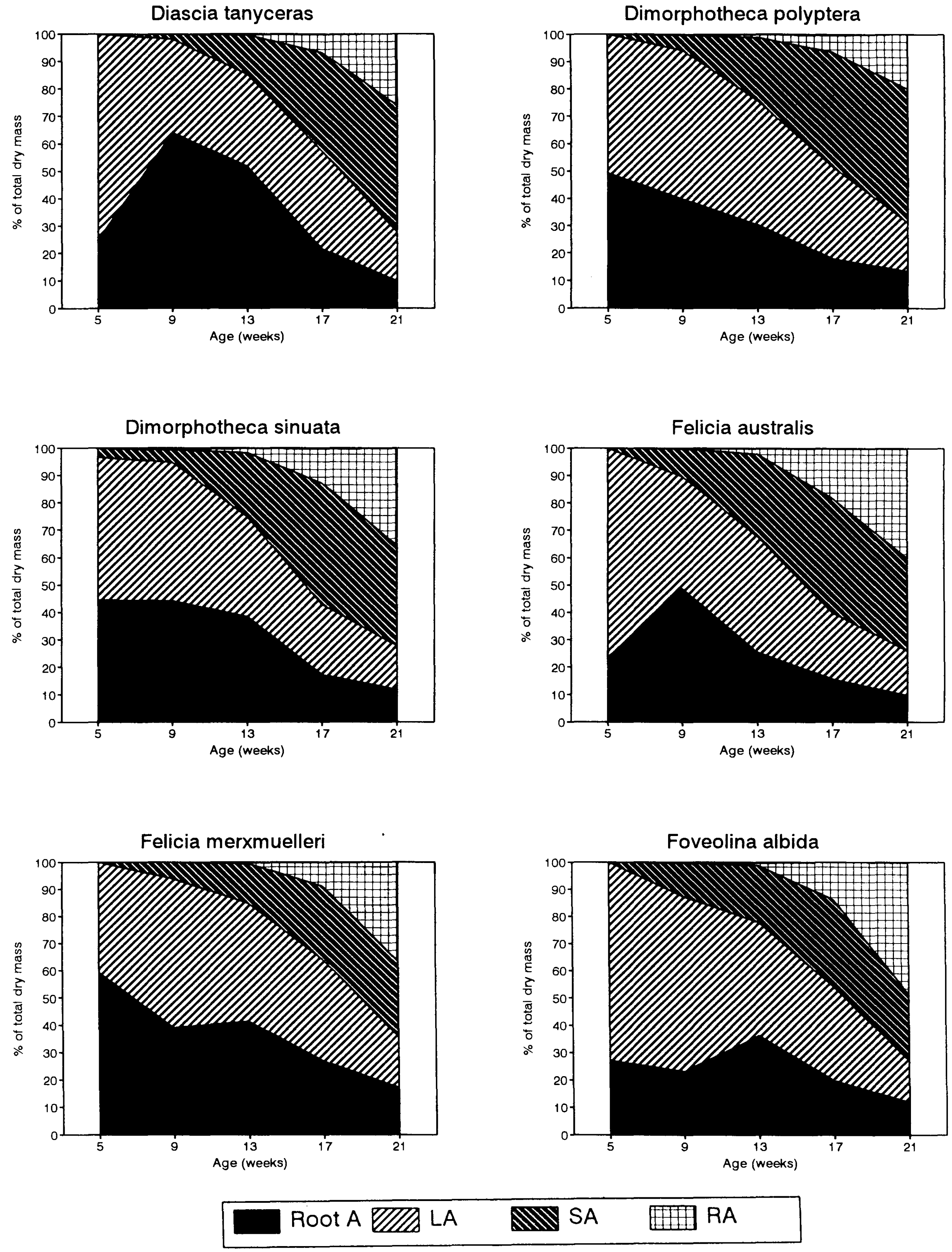
Arctotis diffusa

Arctotis fastuosa

Conicosia elongata

Cotula thunbergii

Figure 4. Changes in dry mass allocation with time. Root A = Root allocation; LA = Leaf allocation; SA = Stem allocation; RA = Reproductive allocation.



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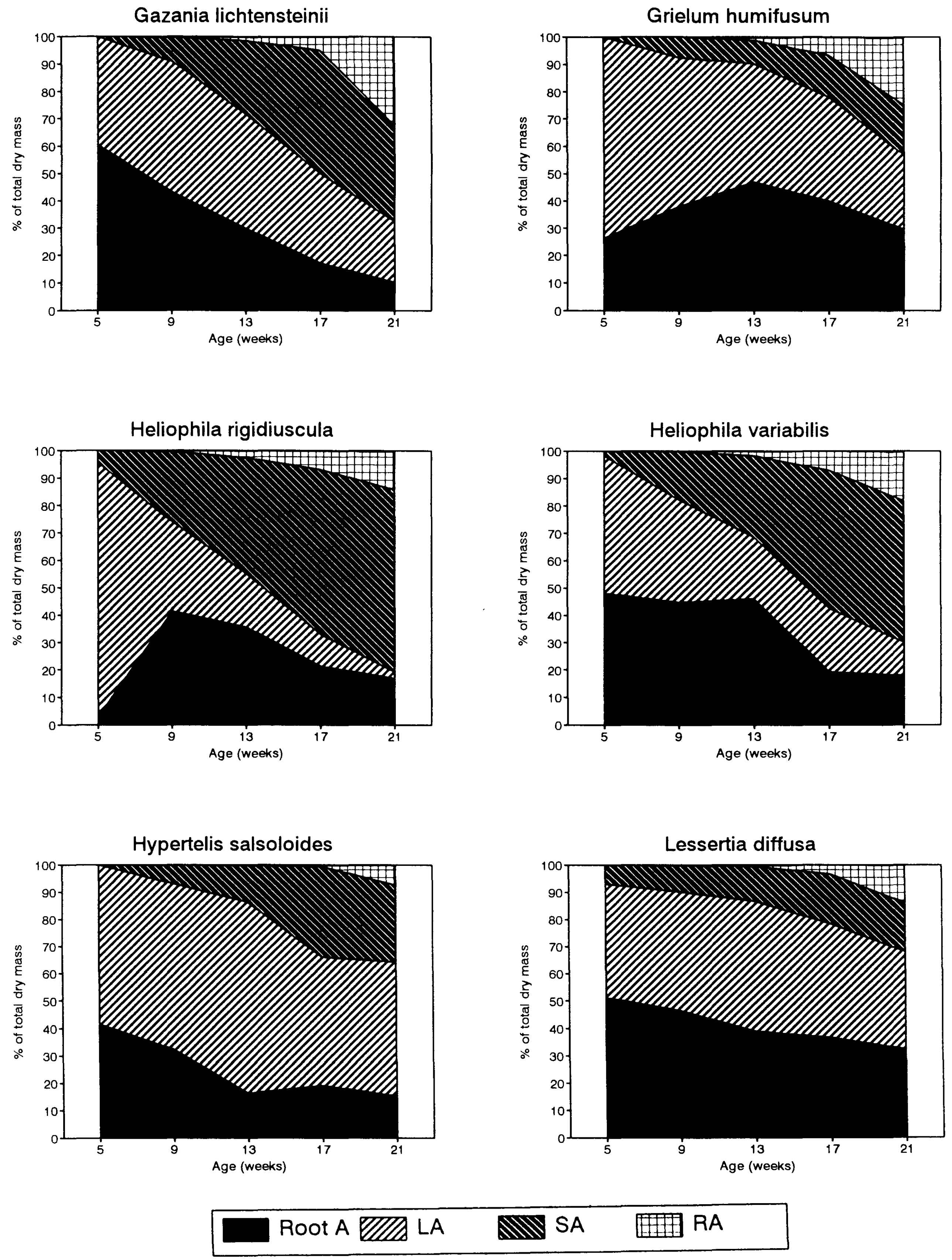

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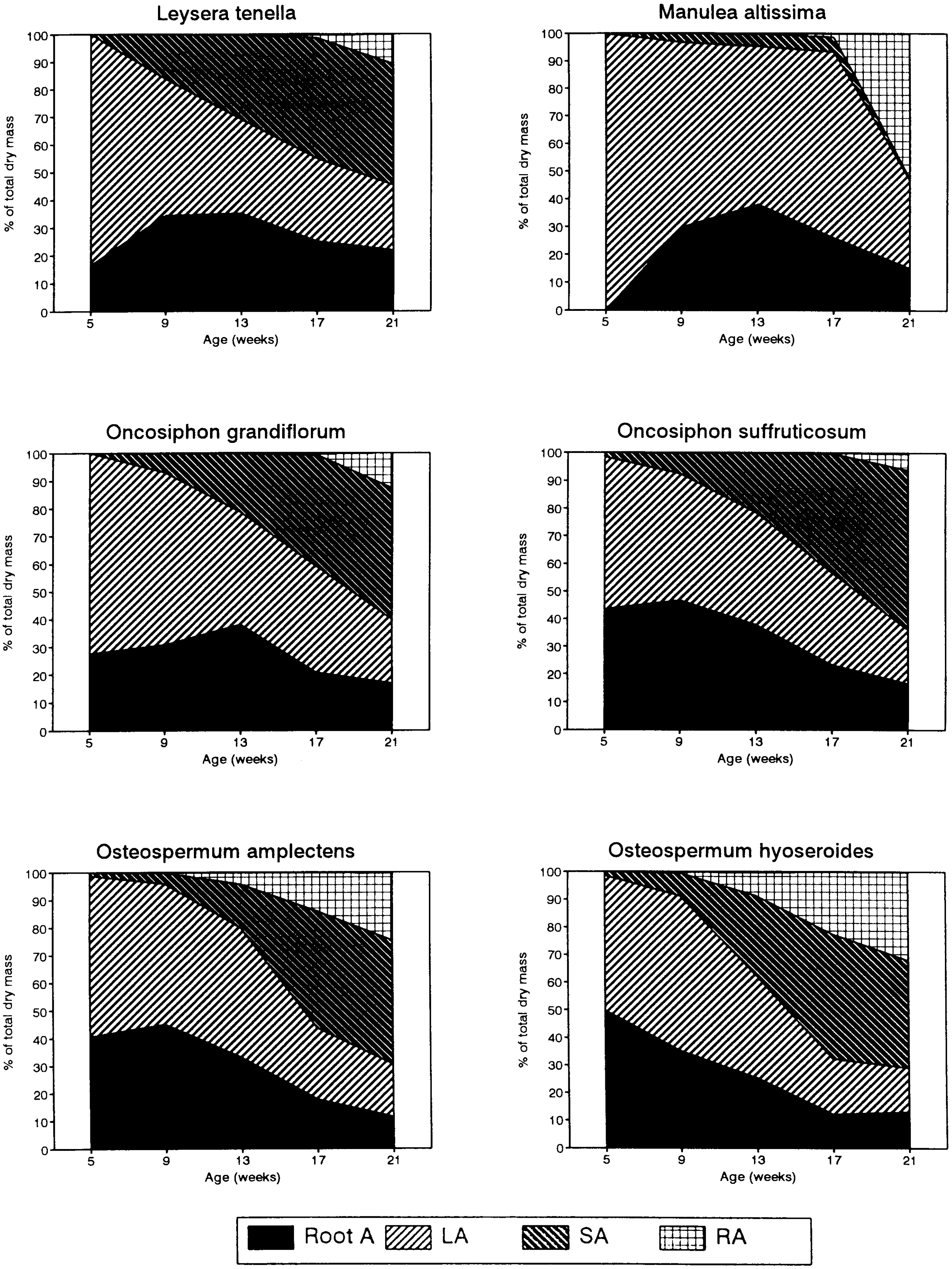

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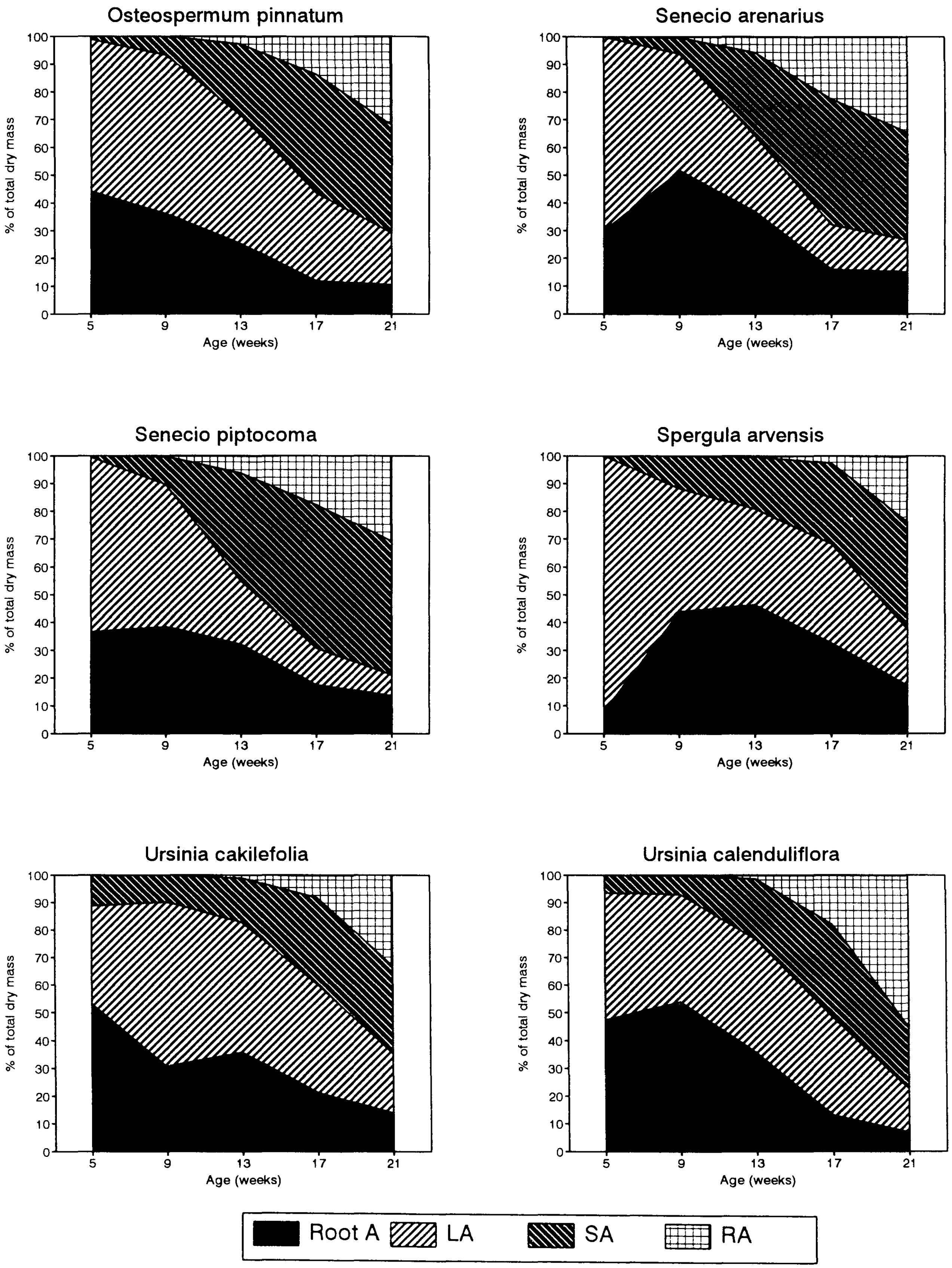


Figure 4. (Continued)

slower than that of the other facultative perennials and annuals (Figure 1), it is thus expected that the RA of these two species would have increased substantially in the next four week period. Perennials possibly have a smaller RA but have the advantage of seed production over many years (Silvertown 1987). The perennial species (*C. elongata* and *G. humifusum*) both produced fewer diaspores over time than most of the annuals. Diaspore production of the facultative perennials (*A. capensis*, *Arctotis diffusa* and *Lessertia diffusa*) was also less than that of the annuals (Table 4).

Table 4. Diaspore production of 15 of the 30 Namaqualand plant species

Species	Number of diaspores produced per plant
Anchusa capensis	599.8
Arctotheca calendula	4406.2
Arctotis diffusa	293.5
Conicosia elongata	1167.0
Dimorphotheca polyptera	5397.8
Dimorphotheca sinuata	4278.8
Gazania lichtensteinii	1559.4
Grielum humifusum	50.6
Heliophila variabilis	4314.8
Lessertia diffusa	960.4
Osteospermum amplectens	2726.4
Osteospermum hyoseroides	2118.3
Osteospermum pinnatum	667.4
Ursinia cakilefolia	3636.6
Ursinia calenduliflora	1602.0

6) Leaf area and leaf area ratio (LAR)

Leaf area increased with age as the leaves on the plant grew and new leaves were produced (Figure 5). This increase in leaf area enables the plant to assimilate enough resources or energy to reproduce.

In all the species the leaf area increased with time. Some species had a reduction in leaf area after the seventeenth week (Figure 5), as a result of leaf loss exceeding the production of new leaves (Figure 4), this was particularly noticeable in species such as *Arctotheca calendula*, *Heliophila rigidiuscula* and *H. variabilis*.

Leaf area ratio (LAR) characterises the relative size of the assimilatory apparatus, thus being a useful measure of differences between plants or stands resulting from genetic factors, environmental factors or different treatments (Kvet *et al.* 1971) (Figure 5). The LAR usually decreases with time (Reekie & Bazzaz 1987), as the increase in plant mass is larger than the increase in leaf area. In *Cotula thunbergii*, *Felicia merxmuelleri*, *Heliophila rigidiuscula* and *Ursinia cakilefolia* LAR first increased then decreased.

7) Reproductive structures

In most species there was an increase in the number of buds after the ninth week (Figure 6). The species that did not show this increase namely *Arctotis diffusa*, *Conicosia elongata*, *Manulea altissima*, *Oncosiphon grandiflorum* and *O. suffruticosum* were all species in which phenological development was slower and flower initiation occurred later (Figure 1). The total number of reproductive structures continued to increase throughout the monitoring period. This increase was greatest after the seventeenth week when the classes of anthesis, withered and fruit increased in number.

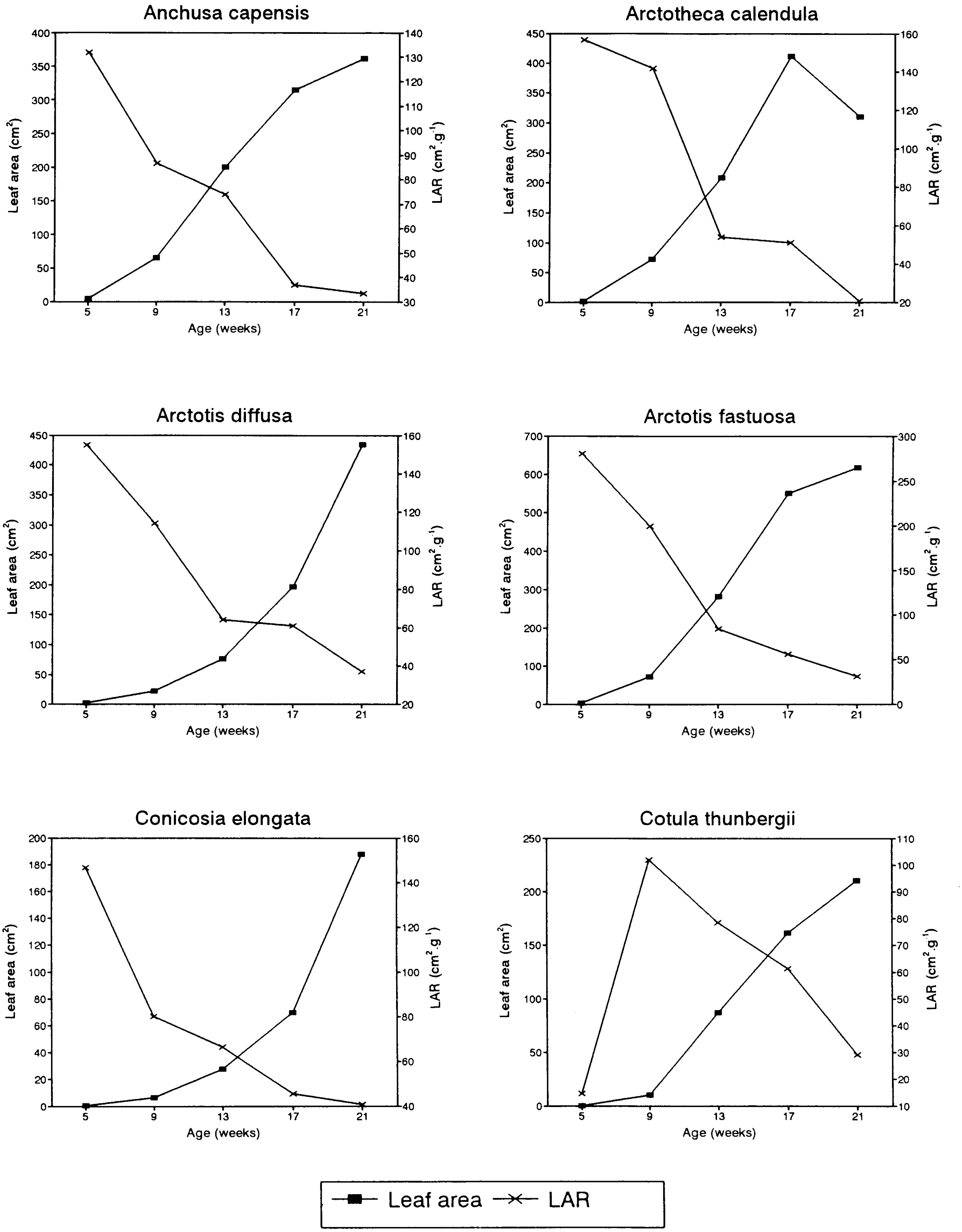
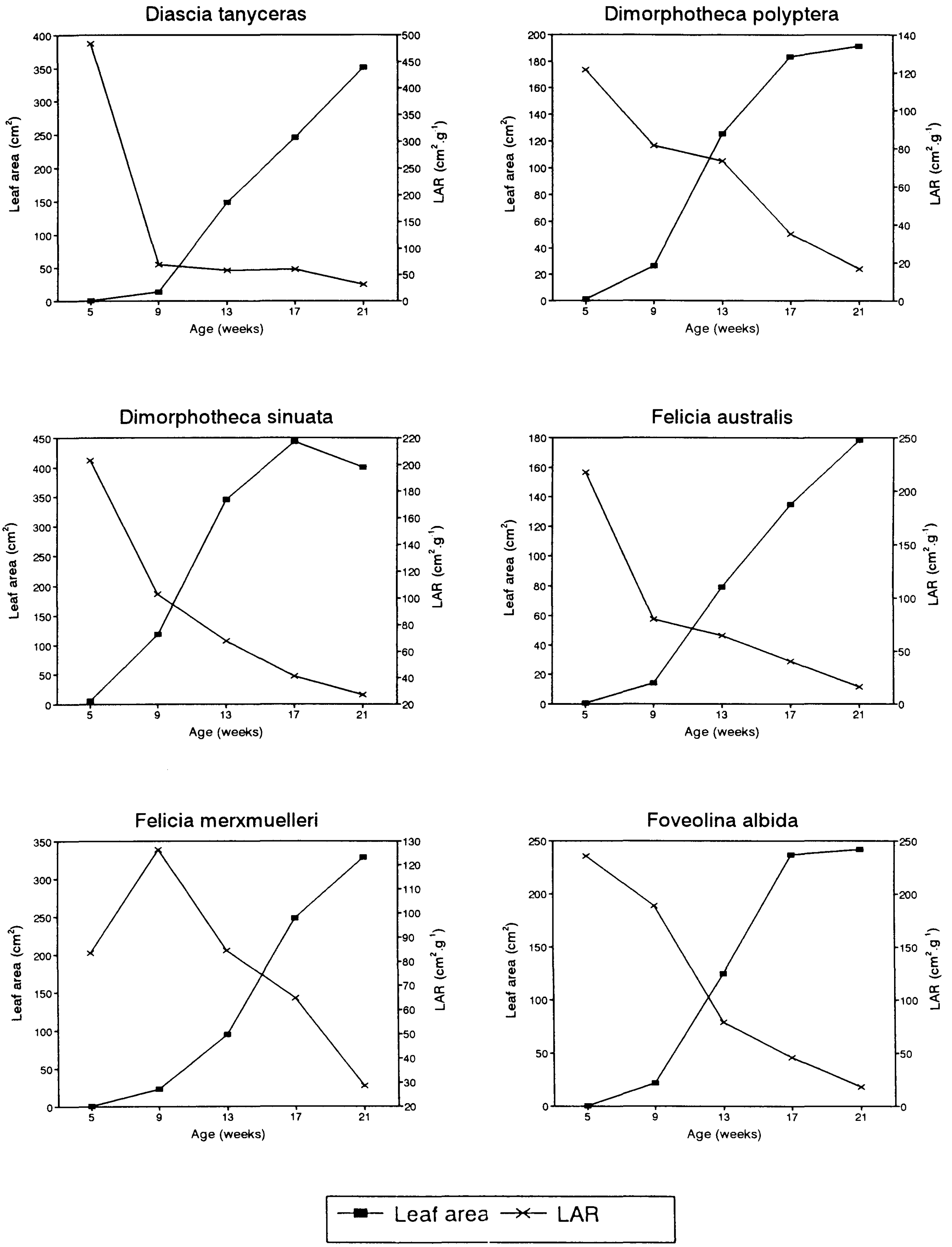


Figure 5. Leaf area and leaf area ratio (LAR) against time of 30 Namaqualand plant species.



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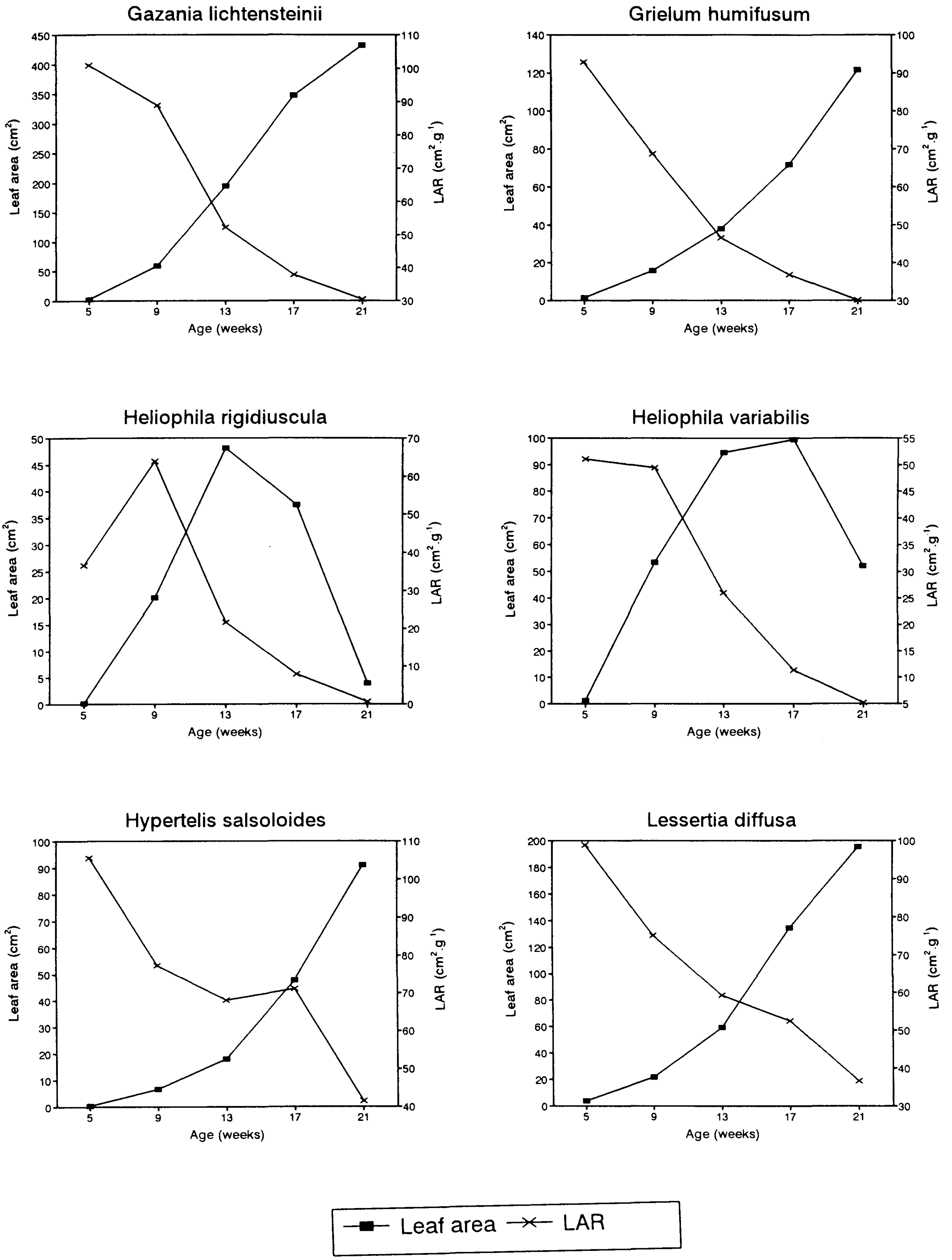

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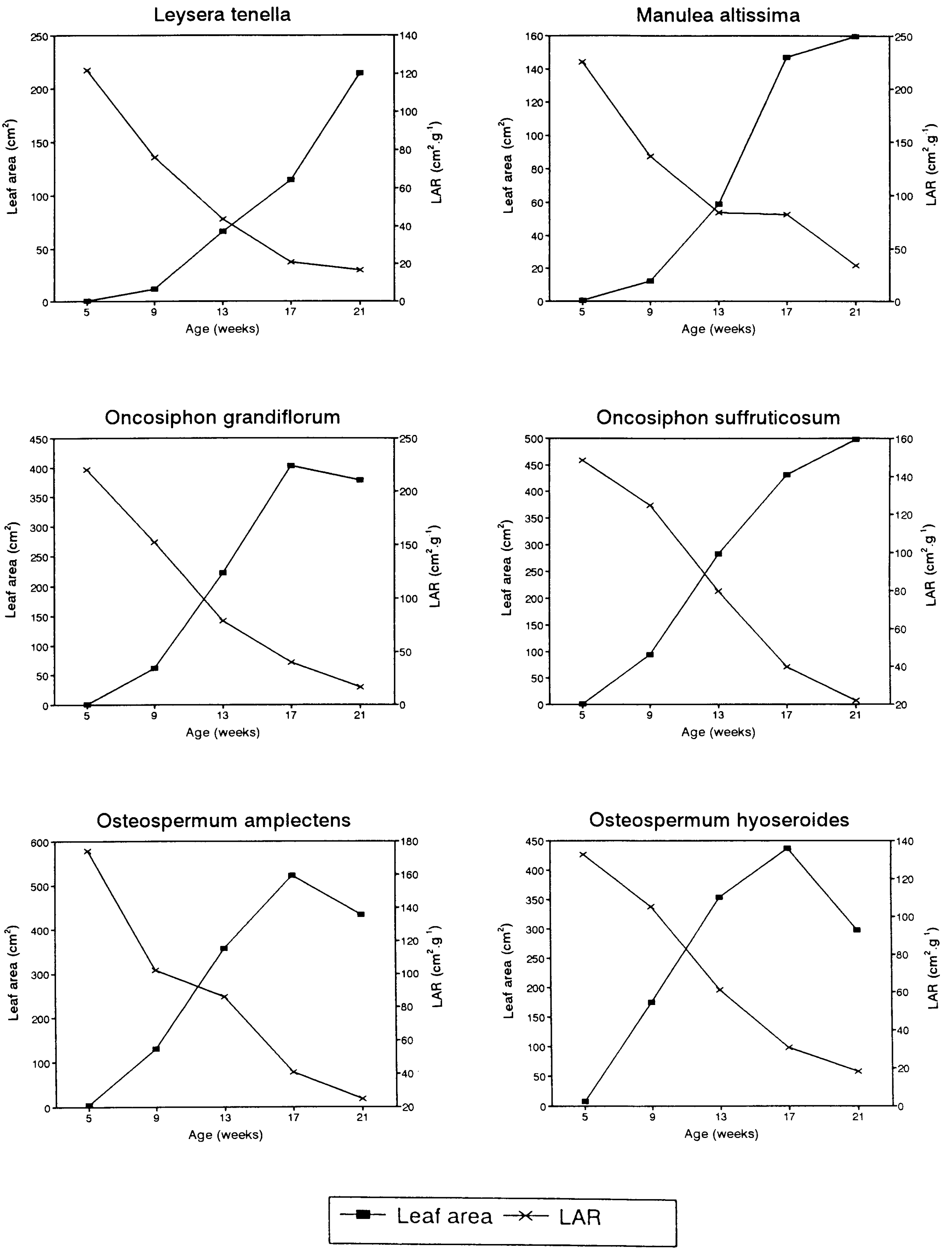

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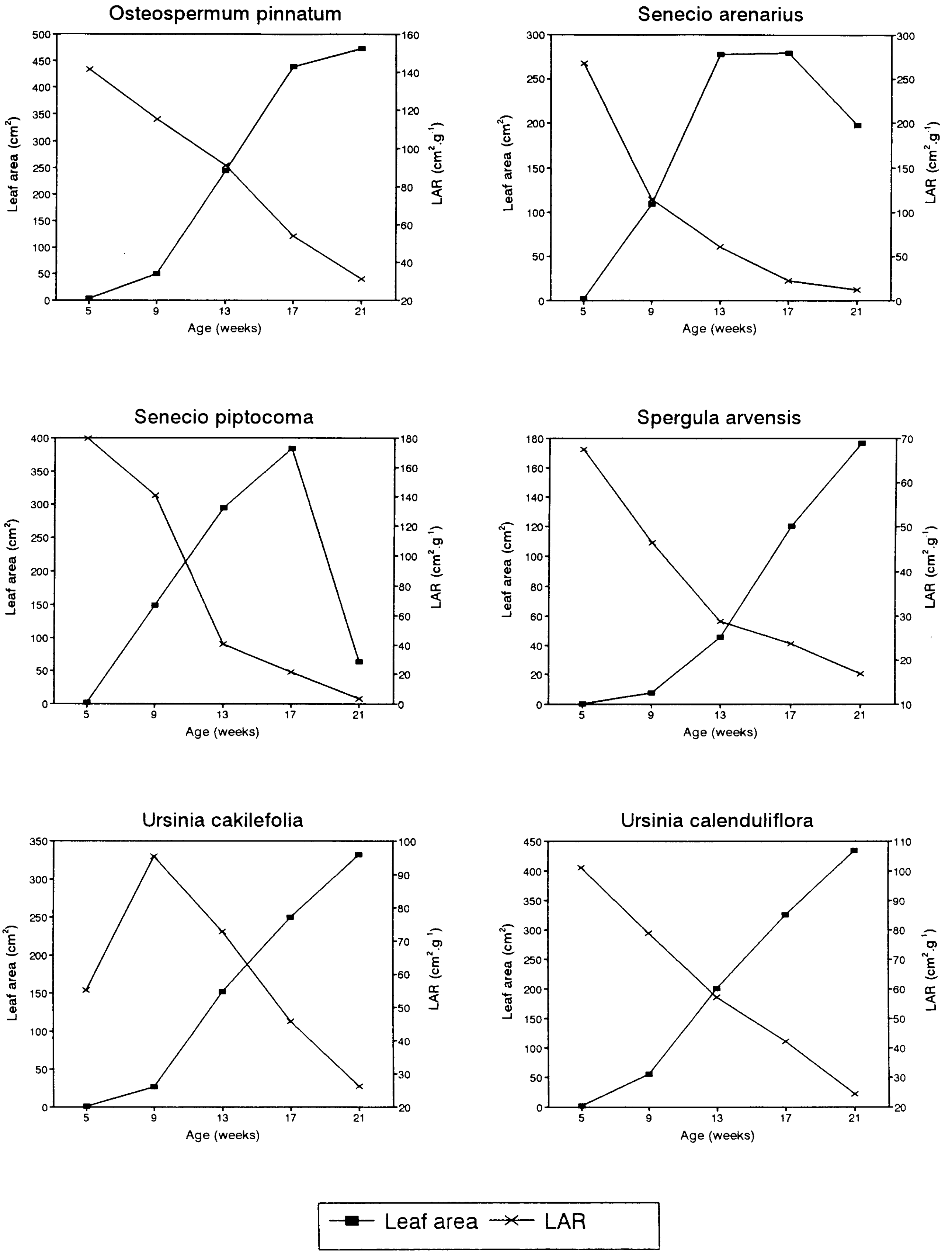

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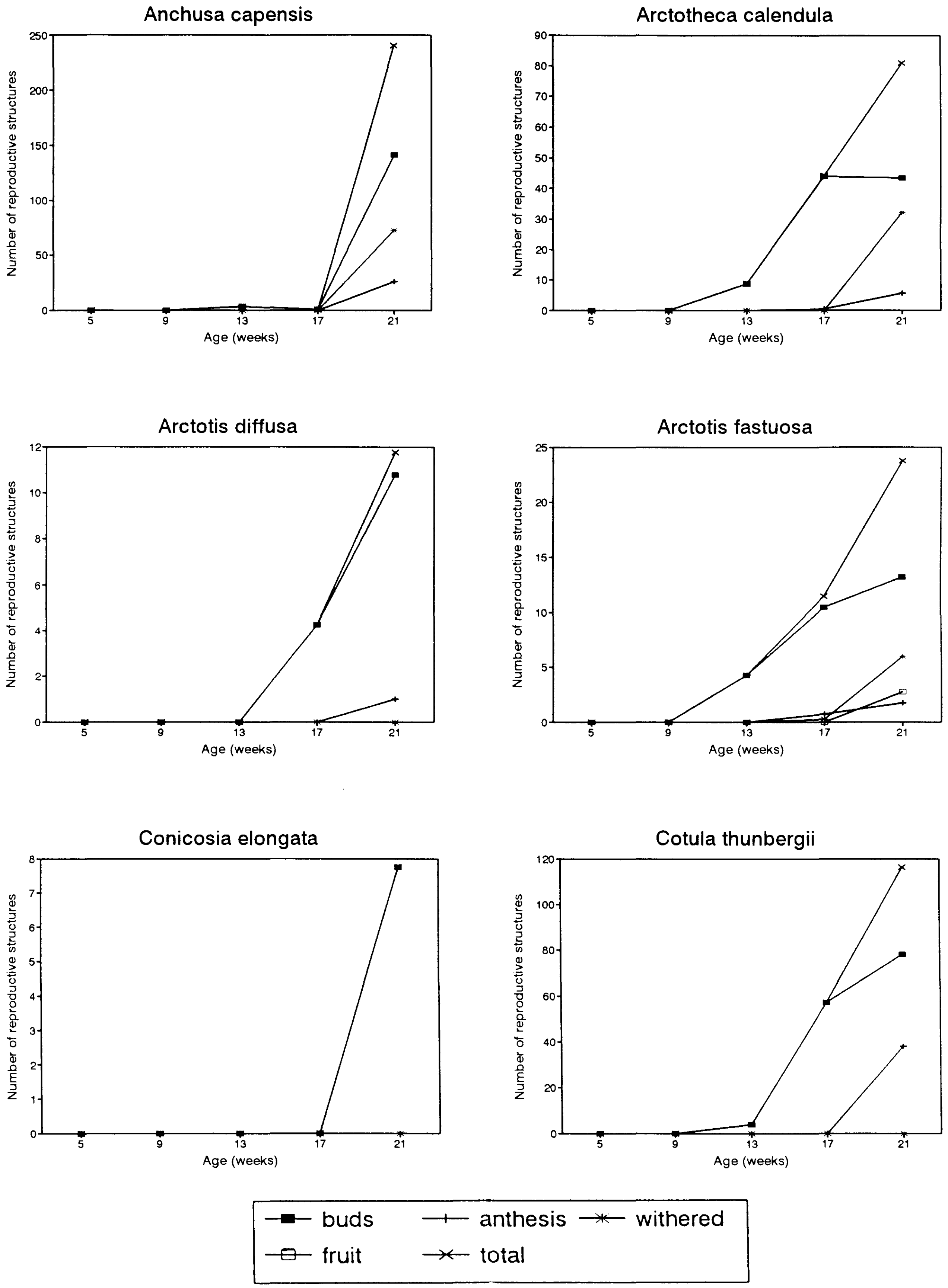
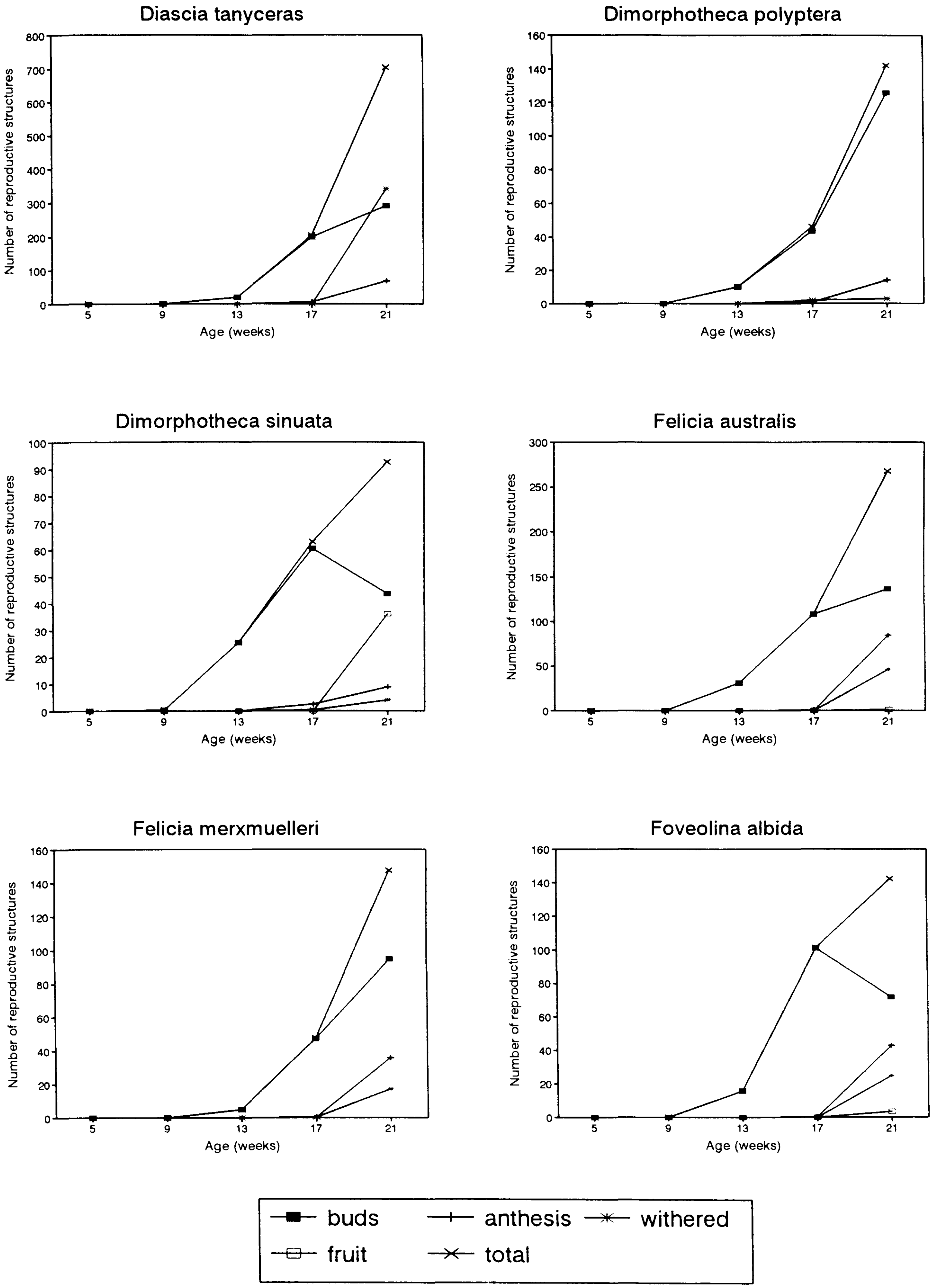


Figure 6. Total number of reproductive structures per plant and number of reproductive structures in classes: buds, anthesis, withered and fruit for 30 Namaqualand plant species.



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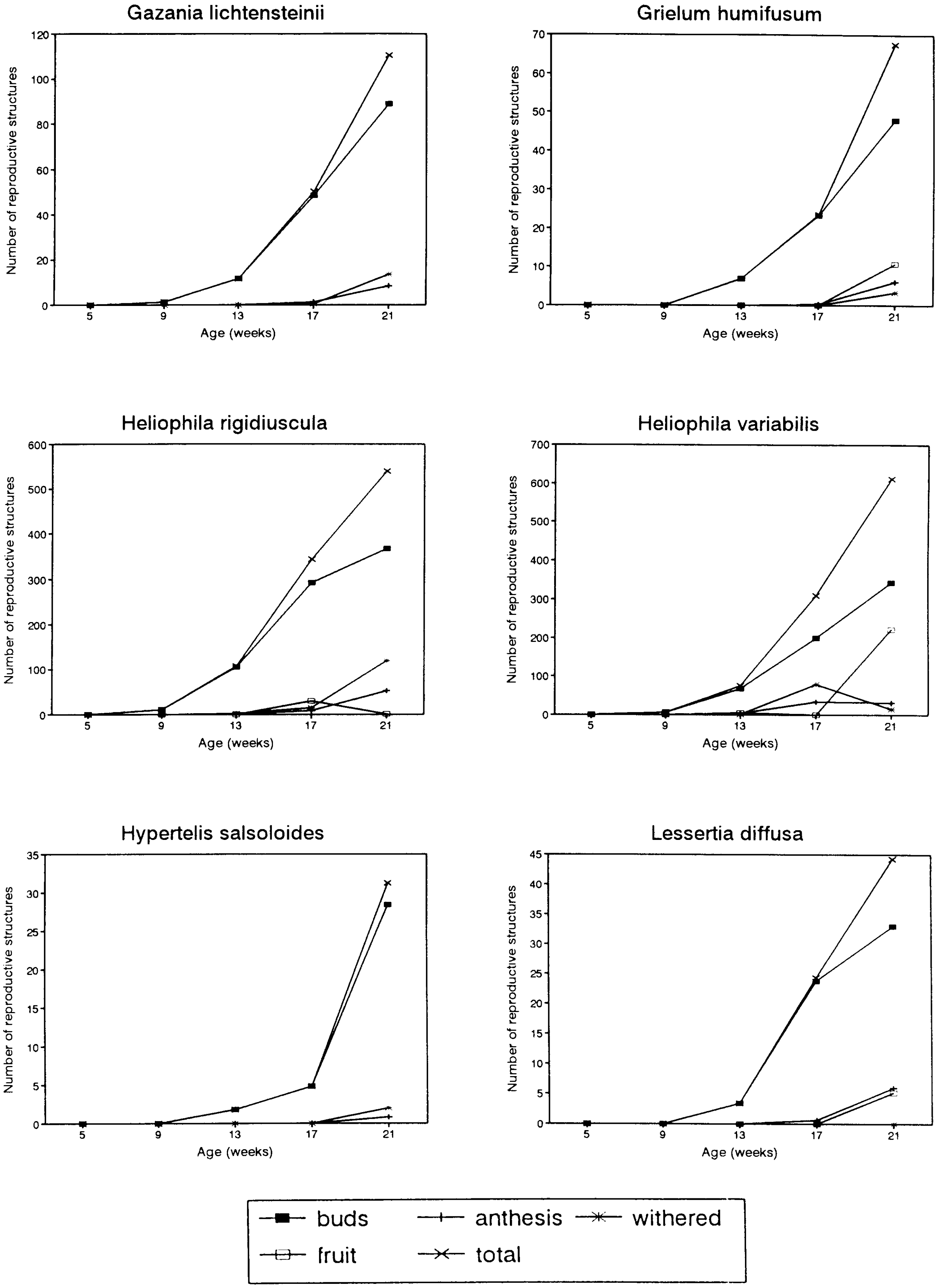

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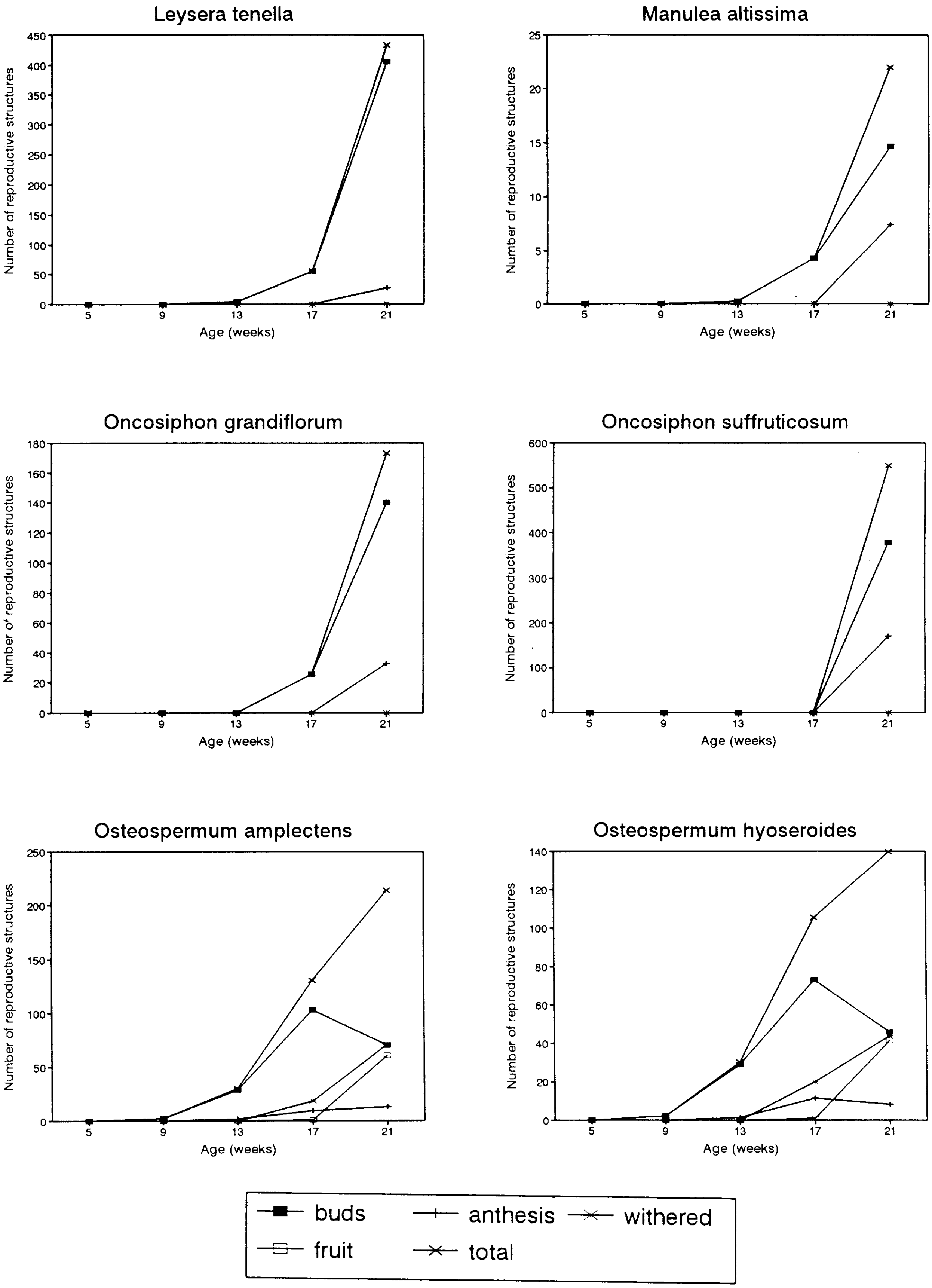

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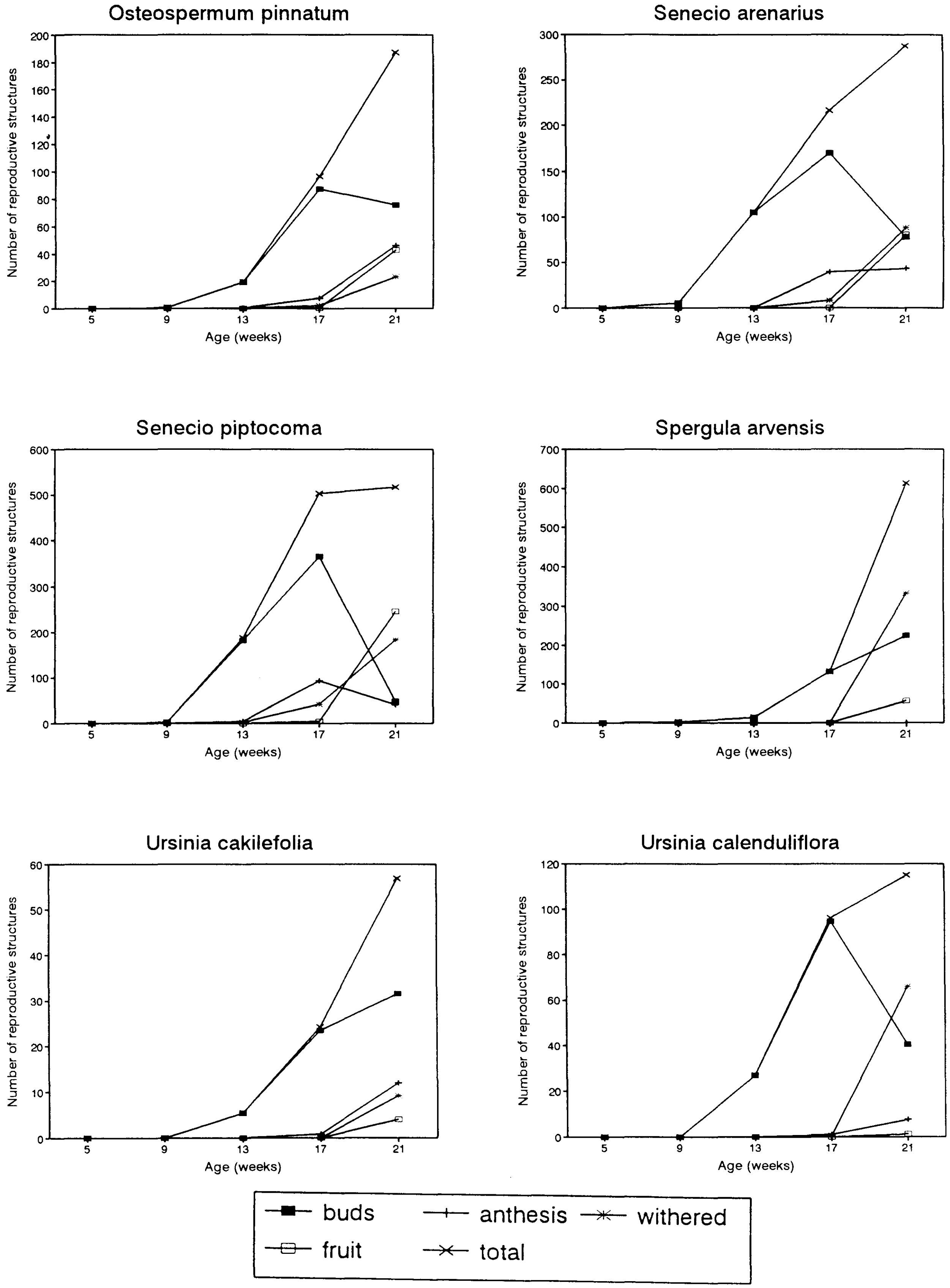

Figure 6. (Continued)

Summary

Life history traits are genetically and environmentally determined for each species in a given environment (Barbour *et al.* 1987). The unpredictable nature of the rainfall in Namaqualand has caused the species to evolve various strategies that have led to different life history patterns and thus different plant traits, which enable the species to survive under these conditions.

Three main strategies (perennial, facultative perennial and annual) were distinguished between the 30 Namaqualand pioneer plant species studied. The perennials (*Conicosia elongata*, *Grielum humifusum* and *Hypertelis salsoloides*) and facultative perennials (*Anchusa capensis*, *Arctotis diffusa*, *Lessertia diffusa* and *Manulea altissima*) are distinguished from the annuals largely by their differing phenological development.

No trends in dispersal type, plant height, root allocation, stem allocation, leaf allocation, and LAR could be found to distinguish the three strategies. However, clear distinction between these three strategies could be seen when considering days to emergence, maximum total mass of the individual and reproductive allocation.

The perennial and facultative perennial species take longer to emerge than most of the annuals. This delay in germination could be as a result of a more cautious strategy of the perennials, whereas the annuals adopt a more opportunistic strategy. The perennial species and *Manulea altissima* (facultative perennial) all have low maximum total masses after 21 weeks, whereas the annuals and *Anchusa capensis* and *Arctotis diffusa* (facultative perennials) have large total masses.

The perennials and facultative perennials greatly increase their RA at the seventeenth week whereas the annuals increase their RA from the ninth or thirteenth weeks. Generally, the perennial species have a much smaller RA than the annuals. Perennials have much smaller RA's as they have the advantage of seed production over many years (Silvertown 1987). The perennial species (*C. elongata* and *G.*

humifusum) both produced fewer diaspores over time than most of the annuals. Diaspore production of the facultative perennials (*A. capensis*, *A. diffusa* and *L. diffusa*) was also less than that of the annuals (Table 4).

Generally, perennial species take longer to emerge, have small maximum total masses and small RA's, while facultative perennials also take longer to emerge and have larger RA's than perennials but smaller RA's than annuals. Annual species emerge quickly, possess large total masses and very large RA's. All these differences in plant traits demonstrate that the different species have evolved different life history patterns to survive the unpredictable environment.

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Chapter 4

PREDICTING THE COMPETITIVE EFFECT OF FIFTEEN NAMAQUALAND PIONEER PLANT SPECIES BY USING PLANT TRAITS

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Abstract

A competitive hierarchy for fifteen Namaqualand pioneer plant species was established by using the average phytometer mass (*Dimorphotheca sinuata*) when grown in combination with itself and fourteen other species. There were no clear groupings of species in the hierarchy. This competitive hierarchy (gradient) indicated which species are strong competitors (causing a low phytometer mass) with *D. sinuata* and which species are weak competitors (causing a large 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 x diameter, leaf area ratio (LAR); and average 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. The equation, y = 17.1265 - 0.4183 (shoot mass) - 0.0163 (SLA) with a r^2 value of 82.77% was established.

KEYWORDS: Competitive hierarchy, *Dimorphotheca sinuata*, Life history strategy, Phytometer.

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, Sivertown & Dale 1991, Lüscher *et al.* 1992, Goldberg & Barton 1992, Duralia & Reader 1993, Shipley & Keddy 1994). Variation in relative competitive ability among environments has been proposed to control the species composition of plant communities (Gaudet & Keddy 1988, Wilson & Tilman 1995).

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 renown for its floral displays of 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, Grobbelaar, Theron & Van Rooyen 1992, Steyn *et al.* 1996), as well as the relative abundance of species from year to year.

The importance, and even existence of competition in arid ecosystems has often been questioned (Fowler 1986). Noy-Meir (1979) argued that the dynamics of populations in deserts are determined mainly by the direct responses of individuals to changes in the abiotic environment, and competitive interactions between and within species are rare. Shmida *et al.* (1986) reasoned that, under the harsh and unpredictable conditions characterising desert environments, the probability is very low that densities increase up to levels in which competition becomes important.

Results obtained in other studies (Klikoff 1966, Friedman & Orshan 1974, Inouye *et al.* 1980, Kadmon & Shmida 1990a, Kadmon & Shmida 1990b) 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 (Beneke *et al.* 1992a & 1992b, Oosthuizen 1994, Rösch *et al.* 1996a). Previous studies have all indicated the importance of intra- as well as interspecific competition on annual plant populations in Namaqualand (Van Rooyen, Theron & Van Rooyen 1992, Beneke *et al.* 1992a, 1992b, Oosthuizen 1994, Rösch *et al.* 1996b)

"Competitive ability" has two components (Goldberg 1990): competitive effect (the ability to depress growth and 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, only competitive effect among a group of "neighbour" species on a single "target" species (phytometer) species 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, Keddy *et al.* 1994). However, different opinions have been expressed as to what particular plant trait confer a competitive advantage to a species. In a study by Gaudet & Keddy (1988) a strong relationship was found between competitive ability and plant biomass. The present study is done with a very different set of species (desert annuals instead of wetland mostly perennial species) and on a much expanded set of plant traits.

The aim of the study was firstly to determine a competitive effect hierarchy of fifteen 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 twenty-six plant traits determined for each species grown singly. All the species chosen are abundant on old fields or in disturbed veld and contribute toward the production of the mass floral displays in Namaqualand. The phytometer is one of the most abundant species in Namaqualand and occurs singly or in mixtures in very dense stands.

Material and Methods

Diaspores of *Conicosia elongata* (Haw.) N.E. Br., *Dimorphotheca sinuata* DC., *Foveolina albida* (DC.) T. Norl., *Gazania lichtensteinii* Less., *Grielum humifusum* Thunb. var. *humifusum*, *Heliophila rigidiuscula* Sond., *Hypertelis salsoloides* (Burch.) Adamson., *Lessertia diffusa* R. Br., *Leysera tenella* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo, *Osteospermum pinnatum* (Thunb.) T. Norl. var *pinnatum*, *Senecio arenarius* Thunb. and *Ursinia calenduliflora* (DC.) N.E. Br. were collected at Goegap Nature Reserve near Springbok (29° 41' S, 17° 55' E). The diaspores of *Manulea altissima* L.f. subsp. *glabricaulis* (Hiern) Hilliard and *Spergula arvensis* L. were collected at Skilpad Wildflower Reserve (17° 47' East and 30° 09' South) near Kamieskroon. Voucher specimens of all species are stored 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).

Each plant species was grown singly and in combination with the phytometer. In the beginning of April 1994 seeds were sown, out of doors, in quartz sand filled pots (particle size 0.8 - 1.6 mm) with a volume of 1000cm^3, at the University of Pretoria. The 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 pots where the plant species were grown singly, the seedlings were thinned out to a density of one per pot, two weeks after sowing. These plants were used to determine various plant attributes for each species.

Competitive effect of the fifteen species was assessed as the relative ability of each species to suppress the growth of a common indicator species, or phytometer, in this case *Dimorphotheca sinuata*. The phytometer seeds were sown in the centre of the pot and the seeds of the other species were sown around the phytometer. The seedlings were thinned out after four weeks to the desired density of one phytometer (in the centre) and the four individuals of the other species (symmetrically around the centre phytometer). The 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 September (eighteen weeks after sowing) the phytometer plants were harvested and the dry mass of the leaves, stems and reproductive organs were determined. The average dry mass of *Dimorphotheca sinuata* with each species combination was used to determine a competition gradient between the species.

The following phenological attributes were determined for each species grown singly:- The average number of days to emergence was calculated by noting when the first seedling in each of ten 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 an average mass per diaspore calculated.

To determine the maximum values for each trait in the first 25 weeks of the plant life, five replicates of each species were harvested every four weeks, for five harvests, commencing in May. The following plant attributes were measured at each harvest:

1) Leaf area (cm^2) - A
2) Leaf mass (g) - W_l
3) Stem mass (g) - W_s
4) Reproductive mass (g) - W_i
5) Root mass (g) - W_r
6) Plant height (mm)
7) Plant crown diameter (mm)

The following calculations based on the formulae of Kvet *et al.* (1971), Causton & Venus (1981), Hunt (1982), Coombs *et al.* (1986) and Causton (1991) were made:

1) Shoot mass (g) - W_{sh}

$W_{sh} = W_l + W_s + W_i$

2) Total plant mass (g) - W

$W = W_{sh} + W_r$

3) Relative growth rate

$= (\ln W_2 - \ln W_1)/t_2 - t_1$

where W_1 and W_2 represent total dry mass at times t_1 and t_2 respectively.

4) Leaf allocation

$= W_l/W \times 100$

5) Stem allocation

$= W_s/W \times 100$

6) Reproductive allocation

$= W_i/W \times 100$

7) Root allocation

$= W_r/W \times 100$

8) Root : Shoot ratio

$= W_r/W_{sh}$

9) Leaf area ratio (LAR)

$= A/W$

10) Specific leaf area (SLA)

$= A/W_l$

Leaf areas were 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.

The data collected from the species grown singly were used to determine the maximum value over the harvests for each plant trait for each species. A simple linear regression 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 regressions 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. U.S.A..

Results and Discussion

The winter ephemerals of Namaqualand have evolved certain life history characteristics which enable them to survive in their semi-desert habitat (Van Rooyen, Grobbelaar, Theron & Van Rooyen 1992). These plant traits and combinations of plant traits determine the plant's competitive ability. Species can be ranked in order of competitive ability from a competitive dominant, which is able to suppress all other species, to a subordinate, which is suppressed by all other species (Keddy 1989).

A competitive effect hierarchy (Figure 1) was established by using the average phytometer mass when it was grown in combination with itself and fourteen other species. The competitive effect hierarchy can be seen as a competition gradient with the species on the extreme ends ranging from the weakest to the strongest competitor (Figure 1).

Dimorphotheca sinuata's mass (phytometer) was the least when in competition with itself (Figure 1). Other strong competitors with *D. sinuata* are *S. arenarius, Oncosiphon grandiflorum, F. albida, U. calenduliflora* and *Osteospermum pinnatum* (Figure 1). The weaker competitors were *Hypertelis salsoloides, Lessertia diffusa, Spergula arvensis, C. elongata*, *M. altissima* and *G. humifusum* (Figure 1). The weaker competitors are all perennial or facultative perennial species (except *S. arvensis*), while the annual species are the stronger competitors. In competition experiments using four other target species at two nutrient levels it was found that the perennial and facultative perennial species are weaker competitors and that this could be as a result of a delay in phenological development compared with annuals (Rösch *et al.* 1996a).

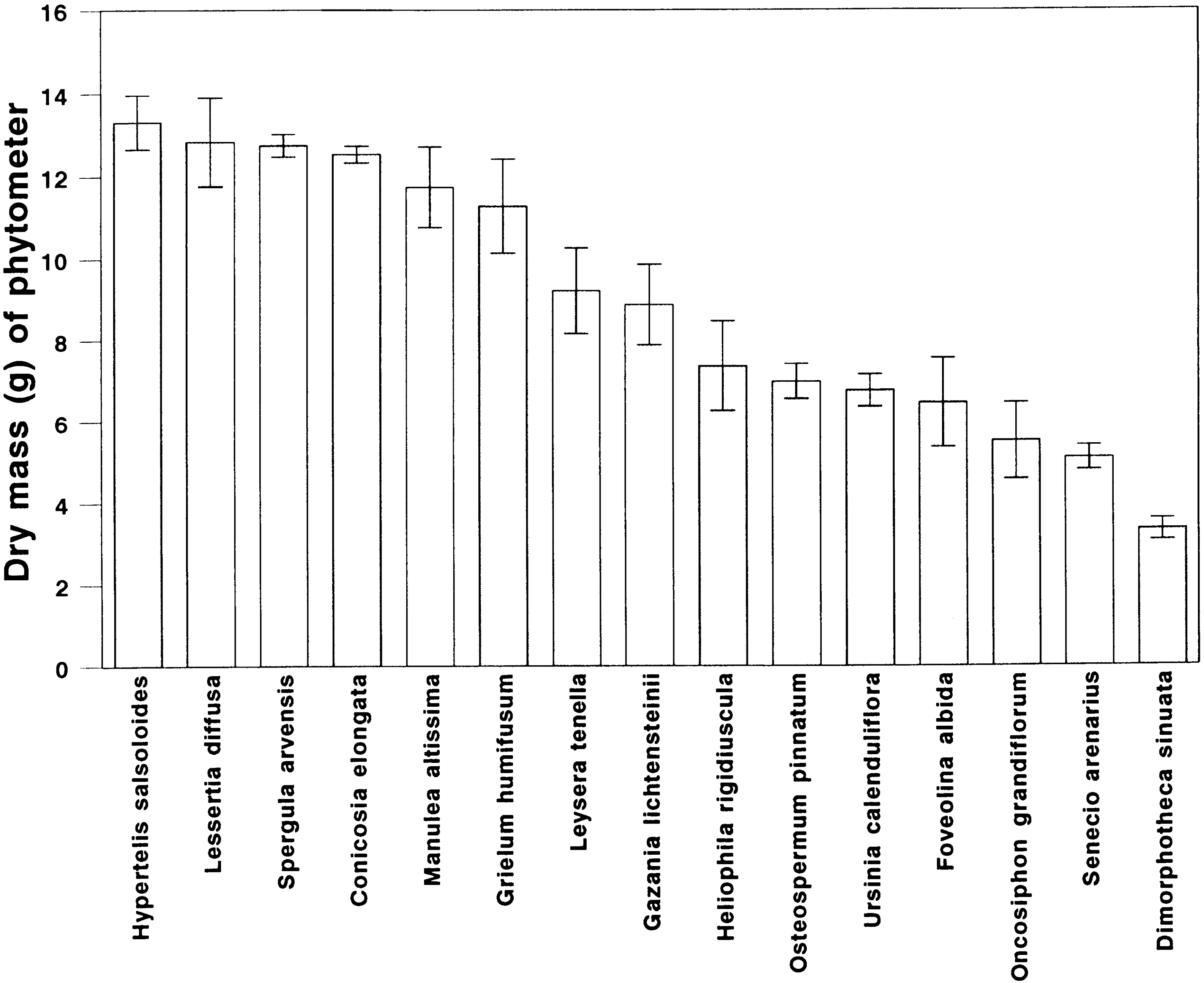

Figure 1. Competitive hierarchy determined by using the above-ground dry mass of the phytometer (*Dimorphotheca sinuata*) when grown in combination with the other species.

Gaudet and 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 morphological traits used by Gaudet & Keddy (1988) in their study were measured on plants interacting with the phytometer. The same traits were also measured on each test species grown singly, and when regressed against phytometer biomass, similar results were obtained with both sources of measurement and test species biomass was still strongly correlated with competitive ability ($r^2 = 0.74$, $P<0.001$) (Gaudet & Keddy 1988).

Table 1 shows the correlation coefficients of the linear regression of a plant trait, 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 (r-values of -0.812 and -0.800 respectively, Table 1, Figure 2 & 3). Thus there was a strong relationship between these traits and the competitive effect (Figure 1). Other traits with highly significant ($P< 0.01$) r-values were those of maximum stem mass, maximum reproductive mass and maximum leaf area (Table 1). Significant correlations ($P< 0.05$) were obtained with maximum stem allocation, SLA, vegetative height x diameter, LAR and average number of days to flower initiation.

All significant traits (with the exception of the average number of days to flower initiation) have a negative correlation coefficient i.e. phytometer mass decrease as the traits magnitude increases. All these traits are related to the plant size i.e. the species with large masses such as *D. sinuata* on the right hand side of the hierarchy, are strong competitors whereas those species on the left hand side have smaller masses and are the weaker competitors (Figure 1).

Table 1. Linear regressions between plant traits of 15 Namaqualand species and phytometer (*Dimorphotheca sinuata*) above-ground mass

Plant trait	Correlation coefficient (r)
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 x maximum diameter	-0.561 *
Maximum leaf area ratio (LAR)	-0.528 *
Average 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 x 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.

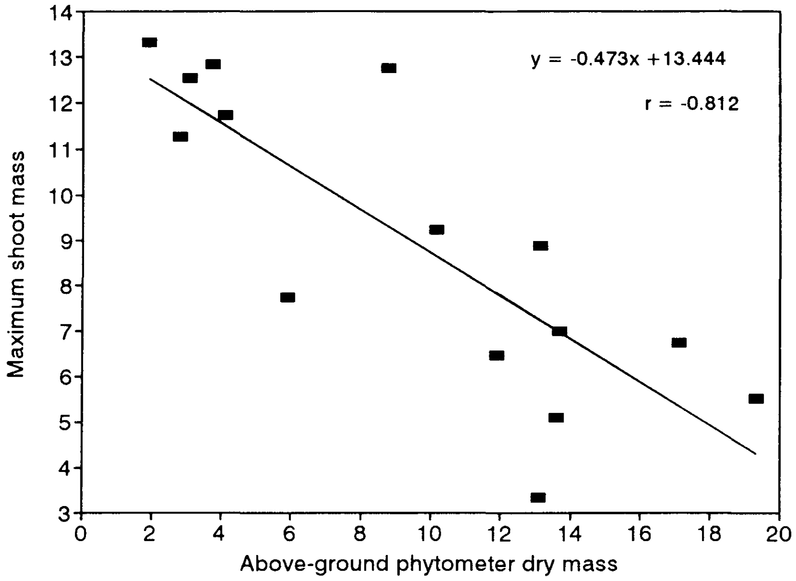

Figure 2. Linear regression of shoot mass on phytometer dry mass.

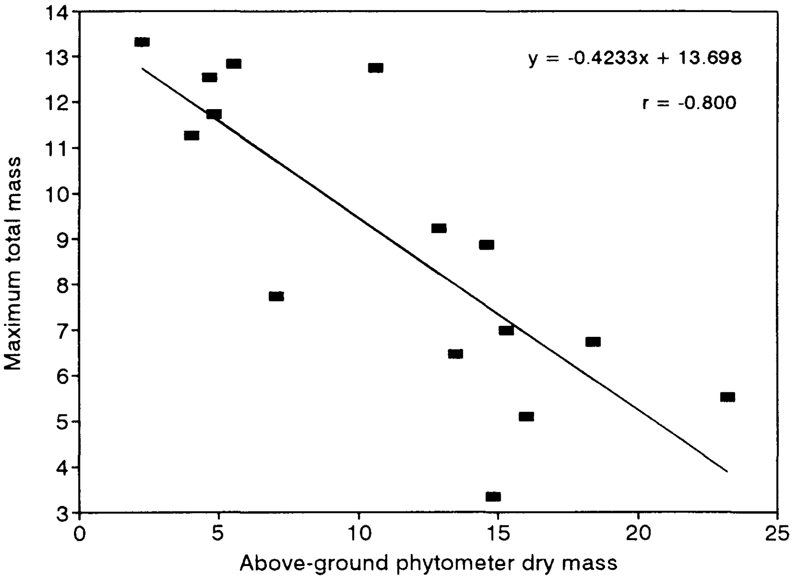

Figure 3. Linear regression of total mass on phytometer dry mass.

That size related traits (Table 1) 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.

Average number of days to flower initiation was also found to be significantly related to competitive effect (Table 1). 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 x maximum diameter was a better indicator of competitive effect than maximum total height x maximum diameter. Many species for example *Manulea altissima* produce inflorescences at the tip of long slender stems 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 1). Roush & Radosevich (1985) stated that LAR showed a strong relationship with relative competitive ability while relative growth rate did not. Their findings are supported by this study, indicating a significant relationship between LAR and competitive effect ($r = -0.528$, Table 1).

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 x maximum diameter were used to determine an equation to predict competitive effect. An equation, y = 17.1265 - 0.4183 (shoot mass) -

0.0163 (SLA) was obtained with a r^2 value of 82.77% i.e. 82.77% of a 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 generalise 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 1996a) 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 generalisations 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, Goldberg & Barton 1992, Campbell & Grime 1992, Grace 1993, Goldberg & Scheiner 1993, Goldberg 1994, Silvertown *et al.* 1994, Keddy *et al.* 1994). A subsequent study (Rösch 1996a) to investigate competitive effect and response of ten 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 1996a).

Conclusion

In high rainfall years, Namaqualand pioneer plant species form dense stands and compete for limited resources. These species can be ranked in an order of competitive effect - the annual species being the stronger competitors, suppressing the perennial and facultative perennial species.

When characteristics, measured on plants grown singly, were regressed against the phytometer mass, certain traits were well related. Maximum total mass, maximum shoot mass, maximum leaf area, maximum stem mass, maximum reproductive mass and maximum vegetative height x maximum diameter were all highly significant while days to flower initiation, stem allocation, LAR and SLA were all significantly correlated to competitive effect ability. Most of these traits are size related. According to Keddy (1989) competitive hierarchies may be inevitable consequences of differences in size. Maximum relative growth rate which is usually considered a good predictor of competitive ability was not significantly correlated to competitive effect ability. The equation, $y = 17.1265 - 0.4183$ (shoot mass) $- 0.0163$ (SLA), was obtained with a r^2 value of 82.77% i.e. 82.77% of a plants competitive ability can be accounted for by the use of the equation.

The results may not be different from those obtained by Gaudet & Keddy (1988) but the experiment was done on a very different set of species i.e. desert annuals and not wetland plants, also many more plant traits were used.

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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Chapter 5

A MULTIVARIATE ANALYSIS OF THIRTY NAMAQUALAND PIONEER PLANT SPECIES USING PLANT TRAITS

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Abstract

Eighteen plant traits were used to arrange thirty Namaqualand pioneer plant species into groups with similar characteristics. The result of the first ordination (Principle Component Analysis) using all species grouped perennial and facultative perennial species together. These species were distinguished from the annual species on the basis of their delayed phenological development.

The second ordination, using only the annual species, produced three main guilds, two of which could be further subdivided into smaller groups. Each guild (group) can be explained in terms of their plant traits such as stem mass, reproductive mass and reproductive allocation.

Plant traits are important in determining and predicting a plant's life history strategy and can be used to group species into guilds.

KEYWORDS: Guild, Life history strategy, Multivariate analysis, Plant traits, Principle Component Analysis.

Introduction

Namaqualand is situated in the arid North-west corner of the Republic of South Africa and covers approximately 55 000km^2. The climate in Namaqualand is warm and dry, and is characterised by sparse, irregular winter rainfall and large daily and seasonal temperature fluctuations (Schulze 1965). The area owes its fame mainly to the display of wild flowers which transforms the normally barren landscape into a land of colour in the spring (Van Rooyen *et al.* 1992).

Desert plants are often subjected to strong natural selection on at least three kinds of interrelated traits:

1) life history traits, i.e. the timing and amount of germination, growth and flowering;
2) plastic responses to environmental influences; and
3) physiological traits affecting growth, reproduction, and survival (Fox 1992).

The unpredictable nature of the rainfall in Namaqualand has been an important selective force in determining the life history strategies of the species indigenous to the region. As a result of the unpredictability of the rainfall, germination of seeds can occur over a long period of time and this in turn determines the length of the growing period. The reaction of the species to this unpredictability is manifested in plastic responses in lifespan, size and biomass allocation (Van Rooyen *et al.* 1992).

Plant traits vary within and among species as well as populations. The relative abundance of species with different attributes varies with the level of stress (water and nutrient availability) and disturbance (grazing and ploughing) (Fernàndes Alés *et al.* 1993). There are many patterns of variation in life history in species that enable them to exist in different parts of a mosaic of disturbed environments (Fernàndes Alés *et al.* 1993). Plant traits are also important in determining and predicting a plant's competitive ability (Grime 1979, Gaudet & Keddy 1988, Tilman 1988, Keddy 1989, Grace 1990, Goldberg & Landa 1991, Keddy *et al.* 1994, Rösch *et al.* 1996).

Multivariate analysis is a branch of mathematics that deals with the examination of numerous variables simultaneously (Gauch 1981). The purpose of multivariate analysis is to treat multivariate data as a whole, summarising the data and revealing their structure (Gauch 1981). Ordination is a multivariate technique, which is used to analyze and visualize the relationships between many species and many environmental variables (Ter Braak 1987a). In community ecology ordination serves to summarize community data by producing a low-dimensional ordination space (Gauch 1981). This is achieved by arranging the points, such that, points that are close together correspond to sites that are similar in species composition, and points that are far apart correspond to sites that are dissimilar in species composition (Jongman *et al.* 1995). In this study species and plant traits were used instead of species and samples.

The most common function of Principal Component Analysis (PCA), which is one of many ordination techniques, is simply descriptive-reduction of the dimensionality of a data set to manageable proportions, while preserving as much of the original structure as possible (Gauch 1981). This descriptive function of PCA is served successfully, however, only for data sets whose properties match the PCA model tolerably well (Gauch 1981).

Originally the term guild was defined by Root (1967), as a group of species that exploit the same class of environmental resources in a similar way while Kindscher and Wells (1995) define plant guilds as groups of species with similar morphological, physiological and ecological traits.

The aim of the study was to a) determine whether annual and perennial species from Namaqualand could be grouped together into guilds by means of an ordination technique; and b) to establish which attributes characterise specific guilds.

Material and Methods

Diaspores of thirty species were collected in Namaqualand. *Anchusa capensis* Thunb., *Arctotheca calendula* (L.) Levyns, *Arctotis diffusa* Thunb., *Cotula thunbergii* Harv., *Diascia tanyceras* E. Mey. ex Benth., *Felicia merxmuelleri* Grau., *Heliophila variabilis* Burch. ex DC., *Manulea altissima* L. f. subsp. *glabricaulis* (Hiern) Hilliard, *Spergula arvensis* L. and *Ursinia cakilefolia* DC. diaspores were collected at Skilpad Wildflower Reserve near Kamieskroon at 17° 47' East and 30° 9' South. The diaspores of the other twenty species were collected near Springbok (29° 41' S, 17° 55' E). The species were: *Arctotis fastuosa* Jacq., *Conicosia elongata* (Haw.) N.E. Br., *Dimorphotheca polyptera* DC., *D. sinuata* DC., *Felicia australis* (Alston) Phill., *Foveolina albida* (DC.) T. Norl., *Gazania lichtensteinii* Less., *Grielum humifusum* Thunb. var. *humifusum*, *Heliophila rigidiuscula* Sond., *Hypertelis salsoloides* (Burch.) Adamson., *Lessertia diffusa* R. Br. *Leysera tenella* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo, *O. suffruticosum* (L.) Kallersjo, *Osteospermum amplectens* (Harv.) T. Norl., *O. hyoseroides* (DC.) T. Norl., *O. pinnatum* (Thunb.) T. Norl. var. *pinnatum*, *Senecio arenarius* Thunb., *S. piptocoma* O. Hoffm. and *Ursinia calenduliflora* (DC.) N.E. Br.. Voucher specimens of all these 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).

The diaspores of the individual species were sown in quartz sand filled pots (particle size 0.8 - 1.6 mm), in the beginning of April 1994 at the University of Pretoria. Two weeks after sowing the seedlings were thinned out to one per pot, and maintained at one plant per pot throughout the duration of the experiment. The plants were watered daily and once a week received Arnon and Hoagland's complete nutrient solution (Hewitt 1952).

Five replicates of each species were harvested every four weeks, for five harvests. The following plant attribute data were measured or calculated:

1) Diaspore mass (mg)
2) Leaf area (cm^2)
3) Leaf mass (g)
4) Stem mass (g)
5) Reproductive mass (g)
6) Root mass (g)
7) Plant height x Diameter (cm^2)
8) Total plant mass (g)
9) Relative growth rate ($g.g^{-1}.day^{-1}$)
10) Leaf allocation (%)
11) Stem allocation (%)
12) Reproductive allocation (%)
13) Root allocation (%)
14) Leaf area ratio (LAR) ($cm^2.g^{-1}$)
15) Number of inflorescences per plant

The following phenological data were collected:

1) Number of days to emergence
2) Number of days to anthesis
3) Number of days until the death of the plant

(For more information on the methods refer to chapter 3.)

The species' average maximum value for each attribute, over all the harvests, was determined. Species were then placed into one of three classes for each attribute, and an ordination, using all the traits, done. The result of this first ordination, which grouped the perennial and facultative perennial species together, enabled the exclusion of these species and a second ordination was done using only the annual species. The ordination technique used was Principal Component Analysis (PCA) (Gauch 1981), in the CANOCO computer program (Ter Braak 1987b). The traits best correlated with the x- and y-axis were determined using Pearson's product moment

(STATGRAPHICS 6.0. 1992, USA.). From the Pearson's product moment the location of each species with respect to the x- and y-axis in the PCA plot was correlated to a trait. This technique has been used previously for correlating multivariate plot points with ecological characteristics (Polley & Collins 1984), to determine which traits most highly influence the position of the species and subsequently the groups or guilds of species (Kindscher & Wells 1995).

Results and Discussion

In the ordination, using all the species, the perennial and facultative perennial species were grouped together on the right hand side of the x-axis, thus enabling the division of the ordination graph into two guilds (Figure 1). The eigenvalues, which represent the relative contribution of each component to the explanation of the total variation in the data (Kent & Coker 1995), for the x-axis is 28,05% and for the first four axes of the analysis 66,95% of the variation can be explained.

Life history strategies of perennial (*Conicosia elongata*, *Grielum humifusum* and *Hypertelis salsoloides*) and facultative perennial species (*Anchusa capensis*, *Arctotis diffusa*, *Lessertia diffusa*, *Manulea altissima*) differ from those of the annual species, in that the perennial and facultative perennial species generally take longer to emerge (except *Lessertia diffusa* and *Manulea altissima*) than the annuals (Table 1). This delay in germination of the perennials could be as a result of a more cautious strategy of the perennials, whereas the annuals adopt a more opportunistic strategy.

Perennial and facultative perennial species have the smallest stem masses (0.10 to 2.56g) (Table 2), and a lifespan of 249 days or longer (Table 1). All the species, except *Anchusa capensis*, have low plant height x diameter values (<900cm^2) (Table 2). Stem allocation of these species is low (0.46% and 18.66%), except for *H. salsoloides* while total mass is also low ranging from 2.26g to 5.54g, except for *Arctotis diffusa* (11.86g) and *Anchusa capensis* (12.35g) (Table 2). In general, the species take longer than 6 days to emerge (Table 1 and Table 3).

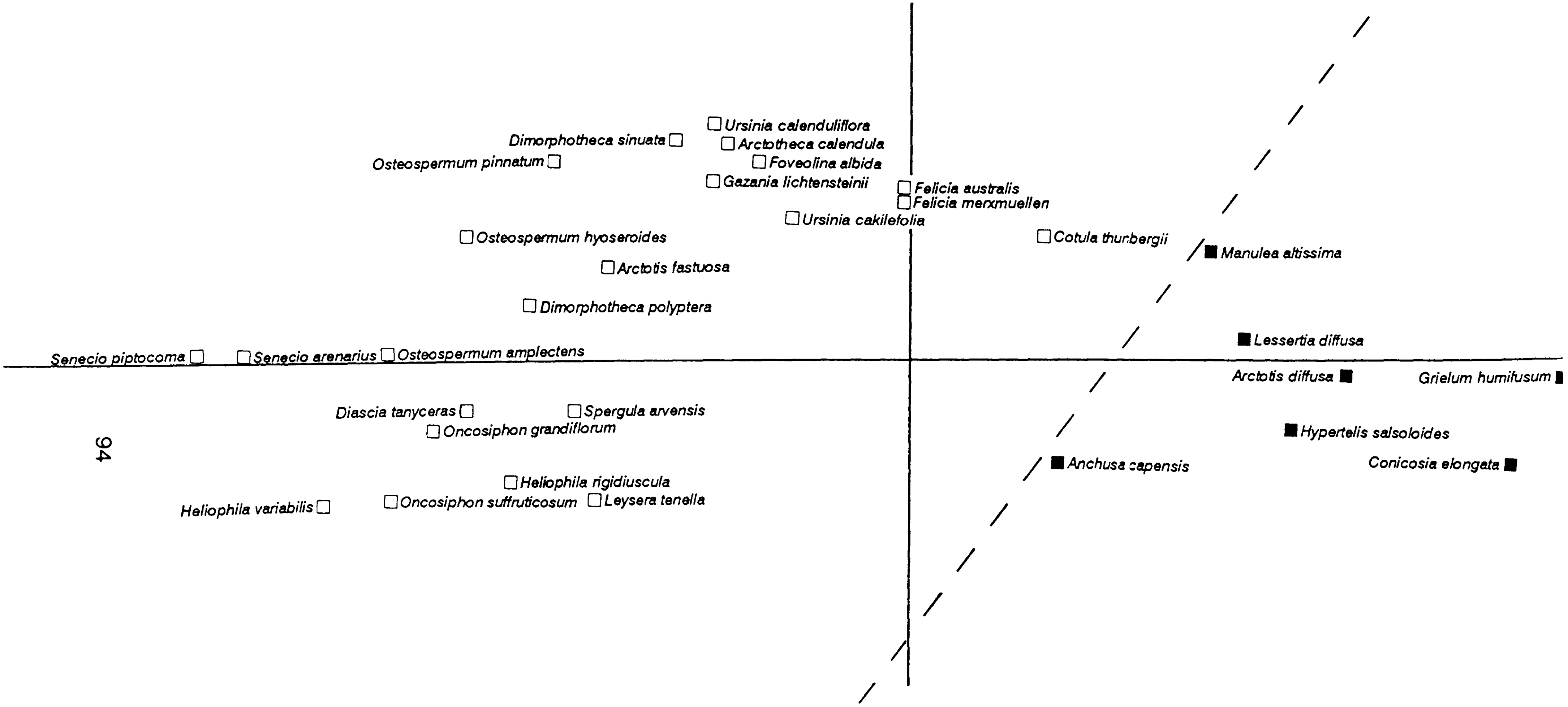

Figure 1. Distribution of 30 plant species from Namaqualand along the x- and y-axis of a PCA ordination of different plant attributes.

■ Perennial and facultative perennial species

☐ Annual species

Table 1. Phenological data used in the ordination of 30 Namaqualand plant species

Group	Species	Days to emergence	Days to anthesis	Days to death
Perennial or Facultative Perennial	Conicosia elongata	8.50	152.00	389.00
	Grielum humifusum	6.50	120.60	389.00
	Hypertelis salsoloides	8.20	99.80	389.00
	Anchusa capensis	10.00	146.00	299.75
	Arctotis diffusa	10.60	137.50	312.00
	Lessertia diffusa	3.60	94.60	249.00
	Manulea altissima	4.70	124.20	309.20
Group 1A	Senecio arenarius	6.00	89.00	221.00
	Senecio piptocoma	4.10	91.80	216.08
Group 1B	Diascia tanyceras	13.00	118.60	190.20
	Dimorphotheca polyptera	4.80	121.00	249.00
	Osteospermum amplecten	5.88	93.40	247.00
	Spergula arvensis	5.40	103.20	229.40
Group 1C	Heliophila rigidiuscula	3.50	79.00	158.00
	Heliophila variabilis	4.77	77.80	172.00
	Leysera tenella	3.20	137.00	240.25
	Oncosiphon suffruticosum	3.00	147.40	252.07
	Oncosiphon grandiflorum	3.00	147.00	244.80
Group 2	Arctotis fastuosa	6.53	83.40	229.75
	Osteospermum hyoseroid	6.40	76.60	244.80
Group 3A	Arctotheca calendula	6.20	93.80	230.80
	Foveolina albida	5.10	96.60	253.20
	Gazania lichtensteinii	4.70	88.60	251.80
	Osteospermum pinnatum	6.77	81.40	222.40
	Ursinia calenduliflora	4.70	115.40	209.80
Group 3B	Cotula thunbergii	4.60	117.80	223.80
	Dimorphotheca sinuata	3.70	103.00	239.20
	Felicia australis	8.70	108.60	215.40
	Felicia merxmuelleri	4.30	119.00	219.60
	Ursinia cakilefolia	4.00	107.40	243.40

Table 2. Attribute data measured or calculated for 30 Namaqualand plant species

Group	Species	Diaspore mass (mg)	Height x diameter (cm^2)	Leaf area (cm^2)	Leaf mass (g)	Stem mass (g)	Reproductive mass (g)	Root mass (g)	Total mass (g)	Leaf allocation (%)	Stem allocation (%)	Reproductive allocation (%)	Root allocation (%)	LAR ($cm^2.g^{-1}$)	RGR ($g.g^{-1}.day^{-1}$)	No. of infloresences
Perennial or Facultative Perennial	Conicosia elongata	1.22	193.87	187.69	2.67	0.21	0.19	1.60	4.67	63.28	0.46	3.69	46.57	146.65	0.15	7.75
	Grielum humifusum	49.14	116.17	121.55	1.09	0.74	0.96	1.25	4.05	73.54	18.66	24.54	46.81	92.81	0.08	67.60
	Hypertelis salsoloides	0.07	185.18	90.90	1.10	0.64	0.19	0.33	2.26	58.59	33.29	7.21	41.41	77.32	0.02	31.20
	Anchusa capensis	1.39	1204.13	362.20	5.91	2.56	1.43	4.34	12.35	58.52	18.41	10.10	50.36	131.76	0.06	240.00
	Arctotis diffusa	5.36	500.57	434.68	4.95	1.51	2.20	3.19	11.86	56.96	13.09	18.46	43.04	154.91	0.31	11.75
	Lessertia diffusa	7.33	259.38	195.10	1.94	0.98	0.82	1.79	5.54	47.77	12.90	13.86	51.06	98.84	0.07	44.20
	Manulea altissima	0.05	899.87	159.60	1.51	0.10	2.56	0.73	4.84	100.00	5.27	52.48	37.89	225.00	0.10	22.00
Group 1A	Senecio arenarius	0.17	2022.76	279.38	2.04	6.20	5.52	2.41	16.01	69.92	45.62	34.55	36.59	267.48	0.06	379.80
	Senecio piptocoma	0.44	2383.14	384.05	2.42	9.15	5.09	3.13	17.83	62.83	51.52	30.71	38.48	140.55	0.05	887.40
Group 1B	Diascia tanyceras	0.08	1991.02	351.09	2.01	4.92	2.78	2.51	10.81	75.00	46.22	26.06	63.83	483.21	0.06	703.20
	Dimorphotheca polyptera	0.84	1185.04	191.16	2.05	5.61	2.33	1.52	11.05	54.66	48.68	20.23	49.26	121.30	0.13	142.25
	Osteospermum amplectens	2.92	2140.03	521.87	3.34	7.64	4.20	2.28	17.19	58.22	44.90	24.39	45.00	174.01	0.07	246.60
	Spergula arvensis	0.32	1312.27	176.71	2.12	4.16	2.48	1.86	10.63	91.99	39.31	23.12	43.96	67.49	0.05	613.20
Group 1C	Heliophila rigidiuscula	0.17	2128.70	48.04	0.57	4.72	1.00	1.17	7.09	92.39	66.67	13.90	41.42	36.62	0.07	568.25
	Heliophila variabilis	0.68	2660.11	99.43	2.05	5.35	1.83	1.89	10.27	50.23	52.02	17.78	48.08	51.01	0.06	676.00
	Leysera tenella	0.08	1336.17	214.31	3.13	5.62	1.42	2.76	12.93	49.23	43.90	10.82	35.21	121.53	0.14	432.80
	Oncosiphon suffruticosum	0.06	1901.33	497.81	4.50	13.21	1.31	3.77	22.80	54.73	57.90	5.88	46.65	148.46	0.07	549.00
	Oncosiphon grandiflorum	0.11	1480.81	402.60	5.36	11.03	2.95	3.89	23.22	72.28	47.44	12.73	38.05	220.39	0.08	173.00
Group 2	Arctotis fastuosa	9.86	1339.06	617.56	4.94	8.13	5.53	2.36	19.89	66.94	40.78	27.98	33.49	280.25	0.07	23.75
	Osteospermum hyoseroides	6.64	1699.44	436.63	2.85	6.72	5.43	2.19	17.02	56.22	45.24	32.03	49.68	132.66	0.05	170.00
Group 3A	Arctotheca calendula	0.72	689.27	411.06	4.04	3.64	5.84	2.23	15.04	56.65	23.69	39.21	51.70	156.66	0.06	81.40
	Foveolina albida	0.12	878.58	241.85	2.03	3.21	6.65	1.59	13.48	73.00	32.13	48.54	36.09	235.67	0.12	171.60
	Gazania lichtensteinii	1.75	380.97	432.32	3.21	5.17	4.76	1.46	14.61	47.71	45.01	32.47	60.58	100.73	0.06	110.40
	Osteospermum pinnatum	2.80	1141.75	472.95	2.86	5.96	4.88	1.63	15.32	54.69	42.89	31.80	44.22	141.33	0.08	198.80
	Ursinia calenduliflora	1.11	795.23	434.09	2.86	4.01	10.19	1.28	18.41	46.05	33.64	54.99	53.96	101.09	0.06	169.20
Group 3B	Cotula thunbergii	0.14	917.63	210.64	1.63	1.86	2.44	1.08	7.00	45.35	26.24	34.87	62.27	29.10	0.25	116.20
	Dimorphotheca sinuata	1.64	1735.01	442.84	2.82	5.46	5.24	2.07	14.82	52.01	44.17	35.42	44.72	202.93	0.34	109.40
	Felicia australis	0.06	739.93	178.17	1.82	3.95	4.61	1.04	11.43	76.33	42.02	39.83	48.82	217.67	0.14	267.80
	Felicia merxmuelleri	0.68	866.09	328.46	2.12	3.21	4.22	2.02	11.58	54.61	27.99	36.38	59.20	126.28	0.43	147.40
	Ursinia cakilefolia	1.67	1217.27	331.96	2.74	4.16	4.24	1.76	12.89	21.48	31.78	32.98	53.23	95.35	0.09	56.80

Table 3. Attributes that singly and/or in combination distinguish the perennial and facultative perennial species from the annual species of Namaqualand

Plant attribute	Distinguishing of perennial and facultative perennial species from annual species
Diaspore mass	
Leaf mass	
Stem mass	YES
Reproductive mass	
Root mass	
Total mass	YES
Plant height x diameter	YES
Relative growth rate	
Leaf allocation	
Stem allocation	YES
Reproductive allocation	
Root allocation	
Leaf area ratio (LAR)	
Number of inflorescences per plant	
Number of days to emergence	YES
Number of days to anthesis	
Number of days until death	YES

In the ordination, using only the annual species, three main guilds (groups) can be distinguished (Figure 2). The first axis of the PCA explains 27,47% of the variation and the first four axes explain 72,25%. Pearson's product moment correlated the location of each species along the x- and y-axis with respect to each plant trait. For the x-axis, plant height x diameter, stem allocation and number of inflorescences per plant had the highest significant positive correlation ($P < 0.001$). The highest

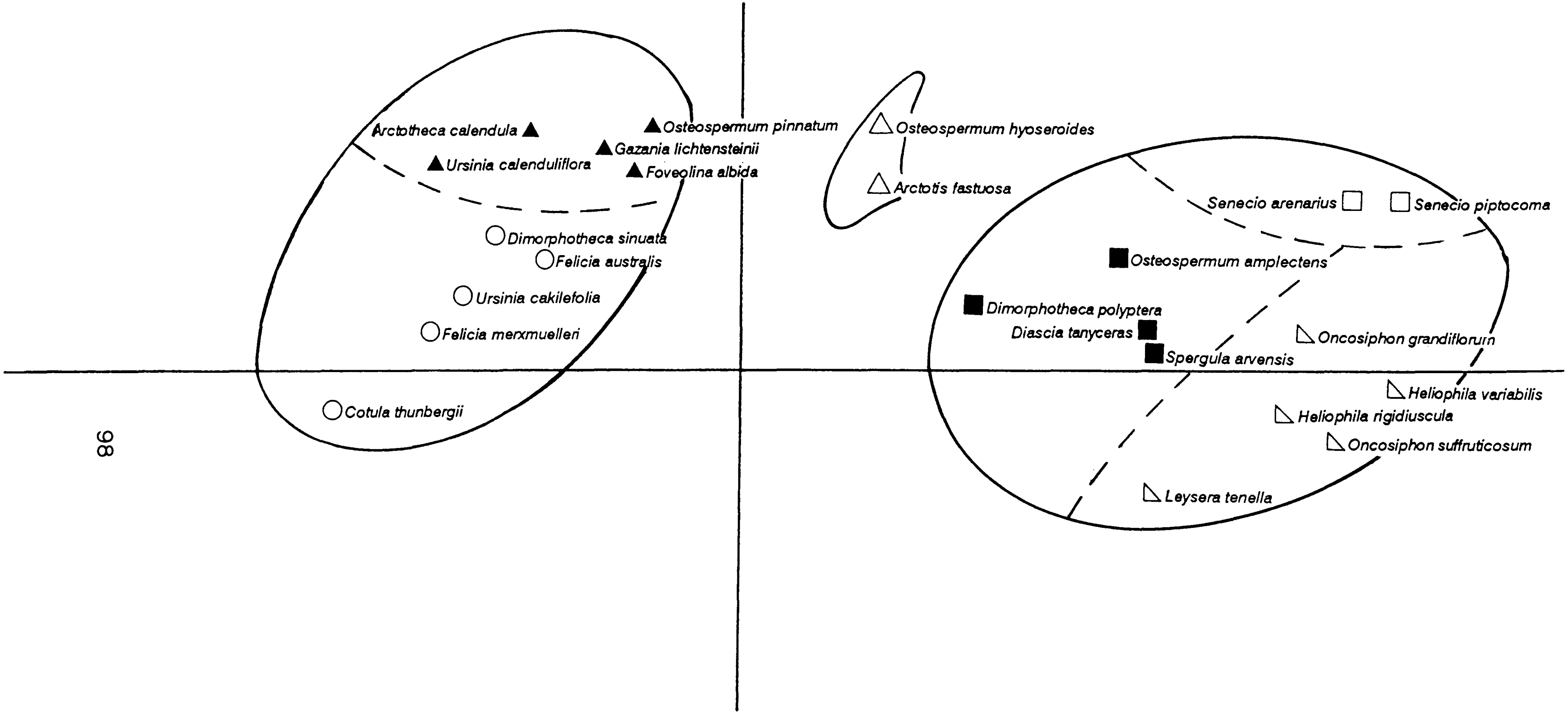

Figure 2. Distribution of annual plant species of Namaqualand along the x- and y-axis of a PCA ordination of different plant attributes.

□ Group 1A ■ Group 1B ◺ Group 1C

△ Group 2

▲ Group 3A ○ Group 3B

significant negative correlation for the x-axis was reproductive allocation. For the y-axis reproductive mass had a highly significant positive correlation and number of days to anthesis a highly significant negative correlation.

The three main groups of species (Figure 2) of which two are further subdivided. The plant attributes that distinguish the three main groups are summarised in Table 4. Group 1 species are all large (plant height x diameter > 1185.03cm^2), but have relatively small reproductive masses (< 5.53g) and reproductive allocations (< 34.56%), while stem mass is large (4.16g or larger) and stem allocation (with the exception of *Spergula arvensis*) is greater than 40% (Figure 2 & Table 2). The number of inflorescences varies from 142.25 to 887.4 per plant (Table 2). Diaspore mass of most of the species is less than 1mg (Table 2) and they take between three and six days to emerge (Table 1).

Group 2, includes only two species and the attributes that characterise these two species are:- high total mass (> 17.02g); relatively high stem (> 6.72g) and reproductive mass (> 5.43g) and relatively high stem and reproductive allocations; large leaf area (> 436.63cm^2) and intermediate height x diameter values (Figure 2, Table 2 & 4). Although these two species take relatively long to emerge (on average 6 -7 days), they are among the first to reach anthesis (Table 1).

Species in Group 3, in general, have the lowest stem masses (< 6g) and the highest reproductive masses (> 4.22g, except *C. thunbergii*), although the number of inflorescences per plant is low (56.8 - 267.8) (Figure 2 & Table 2). Reproductive allocation ranges from 31% to 55% and stem allocation is less than 45% (Table 2). The dimensions of the plant are smaller than those of Group 1 or 2 (Table 2 & 4).

The plant attributes separating the species within the main groups are summarised in Table 5. *Senecio arenarius* and *S. piptocoma* (Group 1A, Figure 2) have the highest reproductive allocations in Group 1 (34.55% and 30.7% respectively) reproductive masses larger than Group 1B and 1C, a large stem mass and stem allocations of more than 45% (Table 2). *Senecio arenarius* takes on average six days to emerge and *S. piptocoma* 4.1 days (Table 1).

Table 4. Plant attributes that distinguish the three Groups of annual species from one another

Plant attribute	Group		
	1	2	3
Diaspore mass	X	X	
Leaf area		X	
Leaf mass			
Stem mass	X	X	X
Reproductive mass	X	X	X
Root mass			
Total mass		X	
Plant height x Diameter	X	X	X
Relative growth rate			
Leaf allocation			
Stem allocation	X		X
Reproductive allocation	X	X	X
Root allocation			
Leaf area ratio (LAR)			
Number of inflorescences per plant	X		X
Number of days to emergence	X	X	
Number of days to anthesis		X	
Number of days until death		X	

Table 5. Plant attributes that separate the annual species within the main groups

Plant attribute	Group				
	1A	1B	1C	3A	3B
Diaspore mass					
Leaf area					
Leaf mass					
Stem mass	X				
Reproductive mass	X	X	X		
Root mass				X	X
Total mass					
Plant height x Diameter					
Relative growth rate				X	X
Leaf allocation					
Stem allocation	X	X	X		
Reproductive allocation	X	X	X		
Root allocation					
Leaf area ratio (LAR)					
Number of inflorescences per plant					
Number of days to emergence	X	X	X	X	X
Number of days to anthesis					
Number of days until death					

Reproductive masses (2.33g and 4.2g), and reproductive allocations (20% - 26.06%), of Group 1B species (Figure 2) are intermediate between Group 1A and Group 1C (Table 2). All the species in Group 1B except *D. tanyceras* take between 4.8 and 5.8 days to emergence (Table 1 & 5).

The species in Group 1C (Figure 2) have the lowest reproductive masses in Group 1 (between 1g and 1.83g except *Oncosiphon grandiflorum*, 2.95g) as well as the lowest reproductive allocations (less than 18%) (Table 2), this could be as a result of the last harvest occurring before the species peak has been reached. Stem allocation is greater than 47% except in *Leysera tenella* (Table 2). All the species, excluding *Heliophila variabilis*, are quick to germinate and take 3 to 3.5 days to emerge (Table 1 and Table 5).

Group 3 (Figure 2) is subdivided into two groups by three attributes i.e. root mass, relative growth rate and number of days to emergence. Group 3A species have a root mass more than 4.76g while Group 3B species have a root mass less than 4.76g except *Dimorphotheca sinuata* which has a root mass of 5.24g (Table 2). Species in Group 3A take 4.7 days or longer to emerge whereas species in Group 3B take less than 4.6 days (Table 1). Relative growth rate is between 0.06 and 0.12 for Group 3A species and between 0.09 and 0.43 for Group 3B species (Table 2 & 5).

Conclusion

The strong selective forces, brought about by the unpredictable nature of the climate in Namaqualand, have caused the species of the area to evolve certain plant traits and combinations thereof.

As plant traits are important in determining and predicting a plants life history strategy and thus its competitive ability these traits can be used to place species into guilds. Kindscher and Wells (1995) used multivariate analysis to group prairie species together in guilds using morphological, physiological and ecological traits.

Eighteen plant traits were used to arrange 30 Namaqualand plant species into groups with similar characteristics. The result of the first ordination grouped perennial and facultative perennial species together as these species exhibit delayed phenological development. In general, these species are small in size, and have a low stem as well as total mass. An ordination of the annual species resulted in three main guilds (groups), two of which could be further divided into smaller groups. The three main guilds are grouped together such that Group 1 and 2 species, with large individuals possessing large stem masses are separated from Group 3 species, with small individuals possessing small stem masses. Reproductive allocation in Group 1 species is small whereas in Group 3 species it is large.

Since species within a guild have similar morphological, physiological and ecological traits, they probably exploit environmental resources in a similar way and therefore occupy the same niche. It is expected that competition between species of the same guild, that utilize the same resources, should be severe. On the other hand, niche differentiation between species belonging to different guilds, should allow coexistence. In a study to establish a competitive hierarchy of 15 Namaqualand pioneer plant species it was found that the annuals were stronger competitors than the perennials and facultative perennials in the first season when all plants had established from seeds (Rösch 1996). This study clearly demonstrates that the perennials and facultative perennials belong to a guild of plants, that are able to utilize a longer growing season, and accumulate enough resources after most annual species have died. Although these species are at a disadvantage during their early life cycle, they will have a headstart in the second growing season when they are able to resprout from subterranean organs.

As plant traits, which were used to determine the guild, are also important in determining a plants competitive ability, these guilds might be able to be used to group species with similar competitive abilities together. Thus, multivariate techniques may be a powerful tool in determining species guilds and the application of these guilds to, for example, community analysis and competition could be wide.

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Chapter 6

COMPETITIVE EFFECT AND RESPONSE OF TEN NAMAQUALAND PIONEER PLANT SPECIES AT TWO NUTRIENT LEVELS

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Abstract

Competitive effect and response hierarchies between Namaqualand pioneer plant species, across two nutrient levels, were investigated.

Competitive effect as well as response hierarchies were found to be concordant between the two nutrient levels i.e. the fertility of the environment did not have a significant effect on the competitive effect or response hierarchy, as well as among target species. Competitive effect and response were only significantly correlated at the low nutrient level.

Competition intensity for each pairwise interaction showed no significant difference within target species, however between treatment and target species differences were found.

KEYWORDS: Competition intensity, Competitive effect, Competitive response, Nutrient level.

Introduction

One of the major factors influencing growth and survival of an individual plant is competition from its neighbours (Firbank & Watkinson 1985, Beneke 1991, Beneke *et al.* 1992). The immediate effect of competition is to suppress the growth and size (performance) of the individual and not plant numbers (Silvertown 1987).

"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).

A hotly debated issue is whether the intensity of competition varies as a function of habitat productivity (Grace 1993). Grime (1977,1988) and Campbell & Grime (1992), have argued that the traits that determine competitive ability are constant across productivity gradients, whereas Tilman (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). Two "opposing" theories to understand community structure have been developed. Grime's theory of life histories (Grime 1977, 1979) has evoked the processes of disturbance, stress and competition as opposing forces selecting for contrasting syndromes of characteristics (Grace 1991), whereas Tilman's (1977) resource based theory of competition, which has recently been extended (Tilman 1985, 1988), explains suites of traits associated with old-field succession and gradients in soil fertility and disturbance (Grace 1991). Furthermore, variation in relative competitive abilities among environments has been proposed to control the species composition of plant communities (Wilson & Tilman 1995).

Different methods exist to investigate competitive interactions for example, pairwise interactions among many pairs of species produce competition matrices that contain important information (Keddy & Shipley 1989). Additive designs relate to the null hypothesis that two taxa do not compete and are appropriate where it is necessary to quantify intercomponent competition regardless of intracomponent competition (Sackville Hamilton 1994). In contrast, replacement designs are appropriate for questions based on similarity of competing taxa and measures of competitive ability that quantify how limiting resources are partitioned between taxa (Sackville Hamilton 1994).

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 environments, 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) contradict these predictions, and suggest that competitive effects may play a major role in determining the dynamics of desert annual plant populations.

Namaqualand, an arid region, covers an area of approximately 55 000km^2 and is situated in the North-Western corner of the Republic of South Africa. The climate of the area 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 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 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 pioneer plant species form dense stands and compete intensely for limited resources.

The aim of the study was to determine the competitive effect and response of ten prominently displaying plant species of Namaqualand at two fertility levels in order to establish if competitive effect and response hierarchies are consistent a) among target species and b) across nutrient levels.

Material and Methods

Arctotheca calendula (L.) Levyns, *Heliophila variabilis* Burch. ex DC. and *Ursinia cakilefolia* DC. diaspores were collected at Skilpad Wildflower Reserve near Kamieskroon (17° 47' East and 30° 09' South). Diaspores of the other species, *Dimorphotheca sinuata* DC., *Foveolina albida* (DC.) T. Norl., *Gazania lichtensteinii* Less., *Leysera tenella* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo, *Osteospermum hyoseroides* (DC.) T. Norl. and *Senecio arenarius* Thunb., diaspores were collected at Goegap Nature Reserve near Springbok (29° 41' S, 17° 55' E). 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).

The diaspores were sown, out of doors, in sand filled pots with a volume of 1000cm^3 in April 1995 at the University of Pretoria in pairwise combinations using target and neighbour species. The four target species were *Dimorphotheca sinuata*, *Gazania lichtensteinii*, *Heliophila variabilis* and *Ursinia cakilefolia* and all ten species were used as neighbours. The four target species were grown in all possible pairwise mixtures with each other and with the other six neighbour species. The target species were sown in the one half of the pot and the neighbour species in the other half of the pot. Seedlings were thinned out to one target and one neighbour individual per pot after four weeks. Single species were also sown in pots and thinned out after four weeks to one individual per pot. The plants were watered daily with tap water and after the fourth week received, 120ml, 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 treatment (Treatment 1) received 120ml full-strength nutrient solution and those of the low nutrient treatment (Treatment 2) 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.

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.

These measures of relative yield are based on an additive design, not a replacement series design (Keddy *et al.* 1994).

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

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

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 $\alpha = 0.05$ (Statgraphics 6.0., 1992). Target species RYP values were used to determine differences between Treatments 1 and 2 for effect competitive ability while neighbour species RYP values were used for response competitive ability. Differences in competition intensity between treatments or targets were also determined using Bonferroni.

Kendall's rank correlations (Keddy *et al.* 1994) 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 (the ability of each neighbour species to damage each target species), mean effect of each neighbour species on all target species (row means of 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 (the ability of each neighbour species to withstand the effects of 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 by using STATGRAPHICS computer program (STATGRAPHICS 6.0 1992, Inc. USA.).

Results and Discussion

1) 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). The mean effect of each neighbour species on each target species is the ability of each neighbour species to damage each target species, while the mean response of each neighbour species to each target species is the ability of each neighbour species to withstand the effects of each target species (Keddy *et al.* 1994).

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 neighbours was found (Table 2). Effect RYP values between target species differed significantly between *D. sinuata* and *G. lichtensteinii* as well as with *H. variabilis*, and *U. cakilefolia* and *G. lichtensteinii*.

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		

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) for the different nutrient levels (Table 2). Between the target species competitive response of *D. sinuata* differed significantly from the three other target species.

Table 2. Analysis of variance for relative yield per plant values

Effect	Significance level	Response	Significance level
Main effects		Main effects	
A: Treatment	0.7433	A: Treatment	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

Competitive effects of the ten species were significantly correlated (P< 0.05) among the two treatments (Figure 1). 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. strong competitors at the low nutrient level were also the strong competitors at the high nutrient level the same applies for the weaker competitors. In their study on wetland plants, Keddy *et al.* (1994) found competitive effect to be significantly correlated and competitive response not. In this study the r value for competitive response was lower than for competitive effect as well as the significance level being lower (Figure 2). At the high nutrient level competitive effect and response were not significantly (P> 0.05) correlated (Figure 3), whereas the correlation was significant (P< 0.05) at the lower

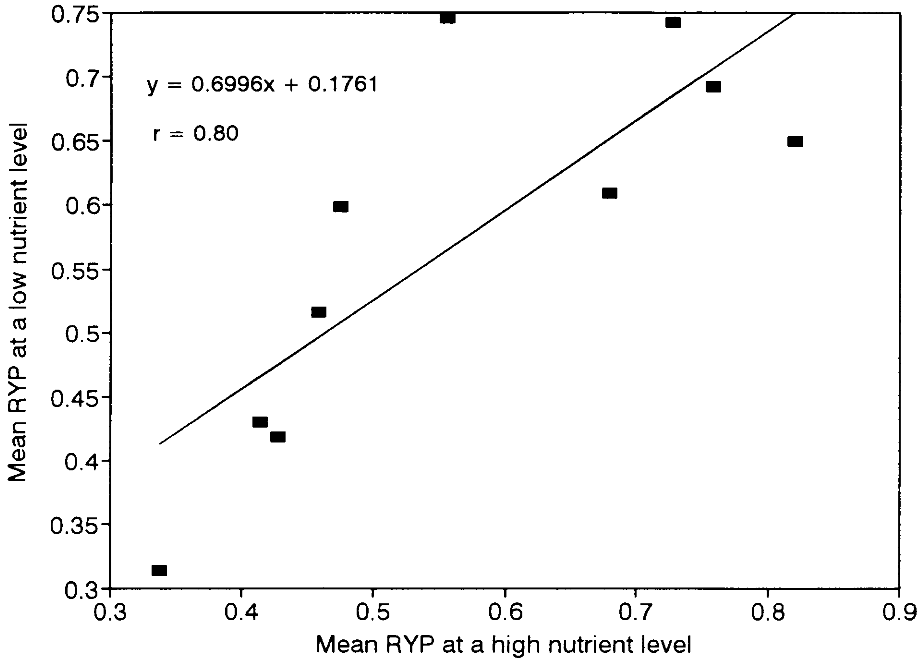

Figure 1. Correlation between relative competitive effect for ten Namaqualand pioneer plant species at two nutrient levels.

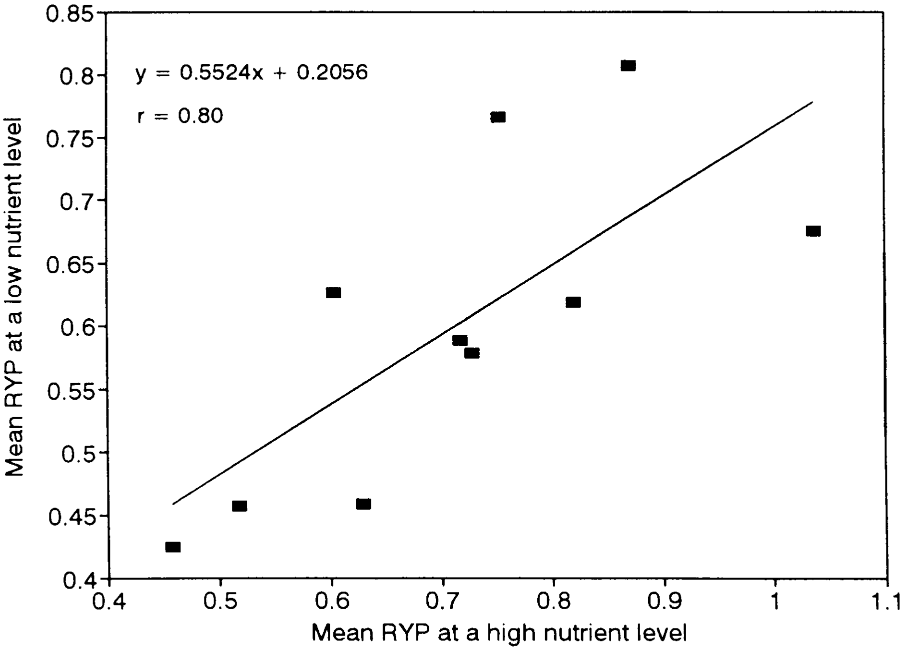

Figure 2. Correlation between relative competitive response for ten Namaqualand pioneer plant species at two nutrient levels.

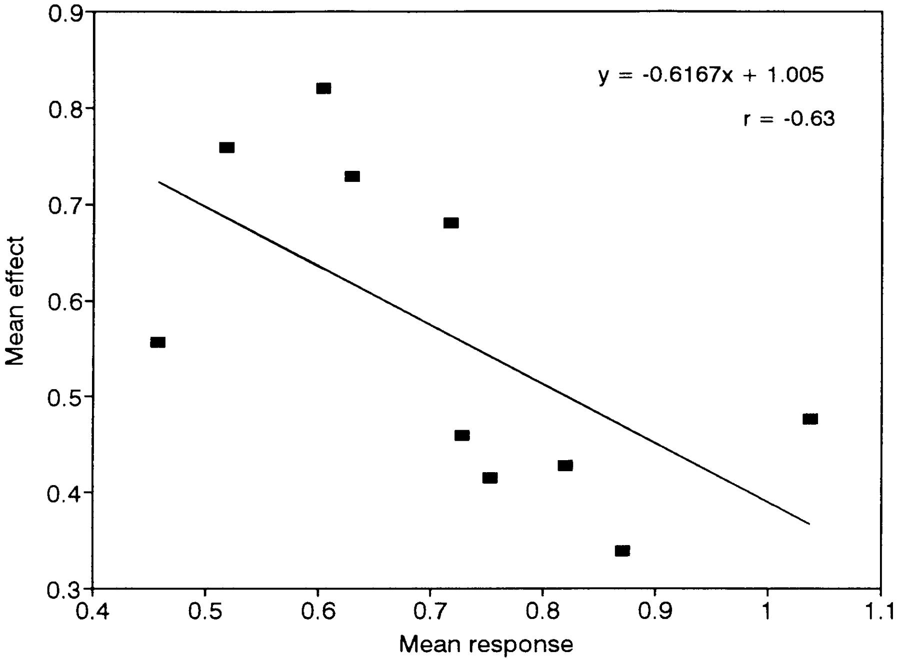

Figure 3. Correlations between mean effect and response in the high nutrient treatment.

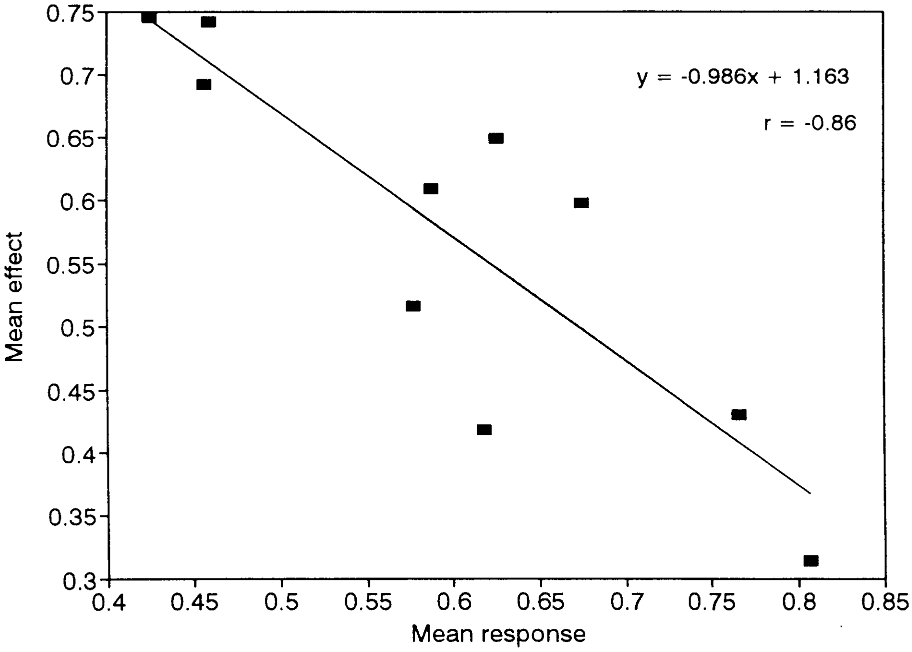

Figure 4. Correlations between effect and response in the low nutrient treatment.

nutrient level (Figure 4). At a low nutrient level a strong effect competitor is a weak response competitor and vice versa. However, this is not the case at the high nutrient level. In their study Keddy *et al.* (1994) found non-significant correlations between competitive effect and response in three environments studied. Goldberg & Landa (1991), found that the mean effect and response were not significantly correlated, although other experiments have revealed different results: a positive relationship was found by Goldberg & Fleetwood (1987) and a negative relationship was found by Miller & Werner (1987).

2) Competitive hierarchy

Kendall's rank correlation coefficient indicated that the mean competitive effect and response rankings of each target species 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 treatments ($P< 0.05$, Table 3).

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 treatments

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

As was the case in this study, Goldberg & 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 1994, Rösch 1996a, Rösch 1996b). Harper (1977) states that competitive hierarchies are consistent and Keddy *et al.* (1994) has also shown that competitive effect hierarchies are unaffected by soil fertility. Keddy *et al.* (1994), suggests concentrating on determining which traits enable some plants to compete better than others as competitive effect hierarchies across soil fertility gradients are unaffected (Keddy *et al.* 1994). The competitive effect for fifteen Namaqualand pioneer plant species was determined and correlated to various plant traits (Rösch *et al.* 1996b). It was found that the traits best related to competitive effect ability were size related, that is - the larger the plant the stronger the competitor.

Competitive response in this study showed the same pattern as competitive effect i.e. perfect agreement between treatments. Goldberg & 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). 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).

Keddy *et al.* (1994) found that from the largest data set to date, one cannot generalize from competitive effect to competitive response and that much more study is needed with respect to these two components of competition.

3) Competition intensity

Mean competition intensity for each pairwise interaction showed no significant difference within a target species (Table 4). However, between treatments and neighbours there was a significant difference in competition intensity (P< 0.05, Table 4). That competition intensity does not vary with nitrogen addition was found by many authors (Campbell & Grime 1992, Wilson & Tilman 1993). The next steps needed in the testing and validation of their model using controlled gradients of stress and disturbance are to distinguish between the relative contributions of above- and below-ground competition and the relative contributions of mechanisms of tolerance of resource shortage and mechanisms of resource capture to individual plant fitness and vegetation dominance (Campbell & Grime 1992).

Keddy *et al.* (1994) suggests 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. Targets should be chosen to represent a range of competitive abilities and not either a strong or a weak competitor. A species of intermediate competitive performance may be the best choice as it will produce the best spread of relative competitive performances, enhancing resolution for the next stages of analysis (Keddy *et al.* 1994), such as determining the importance of competitive effect and response in the distribution of plant species in nature. In this case the use of species with a range of competitive abilities produced resultant effect and response hierarchies that were consistent among the four species and the two treatments.

Table 4. Analysis of variance for competition intensity

Competition intensity	Significance level
Main effects	
A: Treatment	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**

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. While RYP values for competitive response differed significantly between treatment, target species and neighbour species.

Competitive effect hierarchies as well as competitive response hierarchies across two nutrient levels and between targets within a nutrient treatment were found to be concordant. Competitive effect and response hierarchies within treatments were found to be in perfect disagreement. In general, competitive hierarchies are consistent (Harper 1977). However, several studies have shown that competitive hierarchies change over time and within the same environment (Connolly *et al.* 1990, Mechaca & Connolly 1990), and therefore which traits determine competitive ability must depend on factors such as relative sizes or stages of the life cycle of 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 intensity for each pairwise interaction showed no significant difference within target species, however between treatments and neighbour species differences were found.

Testing of hypotheses regarding effect versus response competitive ability or any other relationship between individual's competitive ability requires a good understanding of interactions between plants as a whole as well as plant traits that may give one species an advantage over another.

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Chapter 7

COMMUNITY LEVEL COMPETITION BETWEEN FIVE NAMAQUALAND PIONEER PLANT SPECIES

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Abstract

Namaqualand is renown for its floral displays of many annuals and few perennials, 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 species composition and consequently the floral display?

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 a 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* most. *Senecio arenarius*, *D. sinuata* and *O. grandiflorum* have similar competitive abilities while, *H. variabilis* and *U. cakilefolia* also have similar, yet weaker competitive abilities.

KEYWORDS: Competitive ability, Competitive hierarchy, Community level competition, Relative yield per plant.

Introduction

Competitive interactions are classified as those occurring among individuals of the same species (intraspecific competition) and those occurring among individuals belonging to different species (interspecific competition) (Keddy 1989). The immediate effect of competition is to suppress the growth and size (performance) of the individual and not plant numbers (Silvertown 1987).

Competitive ability is an important determinant of community pattern (Gaudet & Keddy 1988) and ecologists have long been interested in competitive interactions because of their great potential for shaping patterns of distribution and abundance (Goldberg & Barton 1992). Kadmon & Shmida (1990), indicated that the effect of competition on fitness components may vary considerably over both space and time, and that spatial and temporal variations in resource availability may interact with each other to determine the intensity of competitive effects.

Goldberg's (1994) approach to community level competition gives a means to quantify interspecific interactions in the community. Because, in an additive design, the initial density of each species and hence initial levels of intraspecific competition, are the same in the monoculture and the mixture, the method quantifies only effects of interspecific competition (Goldberg 1994).

Goldberg (1994) uses monocultures to calculate what the species composition of a community would look like in the absence of competition and then quantifies the difference between this null community and the observed community. The null community is characterised 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 vegetation of Namaqualand, situated in the north-western arid corner of the Republic of South Africa, is particularly rich in ephemeral species (Van Rooyen *et al.* 1990). The area is renown for its floral displays of many annuals and few perennials, with many tourists visiting the area during the flowering season.

The ephemeral population of Namaqualand varies considerably in species composition and abundance between seasons and localities within a single year and also from year to year (Van Rooyen 1988). The annual variation in species composition is primarily due to the unpredictability of the timing of the first rains. Because each species has its own temperature at which germination is optimal and the first showers may fall from April to July, different species are favoured in different years, giving no one species a clear advantage over the other as a result of the changing competitive environment (Oosthuizen 1994).

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.

Material and Methods

Diaspores of five species were collected in Namaqualand. *Dimorphotheca sinuata* DC., *Oncosiphon grandiflorum* (Thunb.) Kallersjo and *Senecio arenarius* Thunb. diaspores were collected at Goegap Nature Reserve near Springbok (29° 41' S, 17° 55' E), and *Heliophila variabilis* Burch. ex DC. and *Ursinia cakilefolia* DC. diaspores were collected at Skilpad Wildflower Reserve near Kamieskroon (17° 47' East and 30° 09' South). Voucher specimens of all the 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 is according to Arnold & De Wet (1993).

Diaspores were sown in May in quartz sand filled pots (particle size 0.8-1.6mm), with a volume of 0.125m^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 ten individuals per pot (per $0.25m^2$) after a four week period. The mixtures were also thinned out from the time of germination to a final density of ten individuals per species per pot (per $0.25m^2$) after four weeks. The plants were watered daily with tap water and from the fourth week received Arnon and Hoagland's complete nutrient solution (Hewitt 1952) weekly.

The above-ground parts of each plant were harvested 105 days (±15 weeks) after sowing and the dry mass per plant 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

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

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

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 (α = 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), however there were more individuals per pot in a 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). Both intra- and interspecific competition affect the size-specific production rates or survivability (fitness) or both (Kozlowski 1992).

The RYP values indicate a hierarchy: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia cakilefolia* (Table 1). That is, for example *S. arenarius* is 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* similar, but weaker, competitors (Table 1). In two species mixtures Oosthuizen (1994) found than intraspecific competition between individuals of *D. sinuata* or *S. arenarius* was stronger than interspecific competition from individuals of *Ursinia 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 (Oosthuizen 1994), thus these two species are unaffected by the identity of the neighbouring plants. The replacement series evaluation also indicated that there was no niche differentiation between *D. sinuata* and *S. arenarius* and that these species utilised the same resources (Oosthuizen 1994). However, Aarssen (1989) stated that competitive exclusion is avoided at the whole population level because no population contains one genotype that is competitively superior to all other genotypes belonging to any other existing population.

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:		Relative yield per plant (RYP)
	Monoculture	Mixture	
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

In Goldberg's (1994) approach to community level competition the expected relative abundance of a species is compared to the final (actual) relative abundance thus "measuring" the effect of interspecific competition (Table 2). The chi-square goodness-of-fit test showed that there was no significant difference between the observed and expected values of the species (Table 2). Thus 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. However, other experiments have shown competitive effect and response between these species to be different (Rösch *et al.* 1996) yet concordant across fertility gradients.

It is possible that if higher densities had been used in this experiment, the effect of interspecific competition would have been large enough to cause significant changes in species abundances. 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.* 1992, Oosthuizen 1994). Oosthuizen (1994) found that *S. arenarius* seemed to be dependent on optimum densities for optimum performance and that densities in excess of the optimum would not produce a larger floral display. Van Rooyen *et al.* (1992) found that for *D. sinuata*, total yield per unit area increased with increasing density until a level is reached where yield remains fairly constant at a further increase in density.

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

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). 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 (Silvertown & Lovett Doust 1993).

Conclusion

Namaqualand, with its floral displays, is visited by many tourists each year. Various species grow in high densities on abandoned fields and other disturbed areas. Does competition between these species affect the species composition and consequently the floral display?

In all five species studied the mass per plant was significantly greater in the monoculture than in the mixture as pots with small populations impose smaller demands on resources than pots with larger populations.

RYP values enabled the establishment of a competitive hierarchy between the species studied: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia cakilefolia* indicating that *S. arenarius* is the least affected by interspecific competition and *U. cakilefolia* most. *Senecio arenarius*, *D. sinuata* and *O. grandiflorum* have similar competitive abilities while *H. variabilis* and *U. cakilefolia* also have similar, yet weaker, competitive abilities.

Goldberg's (1994) approach to community level competition enables the calculation of the expected relative abundance and the actual relative abundance, and these can be compared to determine the effect of interspecific competition. In all the species the overall effect of interspecific competition was not large enough to cause a significant change in relative species abundance in the mixture compared with the monoculture. It seems that Namaqualand ephemeral species do not show a high degree of density-dependent mortality, but that the individuals are able to exhibit large fluctuations in size (Van Rooyen *et al.* 1992, Oosthuizen 1994).

As both intra- and interspecific competition occurs in Namaqualand ephemeral plant species the possibility exists that, as a result of the variable environment, no one species is able to acquire a competitive advantage over another for long enough as to exclude the other. When pure stands of a species occur in Namaqualand it is probably because of the local distribution of seed and/or conditions for germination, rather than competition.

Most ecological experimenters limit themselves to few treatment levels in order to have sufficient replicate observations so that they may have greater confidence in the differences between treatment levels (Austin 1982). This is true of this experiment. Further experiments are needed to provide data, for example, plant traits, nutrient levels and species composition differences to be able to acquire a holistic view of competition between Namaqualand pioneer plant species.

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Chapter 8

CONCLUSIONS

Namaqualand, with its floral displays, is visited by many tourists each year. Various species grow in high densities on abandoned fields and other disturbed areas. These species occur in one or two species dominant stands or in mixtures including numerous species. From a tourist and management point of view the interaction and functioning of the species is necessary for optimal utilization.

Life history traits are genetically and environmentally determined for each species in a given environment (Barbour *et al.* 1987). The unpredictable nature of the rainfall in Namaqualand has caused the species to evolve various strategies that have led to different life history patterns and thus different plant traits.

Annuals of Namaqualand evade the dry period by germinating, growing, flowering and setting seed quickly during the moist winter and spring, then die off and survive the dry summer in the form of seeds (Le Roux & Schelpe 1988).

Three main strategies, perennial, facultative perennial and annual, were distinguished between the 30 Namaqualand pioneer plant species studied. The perennials (*Conicosia elongata*, *Grielum humifusum* and *Hypertelis salsoloides*) and facultative perennials (*Anchusa capensis*, *Arctotis diffusa*, *Lessertia diffusa* and *Manulea altissima*) are distinguished from the annuals by various characteristics.

Clear distinction between these three strategies could be seen when considering days to emergence, maximum total mass of the individual, reproductive allocation and number of reproductive structures per plant. However, no trends in dispersal type, plant height, root allocation, stem allocation, leaf allocation and LAR could be found to distinguish the three strategies.

The perennial and facultative perennial species take longer to emerge than most of the annuals. This delay in germination could be as a result of a more cautious strategy of the perennials, whereas the annuals adopt a more opportunistic strategy. The perennial species and *Manulea altissima* (facultative perennial) all have low maximum total masses after 21 weeks, whereas the annuals and *Anchusa capensis* and *Arctotis diffusa* (facultative perennials) have large total masses.

Namaqualand plants are characterised by their prolific seed production. The seed of many species exhibit various degrees of dormancy, probably to prevent all the seeds from germinating after one good shower. Each species has its own specific temperature at which germination takes place. Because the first rain may fall from April to July, different species germinate from year to year, depending on when the first rains fall (Le Roux & Schelpe 1988).

The perennials and facultative perennials greatly increase their Reproductive allocation (RA) at the seventeenth week whereas the annuals increase their RA from the ninth or thirteenth weeks. Generally, the perennial species have a much smaller RA than the annuals. Perennials have much smaller RA's as they have the advantage of seed production over many years (Silvertown 1987). The perennial species (*C. elongata* and *G. humifusum*) both produced fewer diaspores over time than most of the annuals. Diaspore production of the facultative perennials (*A. capensis* and *L. diffusa*) was also less than that of the annuals.

As plant traits are important in determining and predicting a plants life history strategy and thus its competitive ability these traits can be used to place species into guilds. Kindscher and Wells (1995) used multivariate analysis to group prairie species together in guilds using morphological, physiological and ecological traits.

Eighteen plant traits were used to arrange 30 Namaqualand plant species into groups with similar characteristics. The result of the first ordination grouped perennial and facultative perennial species exhibit delayed phenological development. In general, these species are small in size, and have a low stem as well as total mass.

Generally, perennial species take longer to emerge, have small maximum total masses and small RA's, while facultative perennials also take longer to emerge and have larger RA's than perennials but smaller RA's than annuals. Annual species emerge quickly, possess large total masses and very large RA's. All these differences in plant traits demonstrate that the different species have evolved different life history patterns to survive the unpredictable environment.

An ordination of annual species resulted in three main guilds (groups), two of which could be further divided into smaller groups. The three main guilds are grouped together such that Group 1 and 2 species, with large individuals possessing large stem masses are separated from Group 3 species, with small individuals pressing small stem masses. Reproductive allocation in Group 1 species is small whereas in Group 3 species it is large.

Since species within a guild have similar morphological, physiological and ecological traits, they probably exploit environmental resources in a similar way and therefore occupy the same niche. It is expected that competition between species of the same guild, that utilize the same resources, should be severe. On the other hand, niche differentiation between species belonging to different guilds, should allow coexistence. In a study to establish a competitive hierarchy of 15 Namaqualand pioneer plant species it was found that the annuals were stronger competitors than the perennials and facultative perennials in the first season when all plants had established from seeds (Rösch 1996). This study clearly demonstrates that the perennials and facultative perennials belong to a guild of plants, that are able to utilize a longer growing season, and accumulate enough resources after most annual species have died. Although these species are at a disadvantage during their early life cycle, they will have a headstart in the second growing season when they are able to resprout from subterranean organs.

Thus, multivariate techniques may be a powerful tool in determining species guilds and the application of these guilds to, for example, community analysis and competition could be wide.

Plant traits, which comprised a plants life history strategy, determines the success of a species in an environment. The combination of plant traits which enables the species to continue existing also determines its competitive ability.

Species can be ranked in order of competitive ability (Keddy 1989). A competitive effect hierarchy was determined using the above-ground dry mass of a phytometer, *Dimorphotheca sinuata*, when grown in competition with itself and fourteen other species. Perennials are weak competitors and annuals stronger competitors.

When characteristics, measured on plants grown singly, were regressed against the phytometer mass, certain traits were well related. Maximum total mass, maximum shoot mass, maximum leaf area, maximum stem mass, maximum reproductive mass and maximum vegetative height x maximum diameter were all highly significant while days to flower initiation, stem allocation, LAR and SLA were all related to competitive ability. Most of these traits are size related and according to Keddy (1989) competitive hierarchies may be inevitable consequences of differences in size. Maximum relative growth rate which is usually considered a good predictor of competitive ability was not significantly related to competitive effect.

The equation, $y = 17.1265 - 0.4183$ (shoot mass) $- 0.0163$ (SLA), was obtained with a r^2 value of 82.77% i.e. 82.77% of a plants competitive effect can be accounted for by the use of the equation and thus its position in a hierarchy can be predicted from values obtained from plants grown singly.

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 for competitive effect differed significantly between target species and between neighbour species but not between nutrient levels. While RYP values for competitive response differed significantly between treatments and targets.

Competitive effect as well as response hierarchies across two nutrient levels and between targets in a nutrient level were found to be concordant. While competitive effect and response hierarchies within nutrient levels were found to be in perfect disagreement. In general, competitive hierarchies are consistent (Harper 1977). However, several studies have shown that competitive hierarchies change over time and within the same environment (Connolly *et al.* 1990, Mechaca & Connolly 1990), and therefore which traits determine competitive ability must depend on factors such as relative sizes or stages of the life cycle of the competing plants (Goldberg & Landa 1991). Yet, the changing environmental conditions in Namaqualand do not allow one species to have a competitive advantage over another for long enough to exclude the other species.

Competitive intensity for each pairwise interaction showed no significant difference within target species. However, between the high and low nutrient levels, and neighbour species there was a significant difference in competition intensity.

In five species studied the mass per plant was significantly greater in the monoculture than in the mixture as pots with small populations impose smaller demands on resources than pots with larger populations.

Relative yield per plant (RYP) values enabled the establishment of a competitive hierarchy between the species studied: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia cakilefolia* indicating that *S. arenarius* is the least affected by interspecific competition and *U. cakilefolia* most. *Senecio arenarius*, *D. sinuata* and *O. grandiflorum* have similar competitive abilities while *H. variabilis* and *U. cakilefolia* also have similar, yet weaker, competitive abilities.

Goldberg's (1994) approach to community level competition enables the calculation of the expected relative abundance and the actual relative abundance, and these can be compared to determine the effect of interspecific competition. In all the species the overall effect of interspecific competition was not large enough to cause a significant change in relative species abundance in the mixture compared with the monoculture. It seems that Namaqualand ephemeral species do not show a high degree of density-dependent mortality, but that the individuals are able to exhibit large fluctuations in size (Van Rooyen *et al.* 1992, Oosthuizen 1994).

Further experiments are needed to provide data, for example, plant traits, nutrient levels and species composition differences to be able to acquire a holistic view of a species life history strategy and thus competition between Namaqualand pioneer plant species. Because of the unpredictable nature of the climate in Namaqualand, to extrapolate these results to natural field conditions will be very difficult or even impossible. But, certain aspects will be better understood and could be used to manage this valuable tourism asset.

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Summary

LIFE HISTORY STRATEGIES OF NAMAQUALAND PIONEER PLANT SPECIES

by

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DEPARTMENT OF BOTANY
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Namaqualand, with its floral displays, is visited by many tourists each year. Various species grow at high densities on abandoned fields and other disturbed areas. From a tourist and management point of view the understanding of interactions and functioning of the species is necessary for optimal utilization.

The unpredictable nature of the rainfall in Namaqualand has caused the species to evolve various strategies which have led to different life history patterns with different plant traits and thus different competitive abilities.

Three different strategies, perennial, facultative perennial and annual, were distinguished between 30 Namaqualand pioneer plant species.

Using multivariate analysis, eighteen plant traits were used to arrange Namaqualand pioneer plant species into groups with similar characteristics. The result of the first ordination grouped perennial and facultative perennial species together as these species exhibit delayed phenological development. In general, these species are

small in size and have a low stem as well as total mass. An ordination of annual species resulted in three main guilds, two of which could be divided into smaller groups.

Species can be ranked in order of competitive ability to form a competitive hierarchy. Plant traits that determine this hierarchy are size related and the equation $y = 17.1265 - 0.4183$ (Shoot mass) $- 0.0163$ (Specific leaf area) can be used to predict (from a singly grown plant) the position of a species in the hierarchy.

Individual competitive ability can be compared between species in two ways: competitive effect and competitive response. Relative yield per plant (RYP) values for competitive effect differed significantly between target species and between neighbour species but not between nutrient levels. While RYP values for competitive response differed significantly between treatments and targets.

Competitive effect hierarchies as well as competitive response hierarchies across two nutrient levels and between targets within a nutrient level were found to be concordant. Competitive effect and response hierarchies within a nutrient treatment were found to be in perfect disagreement.

Competitive intensity for each pairwise interaction showed no significant difference within target species. However, between high and low nutrient levels and neighbour species there was a significant difference in competitive intensity.

Five species were grown in a multispecies mixture and compared to their monocultures. A competitive hierarchy was established: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia speciosa*, indicating that *S. arenarius* is least affected by interspecific competition and *U. speciosa* most. However, the overall effect of interspecific competition was not large enough to cause a significant change in relative species abundance in the multispecies mixture compared with the expected abundance.

The constantly changing conditions in Namaqualand, promote coexistence between species as no species is able to retain a competitive advantage long enough to excluded the others.

Opsomming

LEWENSGESKIEDENISSTRATEGIEË VAN NAMAKWALANDSE PIONIER PLANTSPESIES

deur

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Namakwaland, met sy blomtonele, word elke jaar deur baie toeriste besoek. Verskillende spesies groei in hoë digthede op ou lande en ander versteurde gebiede. Meer kennis omtrent hierdie spesies en die interaksies tussen die spesies is belangrik vanuit 'n toerisme en bestuursoogpunt.

Die onvoorspelbaarheid van reënval in Namakwaland het die totstandkoming van verskillende strategieë in spesies tot gevolg gehad, wat aanleiding tot verskillende lewensgeskiedenisstrategieë en planteienskappe gegee het, asook die verskillende kompeterende vermoëns van die species.

Die dertig ondersoeke pionier plantspesies het drie verskillende strategieë openbaar, naamlik meerjarig, fakultatief meerjarig en eenjarig.

’n Multifaktor variansie-analise van agttien planteienskappe is gebruik om dertig Namakwalandse plant spesies in gildes met ooreenstemmende eienskappe te plaas. Na die eerste ordening van dertig spesies, is die meerjarige en fakultatiewe meerjarige spesies, as gevolg van hulle vertraagde fenologiese ontwikkeling, uitgesluit. Die eenjarige spesies is deur multifaktor variansie-analise georden en drie hoofgildes, wat verder verdeel kan word, geïdentifiseer.

Spesies kan volgens hul kompeterende vermoë gerangskik word om ’n kompeteringshiërargie te vorm. Planteienskappe wat die posisie in hierdie hiërargie bepaal, is grootte-afhanklik en die vergelyking y = 17.1265 - 0.4183 (Bogrondse massa) - 0.0163 (Spesifieke blaaroppervlakte) kan gebruik word om (vanaf ’n enkelgroeinde plant) die posisie van ’n spesie in hierdie hiërargie te voorspel.

Individuele kompeterende vermoëns tussen spesies kan op twee maniere vergelyk word: kompeterende effek en kompeterende reaksie. Relatiewe opbrengs per plant (ROP) vir kompeterende effek het betekenisvol tussen indikatorspesies en tussen buurspesies verskil maar nie oor behandelings nie. In die geval van kompeterende reaksie het die ROP waardes betekenisvol verskil tussen behandelings en indikatorspesies.

Kompeterende effek sovel as reaksie hiërgieë oor twee behandelings en tussen indikatorspesies binne ’n behandeling was dieselfde. Kompeterende effek en reaksie hiërargieë binne behandelings stem nie ooreen nie.

Kompeterende intensiteit vir elke paargewyse interaksie binne ’n indikatorspesie was nie betekenisvol nie. Maar, tussen hoë en lae voedingstof vlakke, en buurspesies was daar ’n betekenisvolle verskil in kompeterende intensiteit.

Vyf spesies is saam in multispesiemengsels gekweek en die opbrengs met die monokulture vergelyk. ’n Hiërargie is vasgestel: *Senecio arenarius* > *Dimorphotheca sinuata* > *Oncosiphon grandiflorum* > *Heliophila variabilis* > *Ursinia speciosa*, wat aantoon dat *S. arenarius* die minste deur interspesifieke kompetisie beïnvloed word en *U. speciosa* die meeste. Die invloed van interspesifieke kompetisie was nogtans nie groot genoeg om 'n betekenisvolle verskil in spesiesamestelling vanaf die verwagte teweeg te bring nie.

Die onvoorspelbare veranderinge in die fisiese omgewing in Namakwaland, bevorder die naasbestaan tussen spesies aangesien geen spesie sy kompeterende voordeel lank genoeg behou om die ander uit te sluit nie.

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* a & b's in this list are not necessarily the same as in the proceeding chapters.