AN ECOPHYSIOLOGICAL STUDY OF TWO KEY GRASS SPECIES, ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

by

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`AND GOD SAID, "LET THE EARTH PUT FORTH VEGETATION, PLANTS YIELDING SEED, AND FRUIT TREES BEARING FRUIT IN WHICH IS THEIR SEED, EACH ACCORDING TO ITS KIND, UPON THE EARTH." AND IT WAS SO. THE EARTH BROUGHT FORTH VEGETATION, PLANTS YIELDING SEED ACCORDING TO THEIR OWN KINDS, AND TREES BEARING FRUIT IN WHICH IS THEIR SEED, EACH ACCORDING TO ITS KIND. AND GOD SAW THAT IT WAS GOOD.'

GENESIS 1: 11-12

`AND HE WILL GIVE GRASS IN YOUR FIELDS FOR YOUR CATTLE, AND YOU SHALL EAT AND BE FULL.'

DEUTERONOMY 11:15

`THOU DOST CAUSE THE GRASS TO GROW FOR THE CATTLE, AND PLANTS FOR MAN TO CULTIVATE, THAT HE MAY BRING FORTH FOOD FROM THE EARTH...'

PSALMS 104: 14

`THEY WERE TOLD NOT TO HARM THE GRASS OF THE EARTH OR ANY GREEN GROWTH OR ANY TREE,...'

REVELATION 9:4

TO MY PARENTS

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ABSTRACT

AN ECOPHYSIOLOGICAL STUDY OF TWO KEY GRASS SPECIES, ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

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The effect of competitive stress was studied in two key grass species, Athephora pubescens Nees ecotype VH20 and Eragrostis curvula (Schrad.) Nees cultivar Ermelo. Increasing competition resulted in a decrease in the total yield per plant in both species. Eragrostis curvula proved to be the superior competitor, while A. pubescens was evidently an inferior competitor exhibiting high sensitivity to both forms of competitive interference. Both intra - and interspecific competition failed to have a significant effect on the pattern of biomass allocation to the vegetative organs in both species, while reproductive allocation was absent. A decrease in net CO_2 uptake rate per unit leaf area, exhibited by both species, coincided with a decrease in leaf production per plant. Increasing competition resulted in retarded relative growth rates and restricted morphological development.

A field survey conducted in a natural plant community did not support the findings made of _A_. _pubescens_ in the pot trials.

UITTREKSEL

'N EKOFISIOLOGIESE STUDIE VAN TWEE SLEUTEL - GRASSPESIES, ANTHEPHORA PUBESCENS NEES EN ERAGROSTIS CURVULA (SCHRAD.) NEES

deur

JENNIFER ELIZABETH MYNHARDT

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Die invloed van kompetisie op twee weidingspesies, naamlik Anthephora pubescens Nees ekotipe VH20 en Eragrostis curvula (Schrad.) Nees kultivar Ermelo is ondersoek. Die invloed van kompetisie was deurslaggewend in beide spesies, deurdat die totale opbrengs per plant met toenemende digtheid afgeneem het. Eragrostis curvula was die sterker kompeteerder, terwyl A. pubescens klaarblyklik die swakker kompeteerder was met hoë sensitiwiteit teenoor beide vorms van kompetisie. Nóg intra - of interspesifieke kompetisie het 'n betekenisvolle invloed op die biomassatoewysingspatroon, aan die vegetatiewe organe, van beide spesies gehad, terwyl reproduktiewe toewysing afwesig was. 'n

Afname in netto CO_2 - opnametempo per eenheid blaaroppervlakte, met toenemende digtheid, het ooreengestem met 'n afname in blaarproduksie per plant in beide spesies. Toenemende kompetisie het gelei tot vertraging van relatiewe groeitempo's en beperkte morfologiese ontwikkeling.

'n Veldopname wat in 'n natuurlike plantgemeenskap gemaak is, het die resultate van potproewe met A. pubescens nie ondersteun nie.

CHAPTER 1

INTRODUCTION

In 1859 Darwin wrote: "... if we wish in imagination to give the plant the power of increasing, we should have to give it some advantage over its competitors, or over the animals that prey on it."

Dry matter production in vegetation is subject to a wide variety of environmental constraints. These include shortages and excesses in the supply of solar energy, water and mineral nutrients. According to Grime (1977) plant species and even different genotypes may differ in susceptibility to particular forms of stress, and consequently each stress may exercise a different affect on vegetation composition. One of the most important forms of stress that plants which grow in close proximity face, whether they are of the same or of different species, is competition. Grime (1977) defines competition as the tendency of neighbouring plants to utilize the same light, mineral nutrients, water or space. The ability to compete for light, water, mineral nutrients and space are interdependent to the extent that natural selection has caused their development to a comparable extent in any particular genotype. Competition has therefore been associated with the evolution of a distinct strategy, and competitive ability is associated with characteristic and measurable genetic attributes which, by maximizing the capture of resources, facilitates the exclusive occupation of fertile, relatively undisturbed environments (Grime, 1977).

Three models of succession have been suggested by Connell & Slatyer (1977). In the first model of facilitation, the original species modifies the environment in such a way that it becomes more suitable for the following species in an ongoing process. The most important feature of facilitation succession is that the change in the abiotic environment is caused by the developing community. The entry and growth of the later species depends on earlier species preparing the ground. The tolerance model suggests that a predictable sequence arises because different species use different strategies to exploit resources. Species which develop at a later stage are able to tolerate lower resource levels and are able to grow to maturity in the presence of earlier species. These species are therefore stronger competitors than the earlier species. The inhibition model applies when all species resist the invasion of competitors. Later species gradually accumulate by replacing earlier individuals when they die. In the case of the facilitation and tolerance models, the early colonisers die due to competition. In the case of the inhibition model, however, the early colonisers die due to local disturbances caused by extreme physical conditions or due to the effect of consumers. Noble & Slatyer

(1981) attempted to formulate the role of different features, of different species, which determines their place in succession. The two most important features relate to the method of recovery and the ability of individuals to reproduce in the absence of competitors. According to Harper (1977) species react to selection pressure and develop features which enable them to survive for a longer period in the succession or they may develop more effective mechanisms of escape.

A theory on plant competition, aiming at analysing general principles by using models, suitable for quantitative treatment and formal interpretation of many competition phenomena, was introduced by De Wit & Ennik (1958), and detailed by De Wit & Van den Berg (1965) and Tow et al. (1966). The design of De Wit (1960) has proved popular due to the ability to identify and differentiate between superior and inferior competitors, and the extent of niche overlap between species, by mathematical means.

An understanding of the mechanisms that regulate population size in plant communities is of vital importance to both pure and applied ecologists. Throughout the history of ecology one school of thought (Antonovics & Levin, 1980) maintained that populations of plants are in some way regulated by density - dependent factors, i.e. processes that either increase mortality or decrease fecundity as the density of the population increases. According to Antonovics & Levin (1980) a density - dependent feedback exists that holds the population within certain limits.

A second school of thought (Antonovics & Levin, 1980) maintains that density - independent factors (e.g. weather conditions or disturbance) are more important in determining population size. Whether populations are regulated by density - dependent or density - independent factors has been a subject of intensive debate and controversy. Much of the controversy stems from a lack of adequate information about density - dependent regulation and its effects on a population; and more specifically the effects of density stress on the individual plant.

Populations of higher plants may vary in growth rate or mortality in reaction to stress. Mortality tends to be a continuing process throughout the life of dense populations and Yoda et al. (1963) showed that there was a relationship between the mean size of the surviving plants and the residual density at various stages in the development of a population. The distribution of matter within the plant and the form of the plant are products of complex developmental processes which depend on, among other things, the supply of assimilates, distribution of active growth hormones and environmental history. A technique, known as growth analysis (Kvet et al., 1971), has been developed in which ecological phenomena such as the success of species in various habitats, competition among species, genetic differences in yielding capacity and effects of agricultural treatments on crop growth can be investigated. According to Kvet et al. (1971), growth analysis is useful to analyse net photosynthetic production by plants, net production being defined as the net result of the assimilatory work taking place in a plant during a certain period of time.

The most common criteria for choosing purported competitors have been taxonomic relatedness or morphological similarity on the assumption that these factors imply an overlap in resource use. Brown _et_ _al_. (1979), however, pointed out that the most important competitive interactions are not necessarily among similar pairs of species. All plants use essentially the same resources and thus all individuals in a community are potential competitors. It is therefore critical to have some objective means of determining the most important competitors for a given plant species, particularly if we wish to evaluate the effect of competition on the distribution and abundance of that species.

The aim of the study was therefore to identify the competitive ability of two important key grass species of South African pastures and to determine the effects of competition on their growth and overall production. _Anthephora_ _pubescens_ and _E_. _curvula_ are both perennial tuft grasses which occur on sandy soils in Savanna, Grassland and Nama - Karoo biomes (Gibbs Russel _et_ _al_., 1990). _Anthephora_ _pubescens_ has the ability to resist high temperatures and perform well in warm semi - arid areas with moderate to high maximum and minimum temperatures. A valuable attribute of this species is that it is a palatable climax grass with a high yield on nutrient - poor soil (Roberts & Fourie, 1975). Eragrostis curvula is a cultivated pasture with a wide distribution and is often used for the control of erosion (Gibbs Russel et al., 1990). Much work has been done on the utilisation of both pasture species as hay or grazing crop, but as differential components. Although these two species do not normally occur together in nature, it was aimed to evaluate their yielding potential if intercropped. The economic viability of pasture species in a third world continent is not only essential, but critical.

The thesis is presented in the form of papers. The papers have been submitted for publication in various scientific journals. A general introduction, a brief chapter on methods, a general conclusion and a comprehensive list of references are included in addition to the papers. The papers represented show some stylistic irregularities due to differences in layout and style required by various journals.

CHAPTER 2

MATERIALS AND METHODS

The following is a summary of the materials and methods used in the study. A more detailed description of the materials and methods is given in the relevant articles and chapters by Mynhardt et al. (1992a, b, c & d) and chapters 7 and 8.

The A. pubescens spikelets, ecotype VH20, were obtained from the Biesiesvlakte Research Station (24^{o} 28" E; 25^{o} 57" S) and certified E. curvula seeds of the Ermelo cultivar were obtained from a local seed dealer. The experiment was carried out in pots under greenhouse conditions at the Grassland Research Centre, Roodeplaat. The method used was based on the replacement series of De Wit (1960).

i) Competition, biomass allocation and growth analysis

The plants were cultivated in a sandy - loam soil and grown over a period of five months. The seedlings were thinned to the desired density four weeks after emergence. The pots received tap water every second day and a commercially produced nutrient solution, UAN 32, at monthly intervals. At the end of each consecutive month, a minimum of four replicates of each treatment and species were harvested. The competition analyses used are based upon those of De Wit (1960), where the growth of individual plants in a mixture is compared with the growth of individuals in a monoculture at the same overall density. The indices used and the derived values are explained in Mynhardt et al. (1992a). The allocation of biomass to the separate plant parts was determined as a ratio of the dry mass of the particular plant part to the dry mass of the whole plant multiplied by 100 to present the allocation as a percentage. The relationship between the total mass per plant and the mass of a plant part at various densities was determined with the aid of Bleasdale's (1966) allometric relationship. The calculated values are given in Mynhardt et al. (1992b). The growth analysis of Hunt (1982) was used to analyse the growth characteristics. The calculated rates and ratio's are explained in Mynhardt et al. (1992c).

ii) Morphology

In the morphological investigation the morphological development of four marked plants of each treatment and species was monitored fortnightly. The parameters monitored were the total number of leaves on the primary tiller, the average number of lateral tillers per plant and the average tuft height. The determined values are given in Mynhardt et al. (1992d).

iii) Photosynthesis

The net CO_2 uptake rate per unit leaf area of *A. pubescens* and *E. curvula*, at varying densities, was determined with the aid of a LICOR LI 6250 Infra - Red Gas Analyser. A once - only determination was made of which the values obtained are given in chapter 7.

iv) Field trial

To test the validity of the results found in the pot trials of *A. pubescens*, a field survey was conducted at the Biesiesvlakte Research Station (24° 28" E; 25° 57" S). The survey area lies 1 208 m above sea level and receives a mean annual rainfall of 475 mm. The method used was that of the nearest - neighbour as described by Yeaton & Cody (1976). The measurements made and determined values are given in chapter 8.

v) Statistical analysis

Six replicates were planned per treatment, but due to mortality a minimum of four replicates were used. Due to unbalancedness the regression analysis approach was used to analyse the data and the "student's" t - test was used to determine statistical significance at a level of $p < 0.05$ (Rayner, 1969).

CHAPTER 3

THE EFFECT OF INTRA- AND INTERSPECIFIC COMPETITION ON THE DRY MATTER PRODUCTION OF _ANTHEPHORA_ _PUBESCENS_ NEES AND _ERAGROSTIS_ _CURVULA_ (SCHRAD.) NEES

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Two key grass species, _Anthephora_ _pubescens_ Nees (wool grass) and _Eragrostis_ _curvula_ (Schrad.) Nees (weeping love grass) were established in a replacement series to determine their relative competitiveness. Intraspecific competition had a similar affect on both species, causing a decrease in yield per plant with increasing density. This effect was more pronounced in _E_. _curvula_ than

A. pubescens. Interspecific competition, however, had a greater negative affect on A. pubescens than E. curvula, favouring the yield of the latter species. Eragrostis curvula proved to be the superior competitor, whereas A. pubescens was evidently an inferior competitor which was sensitive to any form of competitive interference.

Twee grasspesies, Anthephora pubescens Nees (borseltjiegras) en Eragrostis curvula (Schrad.) Nees (oulandsgras) is in 'n vervangingsreeks gevestig om hulle relatiewe kompeterende vermoëns te bepaal. Die invloed van intraspesifieke kompetisie was dieselfde in beide spesies met 'n toename in digtheid, wat gelei het tot 'n afname in opbrengs per plant. Dié invloed was meer prominent in E. curvula as in A. pubescens. Interspesifieke kompetisie het 'n groter negatiewe invloed op die opbrengs van A. pubescens gehad, terwyl die opbrengs van E. curvula bevoordeel is. Eragrostis curvula was duidelik 'n sterker kompeteerder, terwyl A. pubescens 'n swak kompeteerder was wat gevoelig was teenoor enige vorm van kompetisie.

Additional index words: Density, weeping love grass, wool grass, yield

INTRODUCTION

Harper (1964) states : "the essential qualities which determine the ecology of a species may only be detected by studying the reaction of it's individuals to their neighbours - and the behaviour of the species in isolation may be largely irrelevant to understanding their behaviour in the community." As cited by Hall (1974) Clements et al. (1929) stated : "Competition is purely a physical process. With few exceptions, such as the crowding of tuberous plants when grown too closely, an actual struggle between competing plants never occurs. Competition arises from the reaction of one plant upon the physical factors about it and the effect of the modified factors upon the competitors. In the exact sense, two plants do not compete with each other as long as the water content, the nutrient material, the light and the heat are in excess of the needs of both. When the immediate supply of a single necessary factor falls below the combined demands of the plants competition begins." Plant interference, a term proposed by Harper (1961, 1964), may be defined as the response of an individual plant or plant species to it's total environment as this is modified by the presence and/or growth of other individuals or species. Competition itself is only one facet of interference between plants, although at times it may be a very dominating one.

Competition can arise between plants of the same species (intraspecific competition) or between plants of different species (interspecific competition). Competition is important in both natural and agricultural communities. The botanical composition of any mature stand of vegetation is largely determined by competition. The first complete separation of the factors for which competition occurred was achieved when Donald (1958) partitioned shoot and root competition between two grasses. Donald (1958) found that root competition had a greater affect than shoot competition, and that there was a positive interaction between the two. He suggested that this was basic to competition.

A technique has been evolved where, by comparing the growth of each species in a mixture with it's growth in a pure stand (monoculture), the degree of "competition" occurring between these species can be described mathematically (De Wit 1960). According to Firbank & Watkinson (1985) this design has proved popular because graphical presentation of the yield data allows identification of the stronger competitor and the extent of niche overlap between species. Based on the design of De Wit (1960) a number of indices, such as relative yield per plant, relative yield total, relative crowding coefficient and aggressivity can be used to evaluate the experimental results. This methodology has been widely used in agronomy (Mead & Riley 1981) and plant competition studies (De Wit 1960; De Wit & Van den Bergh 1965).

It was attempted in this study to determine the effect of intra - and interspecific competition on the yield of two key grass species, *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. These two species were chosen as potential competitors due to their similar growth habit and their ability to produce inflorescences within the first growing season. *Anthephora pubescens* is an important component of permanent pastures due to its palatability and ability to produce high yield on nutrient poor soil, and *E. curvula* has found a permanent niche in South African agriculture as an improved pasture grass. Although much work has been carried out on their utilisation as hay or grazing crop, the effect of stress factors on their production has received little local attention. A full knowledge of the effect of stress factors, such as competition, on the production of agriculturally viable pasture species is therefore essential for the rational use of veld and cultivated pastures for animal production. A knowledge of competitive interactions will contribute greatly to an understanding of mixed communities as pasture, and restrict the possibility of eliminating desirable species. Ecological differences between species should be defined and exploited, as in them may lie the secret of pasture stability (Hall 1978).

PROCEDURE

The experiment was carried out in a greenhouse at the Grassland Research Centre, Roodeplaat. Anthephora pubescens Nees of the VH20 ecotype and Eragrostis curvula (Schrad.) Nees cultivar Ermelo were sown in 170 x 170 mm plastic pots with a depth of 150 mm and perforated bases, which were filled with a 10 mm layer of gravel and topped with a sandy - loam soil. The soil consisted of 82.8 % sand, 8.7 % loam, 8.5 % clay and had a pH of 5.3. The A. pubescens spikelets were obtained from the Biesiesvlakte Research Station, Vryburg (24° 28" E; 25° 57" S). These spikelets were harvested in April 1989 from plants which had been planted in March 1976. Certified E. curvula seeds were obtained from a local seed dealer. The two species were sown in both pure and mixed stands in November 1990. In the pure stands the planting densities were 1, 4, 8, 12 and 16 plants per pot respectively. In the mixed stands, however, the total planting density was kept constant at 16 plants per pot, but the ratio's of A. pubescens to E. curvula were varied at 4:12, 8:8 and 12:4 plants per pot, i.e. the pattern followed was that of a replacement series (De Wit 1960). A surplus spikelets and seeds were sown and thinned to the desired density 4 weeks after emergence. The pots received 500 ml tap water every second day and 100 ml nutrient solution, commercially produced UAN 32, at monthly intervals.

The pots were laid out on trolleys arranged in five replicate blocks. Each block had six replicates per treatment. The trolleys were rotated fortnightly. At the end of each consecutive month, commencing January 1991 and terminating in May 1991, a replicate block was harvested to determine the dry matter production. Each plant of each treatment, and species, was harvested separately by clipping at the soil surface and divided into the separate plant parts, i.e. roots, tillers and leaves. The roots were washed over a fine sieve using a fine spray nozzle. In the case of the mixed stands, however, the roots of the two species were intertwined and were therefore not harvested. The separate plant parts of each treatment, and species, were placed in brown paper bags and dried at 90°C for 48 h and weighed. The dry mass values for the entire plant as well as those of the organs were determined on a per plant and per pot basis for each respective species.

ANALYSES

The analyses used are based upon those of De Wit (1960). The growth of individual plants in a mixture is compared with the growth of individuals in a pure stand (monoculture) at the same overall density. The total density of all the plants is held constant and only the proportions of the different species differ.

From the yield (above - ground biomass) of each species in each pot, the total number of individuals in each pot and the proportions of each species in the pot, two variables were calculated, relative yield per plant (RYP) and relative yield total (RYT) (Fowler 1982).

First let :

p = initial proportion of species i in a mixture
q = initial proportion of species j in a mixture
$p + q = 1$ in a mixture of two species

Y_{ii} = yield of species i in a pure stand
Y_{jj} = yield of species j in a pure stand
Y_{ij} = yield of species i in a mixture
Y_{ji} = yield of species j in a mixture

Given a constant total density, then

$$RYP_{ij} = Y_{ij}/(pY_{ii})$$

$$RYP_{ji} = Y_{ji}/(qY_{jj})$$

$$RYT = pRYP_{ij} + qRYP_{ji}$$

To determine whether the yield of the mixture is greater than the mean of the two monocultures, the relative yield of the mixture (RYM) can be calculated (Wilson 1988).

$$\mathrm{RYM} = (Y_{ij} + Y_{ji})/[(Y_{ii} + Y_{jj})/2]$$

This formula is, however, only applicable to a 50:50 mixture.

The relative competitive abilities of the species were determined in a 50:50 mixture and expressed as the "aggressivity" (McGilchrist & Trenbath 1971; Martin & Snaydon 1982).

$$\mathrm{Aggressivity} = 0.5[(Y_{ij} - Y_{ji})/(Y_{ii} - Y_{jj})]$$

Jolliffe *et al*. (1984) calculated various indices :

Let Y_p = projected yield
Y_m = monoculture yield
Y_x = mixture yield

$Y_p - Y_m$ = species monoculture reaction

$(Y_p - Y_m)/Y_p$ = relative monoculture reaction

$Y_m - Y_x$ = species mixture reaction

$(Y_m - Y_x)/Y_m$ = relative mixture reaction

The relative competitive ability of the components in the 50:50 mixture were calculated and can according to Wilson (1988) be expressed by the "Competitive Balance Index" (C_b) :

$$C_b = \log_e[(Y_{ij}/Y_{ji})/(Y_{ii}/ Y_{jj})]$$

If $C_b = 0$; no competition or equal competitive abilities.

The relative crowding coefficient (K) was calculated for the 50:50 mixture (Hall 1974). The relative crowding coefficient is defined as follows :

$$K_i = Y_{ij}/(Y_{ii} - Y_{ij})$$

Harvesting commenced 4 weeks after thinning. At harvest only those pots which still had the full number of plants (i.e. initial density) were used. If one plant in a pot died the pot was discarded. Due to an unequal number of replicates the regression analysis approach was used to analyse the data. A minimum of four replicates were used. The "student's" t - test was used to determine statistical significance at a level of $p < 0.05$ (Rayner 1969).

RESULTS AND DISCUSSION

Five harvest dates were planned for this experiment, but due to the high mortality rate of A. pubescens under competitive stress only the first three months could be harvested (3 harvests). Although E. curvula survived successfully enabling five harvests, data of only the first three harvests of E. curvula were used for the purpose of comparison. Smith (1983) recorded that plants die sooner at high densities, irrespective of the time of initiation. This was evident in A. pubescens, although E. curvula remained relatively unaffected. Donaldson & Kelk (1970) recorded, in a field experiment, that initial establishment by A. pubescens was best where competition from existing grass species was lowest. Both species failed to produce inflorescences under stress with the result that the dry mass mentioned refers to the total vegetative dry mass. Inhibition of the production of inflorescences with increasing density has been recorded by Fowler (1984) in Linum grandiflorum.

1. DENSITY

Anthephora pubescens

At the first harvest the total vegetative dry mass per plant fluctuated with increasing density (Figure 1a). A relationship between dry matter production and density was not evident at this early stage. This fluctuation in dry mass per plant was, however, not significant ($p < 0.05$). At the second and third harvests an increase in density resulted in a significant decrease in dry mass per plant (Figures 1b & c). There are two possible relationships between density and yield (Harper 1977).The first relationship is asymptotic, i.e. the total yield per unit area increases with an increase in density until a level is reached where yield no longer increases with an increase in density. The second relationship is parabolic where the yield decreases at higher densities. The total vegetative dry mass per pot exhibited a parabolic trend at the third harvest (Figure 1c). The optimum density, producing maximum yield at the third harvest, was 12 plants per pot .

Shinozaki & Kira (1956) observed a linear relationship between the inverse of the average mass per plant and density, referred to as the reciprocal yield law:

$$w^{-1} = Ap + B$$

where w = yield per plant

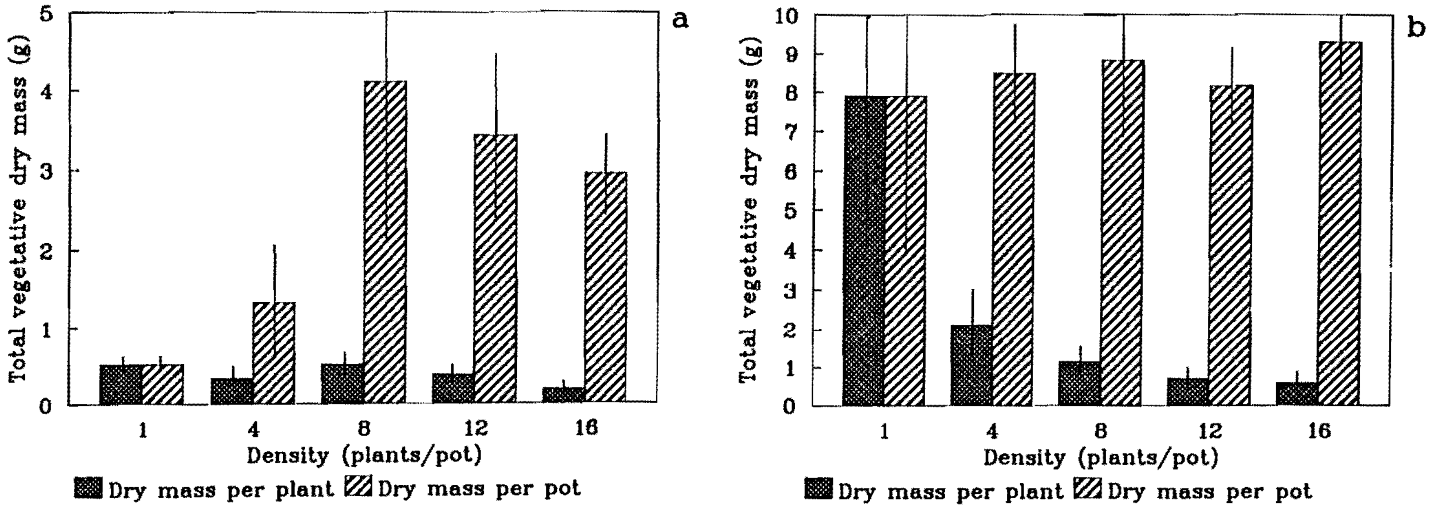
p = density

A and B = constants

This relationship is illustrated in Figure 2 for respective harvest dates. The smaller the slope the sooner the plateau - yield is reached.

According to Harper (1977) higher plants display a great degree of plasticity in their environment. The number of leaves and flowers as well as the size of the whole plant may vary to a great extent, depending on the conditions under which the plants grow. This ability can be clearly seen in the reaction of plants to a changing density.

It was observed that with an increase in density *A. pubescens* exhibited size variation, e.g. in a pot containing 8 plants, 6 plants were small and 2 plants were large. Harper (1977) recorded that plants grown at higher densities were smaller and Weiner & Thomas (1986) recorded greater size variation at higher densities. The increase in size variability in populations grown at higher densities has been interpreted as strong support for the hypothesis that competition between plants is "asymmetric" or "one - sided", i.e. that the larger plants are able to obtain a disproportionate share of resources and suppress the growth of smaller individuals (Weiner & Thomas 1986). Asymmetric competition may be evident in pure stands of *A. pubescens*.



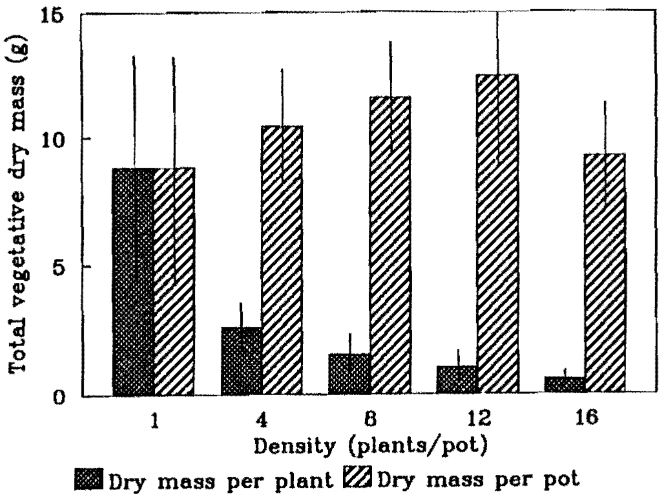


Figure 1 The effect of density on the total vegetative dry mass per plant and per pot of *Anthephora pubescens* at the (a) first (b) second and (c) third monthly harvests.

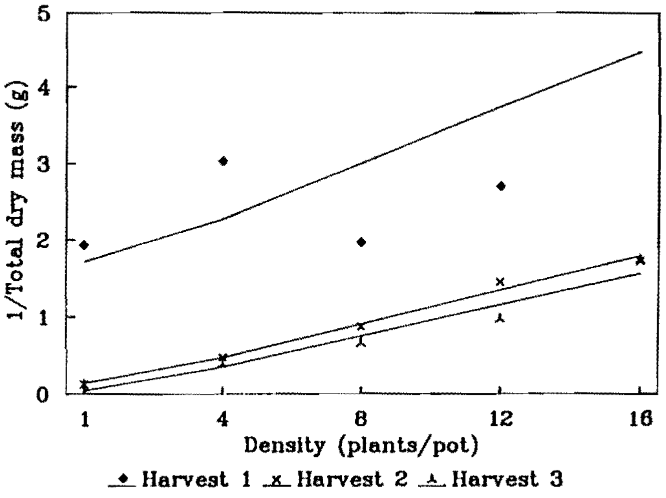
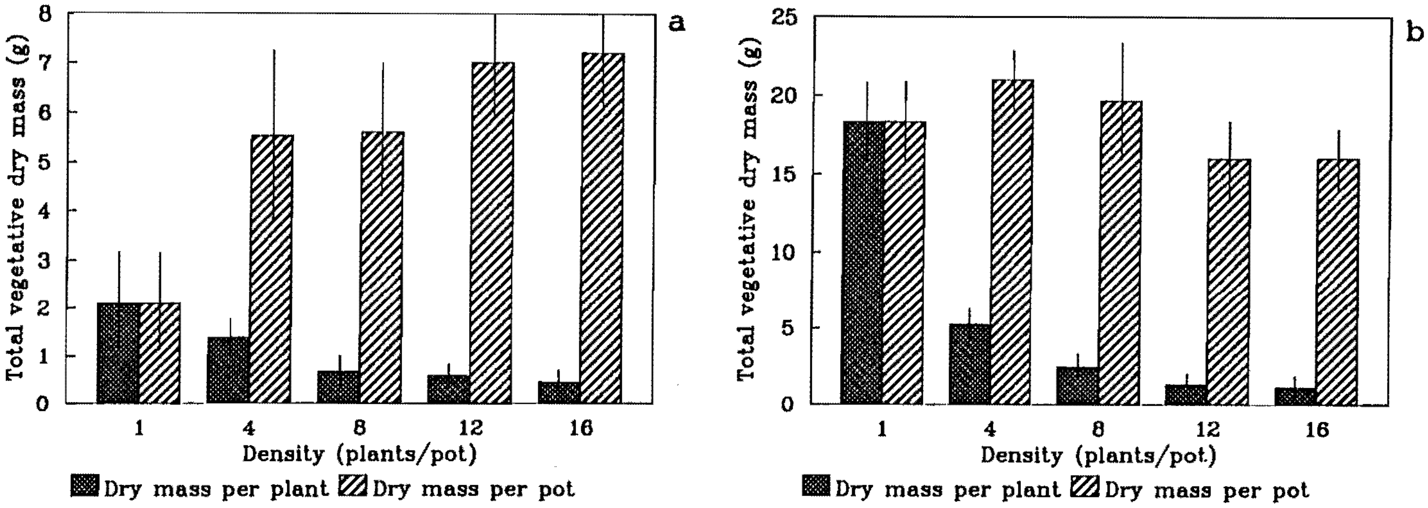


Figure 2 A regression between density and the inverse of the total vegetative dry mass of *Anthephora pubescens* at all three monthly harvests (harvest 1: y = 0; 0.183x + 1.525; r = 0.553; harvest 2: y = 0; 0.109x + 0.029; r = 0.990; harvest 3: y = 0; 0.101x - 0.058; r = 0.947).

Eragrostis curvula

With an increase in density the total dry mass per plant decreased (Figures 3a, b & c). This decrease in dry mass was significant at the second and third harvest ($p < 0.05$). At the first harvest the total dry mass per pot increased with an increase in density (Figure 3a). At the second and third harvest the dry mass per pot initially increased with an increase in density until the maximum yield was reached at an intermediate density and then decreased with a further increase in density (Figures 3b & c). This is known as a parabolic relationship where overcompensation has taken place. At the second harvest 4 plants per pot was the density with the maximum yield per pot, but at the third harvest a density of 12 plants per pot maintained maximum yield.

The reciprocal yield law for *E. curvula* is illustrated in Figure 4. The slope at the first harvest was steep, but got smaller at the second and third harvest indicating that the plateau - yield was being reached; the effect of density increased with an increase in plant size.



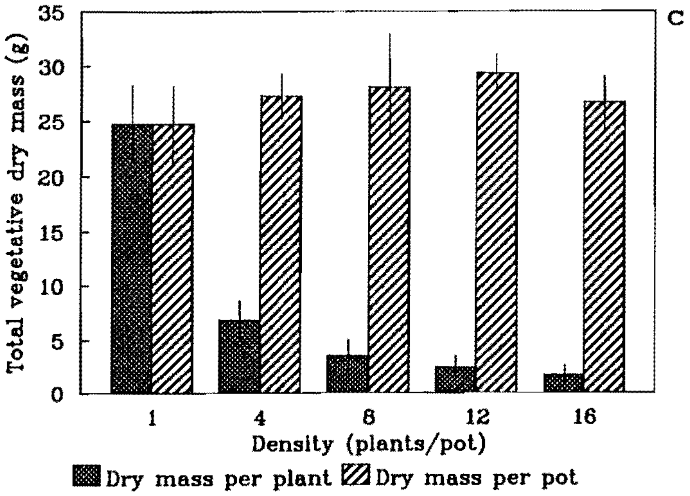


Figure 3 The effect of density on the total vegetative dry mass per plant and per pot of Eragrostis curvula at the (a) first (b) second and (c) third monthly harvests.

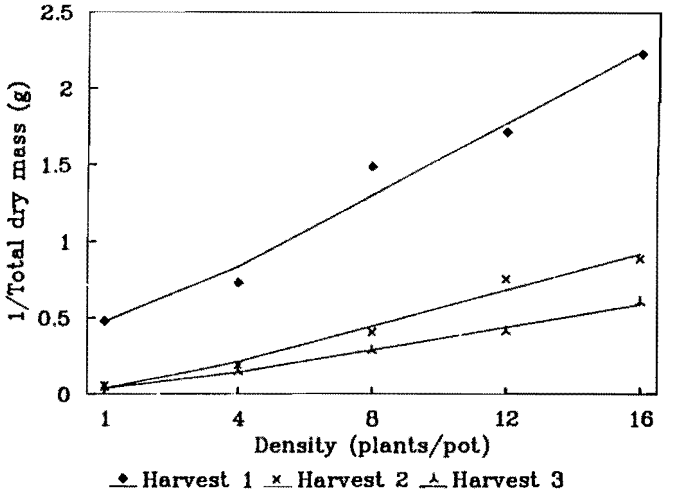


Figure 4 A regression between density and the inverse of the total vegetative dry mass of Eragrostis curvula at all three monthly harvests (harvest 1: y = 0; 0.117x + 0.358; r = 0.976; harvest 2: y = 0; 0.058x + 0.021; r = 0.983; harvest 3: y = 0; 0.036x - 0.002; r = 0.994).

2. COMPETITION

Replacement series

Figure 5a is a schematic representation of the De Wit model (1960). According to this model the effect of I on J is greater than the effect of J on J and the effect of J on I is less than I on I, i.e. intraspecific competition between individuals of I is greater than interspecific competition between I and J. In Figures 5b & c the results of the replacement series is represented graphically. At the first harvest the effect of competition was not as yet evident in *A. pubescens*, but was evident in *E. curvula* (Figure 5b). At the third harvest, however, the effect of competition was evident in both species (Figure 5c). According to Figure 5c intraspecific competition between individuals of *E. curvula* is stronger than the interspecific competition between individuals of *E. curvula* and *A. pubescens*. In the case of *A. pubescens*, the effect of interspecific competition from *E. curvula* is greater than the effect of intraspecific competition between individuals of *A. pubescens*.

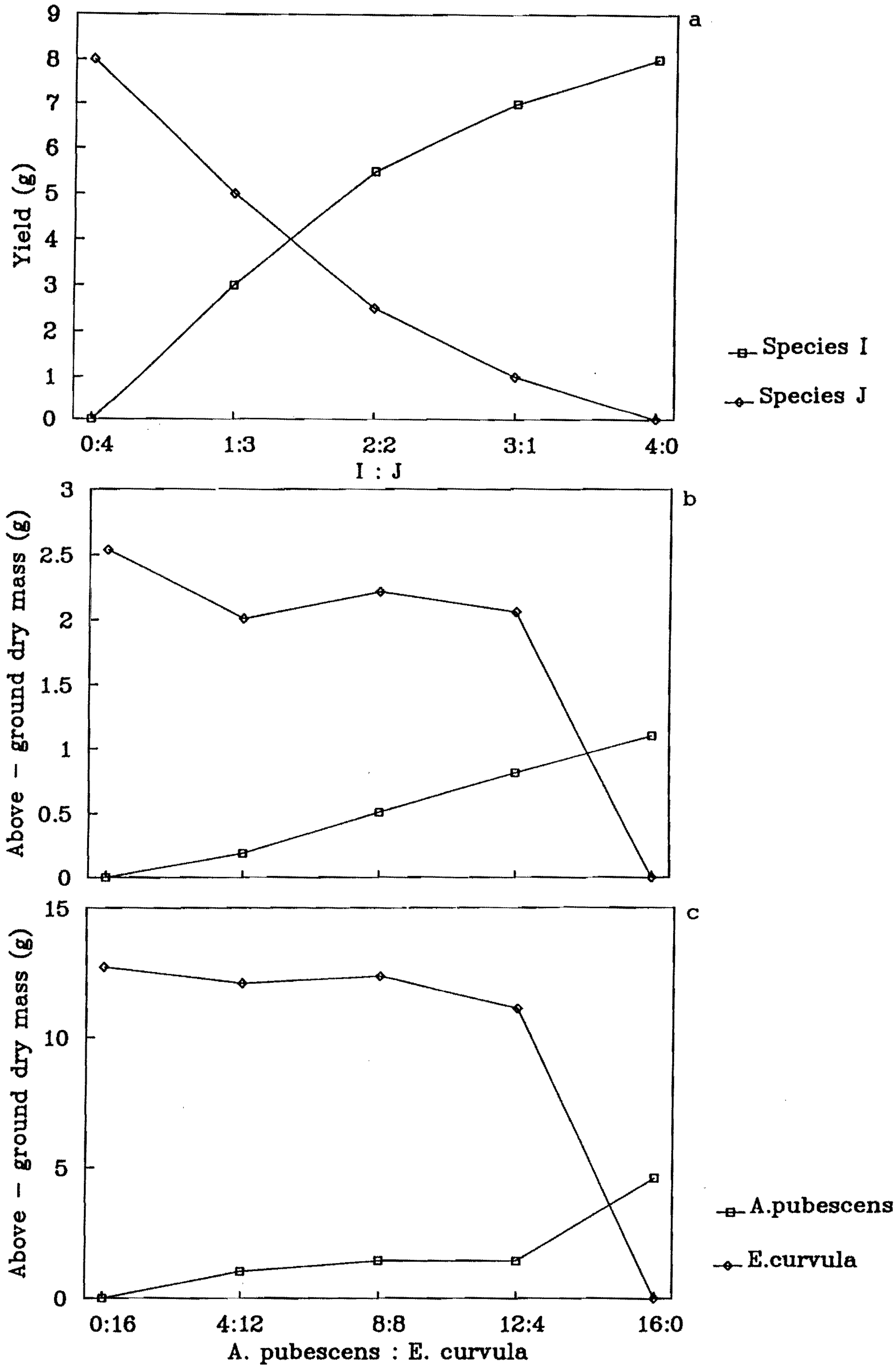


Figure 5 (a) A schematic representation of the relationship between density and yield in a replacement series (De Wit 1960) (b) the effect of competition on the above - ground yield of *Anthephora pubescens* and *Eragrostis curvula* in a replacement series at the first and (c) third monthly harvests.

The replacement series approach has been criticised because of the sensitivity of the results to the total mixture density. Taylor & Aarssen (1989), however, argue that when the component density is at least high enough that each component would be at a constant final yield, indices from replacement series experiments describing interactions in mixtures are more informative because any variation in yield can be interpreted in terms of competition from other species. Therefore if the objective is to use indices to assess relative competitive ability and niche overlap, then it would be sufficient to run the experiment at a single density so long as the component densities are high enough to achieve constant final yield. According to Taylor & Aarssen (1989) indices obtained at these densities may be used in turn to predict species abundance in the field or to interpret competition experiments conducted under the same conditions at any density. The density series used in the present study was sufficient as each component density achieved constant final yield and thus proved satisfactory.

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

In Table 1 the RYP - and RYT - values for the various replacement series are given. The RYP represents the average yield of an individual in a mixed stand in relation to the yield of an individual of the same species in a pure stand at the same density (Fowler 1982). In the case of A. pubescens RYP was < 1 at all three harvest dates. This implies that individuals of

E. curvula have a greater affect on individuals of A. pubescens (interspecific competition) than individuals of A. pubescens have on themselves. In the case of E. curvula RYP was > 1 implying that individuals of E. curvula have a greater affect on themselves (intraspecific competition) than individuals of A. pubescens have on E. curvula.

The RYT represents the sum of the proportional changes in yield which occur in the mixtures (Fowler 1982). The RYT - values at each harvest date are greater than 1 (with the exception of 4 A. pubescens : 12 E. curvula plants per pot at the first harvest), implying that the two respective species compete for different resources and that they utilize their environment more effectively in a mixture than in a pure stand (Berendse 1983). The RYP - and RYT - values of the first harvest are already indicative, revealing the strong competitive interference between the two species at an early stage and increasing with time. Total relative yield - values approximately equal to one have been recorded in many pot trials (Trenbath 1974 ; Berendse 1983). According to Trenbath (1974) RYT - values > 1 seldom occur in agricultural crops, except where a nitrogen - fixing legume is one of the crops. Fowler (1982), however, predicts that RYT - values > 1 should be relatively common in natural communities because the species develop together in the evolutionary pathway. The present results therefore support Fowler's (1982) predictions.

Table 1 Relative yield per plant (RYP) and relative yield total (RYT) of <u>Anthephora pubescens</u> (AP) and <u>Eragrostis curvula</u> (EC) for monthly harvests

Harvest	Density (pl/pot) AP:EC	RYP		RYT
		AP	EC	
1	4:12	0.43	1.06	0.90
	8:8	0.93	1.74	1.34
	12:4	0.98	3.24	1.55
2	4:12	0.30	1.34	1.08
	8:8	0.31	1.76	1.03
	12:4	*	*	*
3	4:12	0.91	1.27	1.18
	8:8	0.64	1.94	1.29
	12:4	0.48	5.20	1.66

* Insufficient replicates

Table 2 The aggressivity values of <u>Anthephora pubescens</u> (AP) and <u>Eragrostis curvula</u> (EC) in a 8:8 mixture for monthly harvests

Harvest	Aggressivity	
	AP	EC
1	-0.205	0.205
2	-0.362	0.362
3	-0.327	0.327

Aggressivity

In Table 2 the values of the aggressivity of the respective species in a 8:8 mixture are given. At all three harvest dates the aggressivity values of *A. pubescens* were negative and those of *E. curvula* were positive. This implies that *E. curvula* is a superior competitor to *A. pubescens*.

Species monoculture reaction and species mixture reaction

The species monoculture reaction is a measure of intraspecific competition. With an increase in density the species monoculture reaction increases, i.e. the higher the density the greater the effect of intraspecific competition (Table 3). The monoculture reaction values of *E. curvula* were higher than the values of *A. pubescens* at each harvest, i.e. the effect of intraspecific competition was greater in *E. curvula* than in *A. pubescens*. The same applies to the relative monoculture reaction (Table 3).

The species mixture reaction represents the decrease in yield due to interspecific competition and any modification in intraspecific competition as a result of the effect of other species in the mixture (Jolliffe *et al*. 1984). The higher the value of the relative mixture reaction the stronger the effect of

Table 3 The species monoculture reaction and species mixture reaction values of _Anthephora pubescens_ (AP) and _Eragrostis curvula_ (EC) for monthly harvests

Harvest	Density (pl/pot) (AP:EC)	Species monoculture reaction	Species mixture reaction	Relative monoculture reaction	Relative mixture reaction
1	4AP	0.580	0.109	0.819	0.851
	8AP	1.245	0.107	0.879	0.626
	12AP	2.020	0.036	0.915	0.346
	4EC	1.408	0.112	0.809	0.337
	8EC	3.240	-0.037	0.931	-0.154
	12EC	5.005	0.848	0.979	0.223
2	4AP	3.530	0.870	0.939	0.946
	8AP	3.696	0.134	0.983	0.848
	12AP	*	*	*	*
	4EC	*	*	*	*
	8EC	5.912	-0.005	0.987	-0.005
	12EC	5.938	-0.092	0.991	-0.147
3	4AP	3.404	0.935	0.919	0.781
	8AP	3.599	0.653	0.972	0.782
	12AP	3.736	0.162	0.994	0.572
	4EC	5.494	0.792	0.917	0.399
	8EC	8.503	0.002	0.978	0.001
	12EC	5.602	0.121	0.989	0.107

* Insufficient replicates

interspecific competition. By comparing the values of the relative mixture reactions of the two species in a replacement series, the effect of interspecific competition of the one species on the other species can be derived. In each case the relative mixture reaction values of E. curvula are smaller than the values of A. pubescens (Table 3). Interspecific competition therefore has a greater affect on individuals of A. pubescens than individuals of E. curvula.

Relative yield of mixtures (RYM)

The relative yield of mixtures can be compared with the monoculture yield of each respective species to determine yield performance. The RYM - values are given in Table 4. At the first and second harvest date the RYM - values in a 8:8 mixture are higher than the monoculture yield values of the respective species. This implies a niche differentiation between the two species and more effective resource utilization in a mixture than in a pure stand.

Relative Crowding Coefficient (K)

The relative crowding coefficient is given in Table 5. If $K_{ij} \times K_{ji} = 1.0$, then species i and j are mutually exclusive; $K_{ij} \times K_{ji} > 1.0$ implies non - competitive interference although they may still be competing for the same resource or resources;

Table 4 The monoculture yield of <u>Anthephora pubescens</u> (AP) and <u>Eragrostis curvula</u> (EC) and their relative yield in a 8:8 mixture (RYM) for monthly harvests

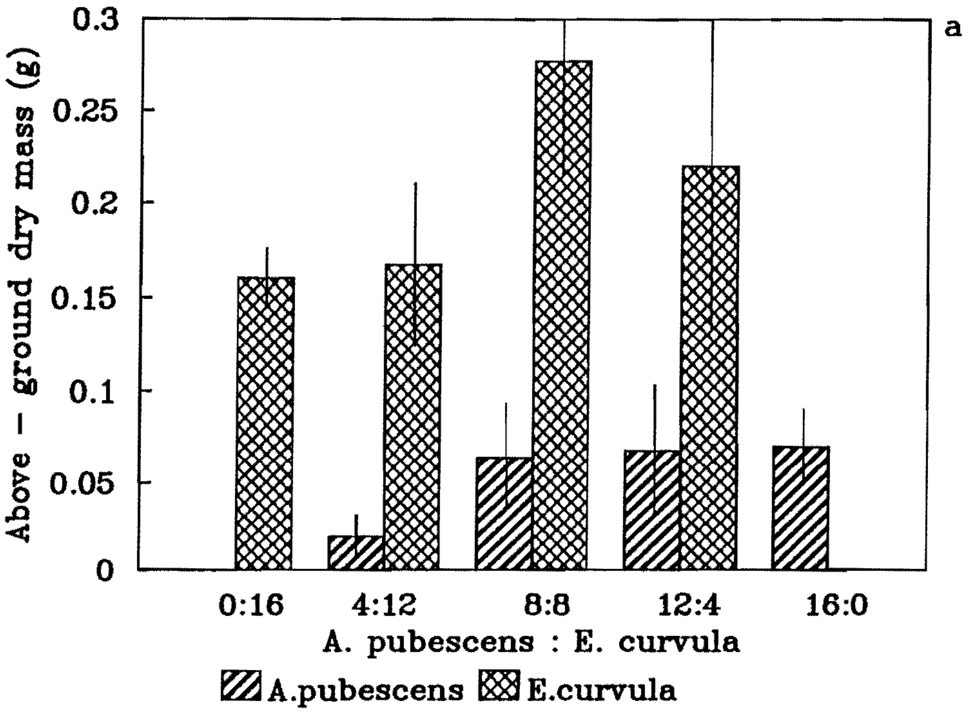
Harvest	Monoculture Yield		RYM
	AP	EC	
1	0.171	0.240	1.655
2	0.512	0.935	1.408
3	0.835	1.546	0.724

Table 5 The relative crowding coefficient (K) of <u>Anthephora pubescens</u> (AP) and <u>Eragrostis curvula</u> (EC) in a 8:8 mixture for monthly harvests

Harvest	K		AP x EC
	AP	EC	
1	12.800	-2.347	-30.042
2	0.451	-2.321	-1.047
3	0.461	-2.061	-0.950

Table 6 The Competitive Balance Index (C_b) of <u>Anthephora pubescens</u> (AP) and <u>Eragrostis curvula</u> (EC) in a 8:8 mixture for monthly harvests

Harvest	C_b	
	AP	EC
1	-0.631	0.631
2	-1.732	1.732
3	-1.118	1.118



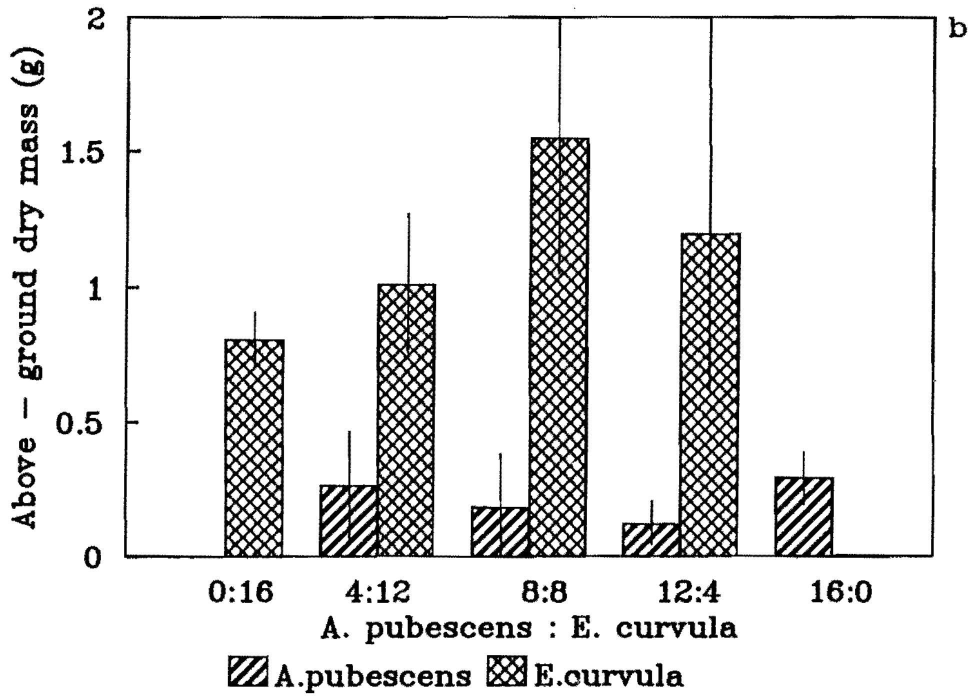


Figure 6 The effect of competition on the above - ground dry mass per plant of Anthephora pubescens and Eragrostis curvula in a replacement series at the (a) first and (b) third monthly harvests.

$K_{ij} \times K_{ji} < 1.0$ implies mutual antagonism. The relative crowding coefficient in the 8:8 mixture is less than one implying that the two species investigated are mutually antagonistic.

Competitive Balance Index (Cb)

The relative competitive ability of the respective species can be represented by the Competitive Balance Index. The Competitive Balance Index of the two species, at the various harvest dates, is given in Table 6. At each harvest date the C_b of *A. pubescens* is negative and that of *E. curvula* is positive. This implies that *E. curvula* is a strong competitor while *A. pubescens* is a poor competitor.

The yield of a population of seedlings is determined by the number of plants present, but as the plants get bigger their growth is determined by the ability of the environment to provide essential resources to the plants. The plateau - yield is therefore directly dependent on the environment and not density. The amount of resources available depends, however, on the number of individuals utilizing the environment. The greater the number of individuals in a restricted environment, the less the amount of resources available to each individual. Density is therefore an indirect factor which affects the plateau - yield of a population.

The effect of interspecific competition on the above - ground dry mass of *A. pubescens* and *E. curvula* at the first and third harvest is illustrated in Figures 6a & b. At the first harvest

A. pubescens exhibited a positive relationship between above - ground dry mass and an increase in the number of A. pubescens individuals in the replacement series. At the third harvest, however, a negative relationship was exhibited (with the exception of 16 plants per pot). Eragrostis curvula exhibited a parabolic relationship at the first and third harvest. The differences in the above - ground dry mass between the various ratio's were, however, not significant in either of the species ($p < 0.05$).

CONCLUSIONS

It is evident from the results that A. pubescens is a poor competitor. Interspecific competition has a greater negative affect on A. pubescens than intraspecific competition. In a pure stand the dry mass per plant of A. pubescens exhibited a negative relationship with increasing density. In a mixture A. pubescens managed a positive relationship at the first harvest, but at the third harvest the relationship between density and dry mass per plant was negative, with the exception of 16 plants per pot. It can therefore be concluded that the yield of A. pubescens suffers loss in a restricted environment and in the presence of other species. Patterson (1990) recorded the same negative relationship between density and yield in Anoda cristata and Abutilon theophrasti. In contrast to A. pubescens, E. curvula is evidently a strong competitor. Intraspecific competition has a greater negative affect on E. curvula than interspecific competition. In a pure stand the yield per plant of *E. curvula* was affected negatively by increasing density. In a mixture, however, *E. curvula* maintained a parabolic trend; the maximum yield per plant being reached at a ratio of 8 *E. curvula* : 8 *A. pubescens* plants per pot.

Robinson & Whalley (1991) examined competition between *E. curvula* and three temperate pasture grasses; *Festuca arundinacea*, *Dactylis glomerata* and *Phalaris aquatica*. *Eragrostis curvula* proved to be more competitive than all three temperate grasses. The competitiveness of the temperate grasses declined with age. This was due to the greater competitive ability of *E. curvula* and a decline in soil fertility which favoured *E. curvula*.

Intraspecific competition became effective from early stages in both *A. pubescens* and *E. curvula* and regulated the amount of dry matter produced. Chandrasena & Peiris (1989) recorded similar results in *Panicum repens* L. Increasing density had a greater affect on the yield per plant of *E. curvula*. The yield per plant of *E. curvula* was, however, favoured in a mixture. The increased yield in the mixtures was due to the contribution by *E. curvula* and not *A. pubescens*. The yield per plant of *E. curvula* in a mixture differed from its yield per plant in a pure stand. The yield per plant of *A. pubescens* in a mixture did not, however, differ significantly from its yield in a pure stand ($p < 0.05$). The yield of *A. pubescens* remained inferior to that of

E. curvula, irrespective of the type of competitive interference (intra - or interspecific competition). It can therefore be concluded that E. curvula is a superior competitor being able to utilize a limited pool of resources effectively so as to ensure survival. Anthephora pubescens, on the other hand, is unable to utilize a restricted environment resulting in inferior competitiveness and eventual mortality.

It is important to keep in mind that this trial was conducted in small pots and that these results cannot be extrapolated unconditionally to a field situation. The trends exhibited are, however, of agricultural importance. The environment plays an important role in the interaction between species by determining the intensity of competition as well as the direction of competitive dominance, and the effect of competition should therefore be examined under field conditions.

It must be mentioned that E. curvula emerged 3 to 5 days ahead of A. pubescens. This headstart may have given E. curvula the competitive edge resulting in competitive superiority. There have been few studies which have addressed the importance of decreased emergence time. It has been suggested that small differences in emergence time can contribute substantially to determining final biomass. For example, Ross & Harper (1972) found that a single day's headstart resulted in an average 222 % increase in the final biomass of Dactylis glomerata. Black & Wilkinson (1963) found that in subterranean clover a 5 - day headstart lead to a 400 % increase. Miller (1987) studied the effect of emergence date on the success of seven species in the field. He found that sensitivity to emergence date was highly variable between species, and within species this sensitivity differed between years and throughout the season. In three out of three species, the probability of emergence decreased significantly with an increase in seed density. The mechanism underlying density - dependent germination is unknown. It has been speculated that chemical modification of the local soil environment, such as the release of CO_2, is responsible for the responses that have been observed (Inouye 1980) and local resource depletion may be another possibility. The observation that seed performance is influenced by the density of heterospecific and conspecific competitors suggests intriguing consequences for species interactions (Bergelson & Perry 1989). Certain species may, for example, suffer reduced emergence at high total densities, whereas their competitors do not; in this case different species may be favoured by situations representing distinct total densities. The relative competitiveness of different species may therefore depend on the total plant density. Such a scenario could potentially produce complex population dynamics.

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REFERENCES

Berendse F. 1983. Interspecific competition and niche differentiation between Plantago lanceolata and Anthoxanthum odoratum in a natural hayfield. J. Ecol. 71: 379-390.

Bergelson J. & Perry R. 1989. Interspecific competition between seeds: Relative planting date and density affect seedling emergence. Ecol. 70: 1639-1644.

Black J.N. & Wilkinson G.N. 1963. The role of the time of emergence in determining the growth of individual plants in swards of subterranean clover (Trifolium subterraneum L.). Aust. J. Agric. Res. 14: 628-638.

Chandrasena J.P.N.R. & Peiris H.C.P. 1989. Studies on the biology of Panicum repens L. II. Intraspecific competition and resource - allocation. Trop. Pest Manage. 35: 316-320.

De Wit C.T. 1960. On competition. Versl. Landbouwkd. Onderz. 66: 1-82.

De Wit C.T. & Van den Bergh J.P. 1965. Competition between herbage plants. Neth. J. Agric. Sci. 13: 212-221.

Donald C.M. 1958. The interaction of competition for light and nutrients. Aust. J. Agric. Res. 9: 421-435.

Donaldson C.H. & Kelk D.M. 1970. An investigation of the veld problems of the Molopo area: I Early findings. Proc. Grassld. Soc. sth. Afr. 5: 50-57.

Firbank L.G. & Watkinson A.R. 1985. On the analysis of competition. J. appl. Ecol. 22: 503-517.

Fowler N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. J. Ecol. 70: 77-92.

Fowler N.L. 1984. The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in Linum. J. Ecol. 72: 307-318.

Hall R.L. 1974. Analysis of the nature of interference between plants of different species. I. Concepts and extension of the De Wit analysis to examine effects. Aust. J. Agric. Res. 25: 739-747.

Hall R.L. 1978. The analysis and significance of competitive interference between species. In: Wilson J.R. (ed.). Plant relations in pastures. Hedges and Bell Pty Ltd, Australia, pp. 163-174.

Harper J.L. 1961. Approaches to the study of plant competition. Symp. Soc. Exp. Biol. 15: 1-39.

Harper J.L. 1964. The nature and consequences of interference among plants. Proc. 11th international conference on genetics, The Hague, 1963, pp. 465-481.

Harper J.L. 1977. Population biology of plants. Academic Press, London.

Inouye R.S. 1980. Density - dependent germination response by seeds of desert annuals. Oecologia (Berl.) 46: 235-238.

Jolliffe P.A., Minjas A.N. & Runeckles V.C. 1984. A reinterpretation of yield relations in replacement series experiments. J. appl. Ecol. 21: 227-243.

Martin M.P.L.D. & Snaydon R.W. 1982. Root and shoot interactions between barley and field beans when intercropped. J. appl. Ecol. 19: 263-272.

McGilchrist C.A. & Trenbath B.R. 1971. A revised analysis of plant competition experiments. Biometrics 27: 659-671.

Mead R. & Riley J. 1981. A review of statistical ideas relevant to intercropping research. J. Roy. Sta. A 144: 462-509.

Miller T.E. 1987. Effects of emergence time on survival and growth in an early old - field plant community. Oecologia (Berl.) 72: 272-278.

Patterson D.T. 1990. Effects of density and species proportion on competition between Spurred Anoda (Anoda cristata) and Velvetleaf (Abutilon theophrasti). Weed Sci. 38: 351-357.

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Robinson G.G. & Whalley R.D.B. 1991. Competition between three agronomic types of the Eragrostis curvula (Schrad.) Nees complex and three temperate pasture grasses of the Northern Tablelands of New South Wales. Aust. J. Agric. Res. 42: 309-316.

Ross M. & Harper J.L. 1972. Occupation of biological space during seedling establishment. J. Ecol. 60: 77-88.

Shinozaki K. & Kira T. 1956. Intraspecific competition among higher plants. 7. Logistic theory of the C - D effect. J. Inst. Polytech. Osaka Cy Univ. 7: 35-72.

Smith 1983. Demography of Floerkia proserpinacoides, a forest floor annual. 1. Density - dependent growth and mortality. J. Ecol. 71: 391-404.

Taylor D.R. & Aarssen L.W. 1989. On the density dependence of replacement series competition experiments. J. Ecol. 77: 975-988.

Trenbath B.R. 1974. Biomass productivity of mixtures. Adv. in Agron. 26: 177-210.

Weiner J. & Thomas S.C. 1986. Size variability and competition in plant monocultures. Oikos 47: 211-222.

Wilson J.B. 1988. Shoot competition and root competition. J. appl. Ecol. 25: 279-296.

CHAPTER 4

THE EFFECT OF INTRA - AND INTERSPECIFIC COMPETITION ON THE PATTERN OF BIOMASS ALLOCATION OF ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

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The effects of intra - and interspecific competition on the biomass allocation of Anthephora pubescens Nees (wool grass) and Eragrostis curvula (Schrad.) Nees (weeping love grass) were studied under greenhouse conditions. Intraspecific nor interspecific competition had a significant affect on the pattern of biomass allocation to the vegetative structures of either species. Eragrostis curvula exhibited an increase in root allocation over the growing season, following an initial decrease. The allocation of biomass to reproductive structures was absent in both species. This effect was attributed to the limited space and soil volume, which restricted the nutrient and water status of the soil. This study provides an insight into the highly adaptive nature of these respective species in response to competitive stress.

Die invloed van intra - en interspesifieke kompetisie op die biomassatoewysingspatroon van Anthephora pubescens Nees (borseltjiegras) en Eragrostis curvula (Schrad.) Nees (oulandsgras) is onder kweekhuistoestande ondersoek. Nóg intraspesifieke nóg interspesifieke kompetisie het 'n betekenisvolle invloed op die biomassatoewysingspatroon aan vegetatiewe strukture, van beide spesies, gehad. Eragrostis curvula het 'n toename in worteltoewysing oor die groeiseisoen getoon, na 'n aanvanklike afname. Die toewysing van biomassa aan reproduktiewe organe was afwesig in beide spesies. Dié invloed kan egter toegeskryf word aan die beperkte spasie en volume grond waarin die plante gegroei het, wat die voedingstof en waterstatus van die grond beperk het. Dié studie werp lig op die hoogs aanpasbare geaardheid van die ondersoekte spesies, in reaksie op kompeterende stres.

Additional index words: Allocation strategy, density, weeping love grass, wool grass

INTRODUCTION

Schoener (1974) states : "Biologists have long been intrigued by differences in morphology and habit among closely related species, for to comprehend the manner and extent of such differences is to comprehend much of the natural control of organic diversity." According to Schoener (1974), ecologists have especially concentrated on differences in the way species in the same community utilize resources. The major purpose of resource - partitioning studies is to analyse the limits interspecific competition place on the number of species that can coexist stably (Schoener 1974).

Growth is dependent upon the availability of supplies to the growing organs, and correlations between the growth of different structures seem to be at least in part a function of competition for such essentials (Harper & Ogden 1970). A change in the environment affecting the availability of some essential resource (e.g. light or water) may therefore change the growth rate of different organs to different extents so that the overall pattern of dry matter distribution becomes altered (Harper & Ogden 1970). In a crowded community where resources are more limiting, individual success is much more dependent on the ability to capture a share of the resources. According to Bazzaz & Reekie (1985) an individual which sacrifices competitive ability for fecundity may not survive to reproduce. Competition between crop plants is usually thought of as an enforced sharing of the supplies of water, nutrients and light. With a given level of supply of these factors, increasing the plant density reduces the weight per plant (Bleasdale 1966). The effect of plant density on the distribution of accumulated assimilates is therefore of agronomic importance.

A plant species has a pattern of resource allocation (biomass allocation) which improves it's chance of survival. Biomass allocation refers to the proportion of total biomass stored in each organ (Harper & Ogden 1970). Such patterns are retained and refined through the process of natural selection. According to Barbour et al. (1980) the biomass allocation of a species determines to an extent it's niche in a community. Reproductive allocation refers to the allocation of biomass to all reproductive structures (Gadgil & Solbrig 1972). Reproductive allocation is to an extent a fixed genetic characteristic, but it can be modified by the plant's environment.

Van Dobben (1966, in Bleasdale 1966) has suggested that the main contribution of the plant breeder to increased cereal yields has been through an increase in the proportion represented by grain and not by affecting total dry matter production. According to Bleasdale (1967), the way in which plant density affects the partitioning of assimilates to the plant parts clearly affects the ability of the horticulturist to use plant density as a means of achieving the control of plant size required for todays markets.

It was attempted in this study to determine the effect of intra - and interspecific competition on the pattern of biomass allocation of two key grass species, Anthephora pubescens Nees and Eragrostis curvula (Schrad.) Nees. Anthephora pubescens and E. curvula are important components of South African pastures due to their palatability and utilisation as hay or grazing crops. An understanding of how the allocation pattern of pasture grasses may be altered under stress could aid pasture management in the manipulation of the vegetation to attain highly productive and stable pastures.

PROCEDURE

The experiment was carried out in a greenhouse at the Grassland Research Centre, Roodeplaat. Anthephora pubescens Nees of the VH20 ecotype and Eragrostis curvula (Schrad.) Nees cultivar Ermelo were sown in 150 mm deep 170 x 170 mm plastic pots with perforated bases in November 1990. The pots were filled with a 10 mm layer of gravel and topped with a sandy - loam soil, which had 82.8 % sand, 8.7 % loam, 8.5 % clay and a pH of 5.3. The A. pubescens spikelets were obtained from the Biesiesvlakte Research Station, Vryburg (24^{o} 28" E; 25^{o} 57" S). The spikelets were harvested in April 1989 from plants which had been planted in March 1976. Certified E. curvula seeds were obtained from a local seed dealer. The two species were sown in both pure and mixed stands. In the pure stands the planting densities were 1, 4, 8, 12 and 16 plants per pot respectively. In the mixed stands, however, the total planting density was kept constant at 16 plants per pot, but the ratio's of A. pubescens to E. curvula varied at 4:12, 8:8 and 12:4 plants per pot, i.e. the pattern followed was that of a replacement series (De Wit 1960). A surplus spikelets and seeds were sown and thinned to the desired density 4 weeks after emergence. The pots received 500 ml tap water every second day and 100 ml nutrient solution, commercially produced UAN 32, at monthly intervals.

The pots were laid out on trolleys arranged in five replicate blocks. Each block had six replicates per treatment. The trolleys were rotated fortnightly. At the end of each consecutive month, commencing January 1991 and terminating in May 1991, a replicate block was harvested to determine the biomass allocation of each treatment and species. Each plant of each treatment, and species, was harvested separately to determine dry matter production. The plants were clipped at soil surface and divided into the separate plant parts, i.e. roots, tillers, leaves. The roots were washed over a fine sieve using a fine spray nozzle. In the case of the mixed stands, however, the roots of the two species were intertwined and were therefore not harvested. The plant parts of each plant were placed in separate brown paper bags and dried at 90°C for 48 h and weighed. The dry mass values of the entire plant as well as those of the plant parts were determined on a per plant and per pot basis for each species.

ANALYSES

The data were analysed with the aid of biomass allocation formulae (Van Rooyen 1988). The allocation of biomass to the separate plant parts was determined as a ratio of the dry mass of the particular plant part to the dry mass of the whole plant multiplied by 100 to present the allocation as a percentage.

The relationship between the total mass per plant and the mass of a plant part (roots, tillers, leaves) at different densities was determined as follows (Bleasdale 1966) :

$$\log W_{\text{whole plant}} = \log k + a \log W_{\text{plant part}}$$

The derivation of this allometric relationship can be found in Bleasdale (1966). If $a = 1.0$, the plant part is a constant portion of the whole plant; $a > 1.0$ implies that the plant part increases with increasing density; $a < 1.0$ implies that the plant part decreases with increasing density.

At harvest, only those pots which still had the full number of plants (i.e. initial density) were used. If one plant in a pot died the pot was discarded. A minimum of four replicates were used. Due to an unequal number of replicates the regression analysis approach was used to analyse the data. The "student's" t - test was used to determine statistical significance at a level of $p < 0.05$ (Rayner 1969).

RESULTS AND DISCUSSION

Anthephora pubescens suffered large - scale mortality under competitive stress. Individuals of A. pubescens, planted at higher densities, could as a result only be harvested the first three months of the experiment's duration. Eragrostis curvula, however, did not suffer loss and could be harvested throughout the experiment's duration. These findings were already indicative of the competitive superiority of E. curvula and the competitive inferiority of A. pubescens.

INTRASPECIFIC COMPETITION

There were no significant differences in the biomass allocation patterns, in either species, subjected to varying amounts of intraspecific competitive stress ($p < 0.05$). As illustrated in Figures 1a, b & c and Figures 2a, b, c, d & e, the percentage dry mass partitioning calculated on the basis of total dry mass, in A. pubescens and E. curvula respectively, remained unchanged with an increase in density, irrespective of the harvest date. The greatest percentage dry mass was allocated to the roots (50 - 80 %) in both A. pubescens and E. curvula. Approximately an equal percentage dry mass was allocated to tillers and leaves in both species (Table 1). In E. curvula, however, the percentage dry mass allocated to the roots decreased with increasing density at

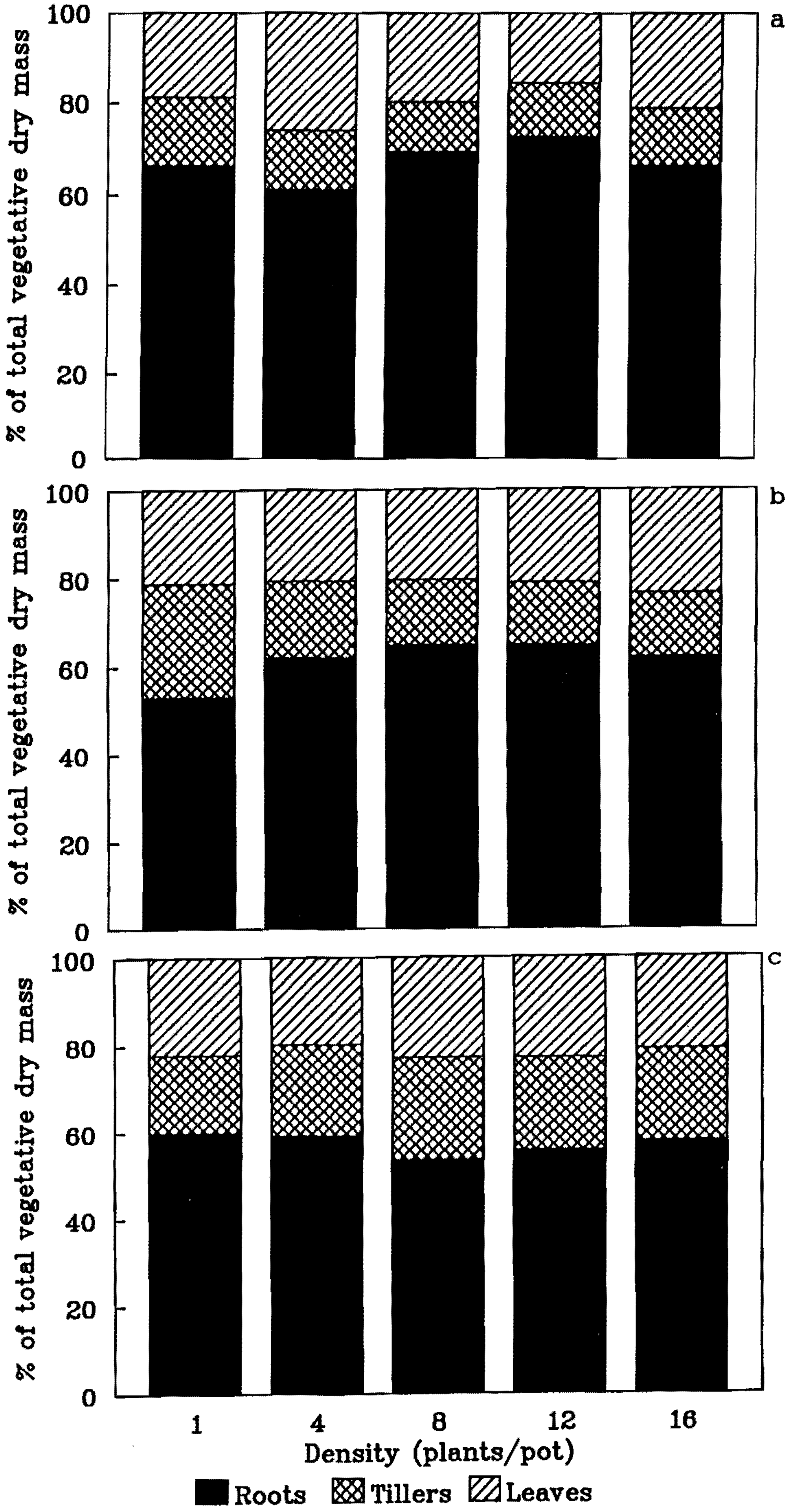

Figure 1 The effect of intraspecific competition on the percentage biomass allocation to vegetative structures of <u>Anthephora pubescens</u> at the (a) first (b) second and (c) third monthly harvest.

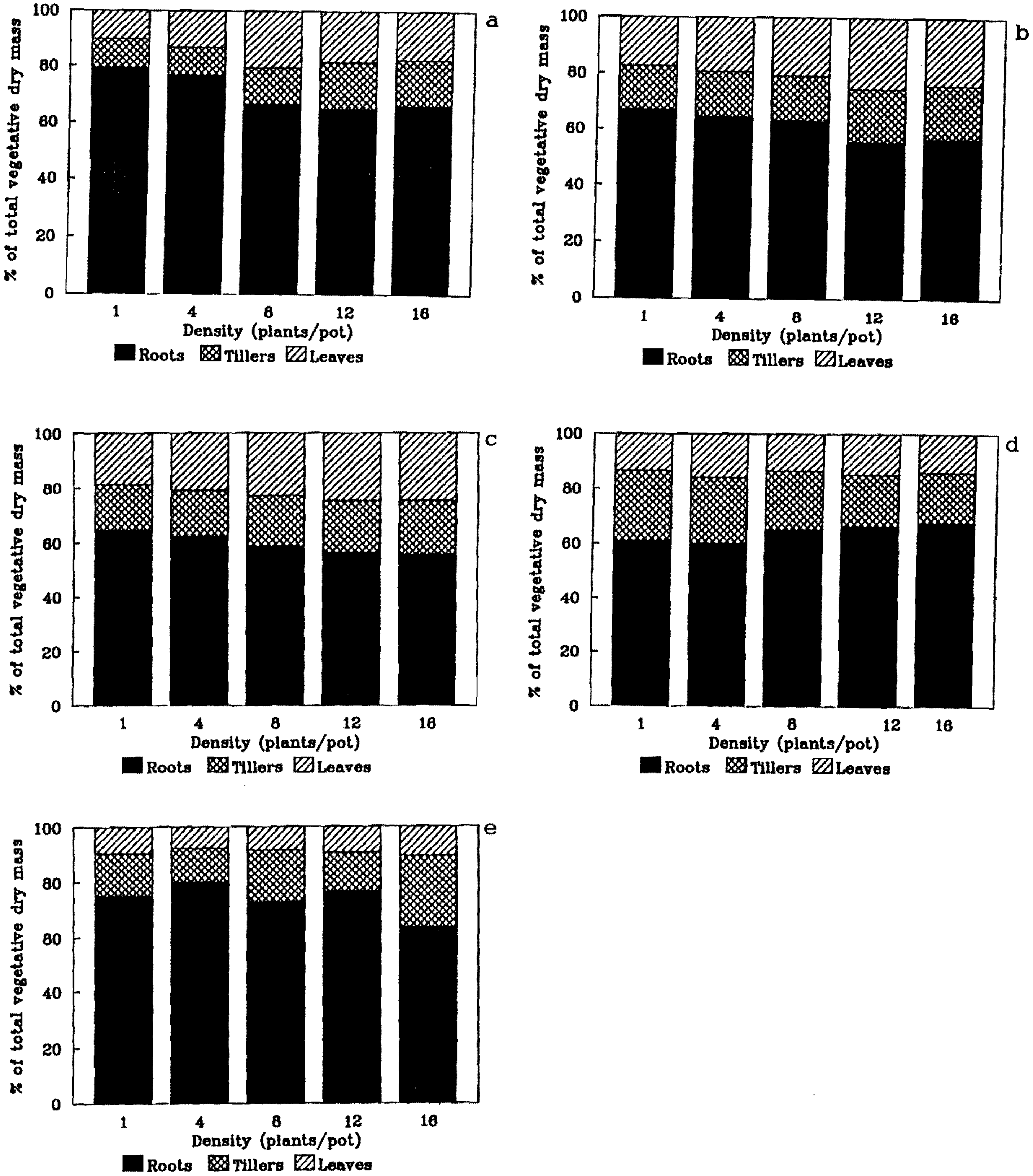

Figure 2 The effect of intraspecific competition on the percentage biomass allocation to vegetative structures of *Eragrostis curvula* at the (a) first (b) second (c) third (d) fourth and (e) fifth monthly harvest.

the first three harvests. This decrease in allocation to the roots was compensated for by a concomitant increase in allocation to tillers and leaves as illustrated by the a - values (Table 1). This shift of dry matter partitioning with changing density was, however, not significant ($p < 0.05$). It is therefore evident that intraspecific competition had a greater affect on the partitioning of dry matter in E. curvula than in A. pubescens. A decrease in root allocation, in E. curvula, with increasing density may be attributed to the limited space offered by the small pots. A finite pool of water, nutrients and space may have resulted in increased competition in below - ground organs causing a shift to above - ground allocation. Harper (1977) has cited cases where the pattern of biomass allocation of the plants have been altered under density stress.

INTERSPECIFIC COMPETITION

The pattern of biomass allocation remained unaltered in both species, irrespective of the species combination (Figures 3a, b, c & d). The partitioning of percentage dry mass, calculated on the basis of above - ground dry mass, in a pure stand did not differ significantly from the partitioning patterns in a mixture in either species. Similar results have been recorded by Chandrasena & Peiris (1989) in Panicum repens L.

Table 1 The log regression values of _Anthephora pubescens_ and _Eragrostis curvula_ for each monthly harvest

Harvest	Roots		Tillers		Leaves	
	a*	r^2	a*	r^2	a*	r^2
Anthephora pubescens						
1	0.923	0.985	1.230	0.941	0.943	0.808
2	1.035	0.999	0.835	0.998	1.090	0.999
3	0.937	0.997	1.110	0.998	1.051	0.999
Eragrostis curvula						
1	0.863	0.998	1.609	0.973	1.519	0.903
2	0.920	0.999	1.100	0.996	1.186	0.998
3	0.926	0.999	1.088	0.999	1.163	0.999
4	1.022	0.999	0.922	0.997	1.024	0.995
5	0.928	0.994	1.156	0.922	1.060	0.989

* $\log W_{\text{whole plant}} = \log k + a \log W_{\text{plant part}}$ (Bleasdale 1966)

TIME

Anthephora pubescens

The pattern of biomass allocation of A. pubescens over the growing season is illustrated in Figures 4a - e at all densities. At the lowest density the allocation of biomass to the roots remained approximately constant, while allocation to the tillers and leaves increased and decreased respectively over the growing season. At higher densities, however, the allocation of biomass to the roots decreased resulting in an expectant smaller root system, while that of the tillers increased; the leaves remained approximately constant. These alterations in allocation pattern were, however, not significant ($p < 0.05$).

Eragrostis curvula

The pattern of biomass allocation of E. curvula over the growing season is illustrated in Figures 5a - e at all densities. All the densities exhibited an initial decrease in root allocation at the first three harvests after which an increase in root allocation was exhibited, with the exception of 16 plants per pot at the fifth harvest which may be accrued to experimental error. It appears that E. curvula exhibits a shift toward above - ground allocation during seedling establishment. Once the plants have established, a shift toward below - ground allocation is

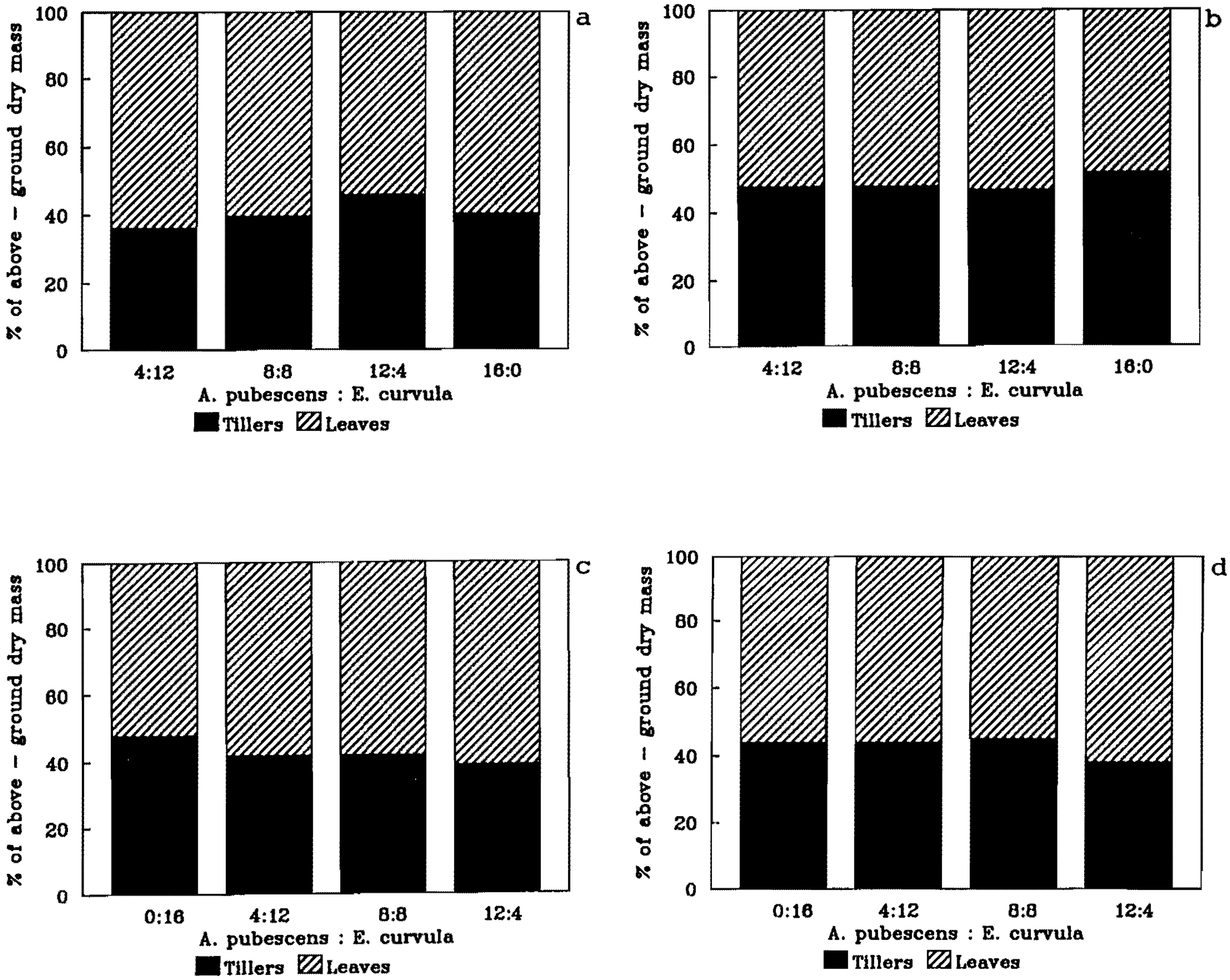

Figure 3 The effect of interspecific competition on the percentage biomass allocation to vegetative structures of (a) *Anthephora pubescens* at the first and (b) third monthly harvest (c) *Eragrostis curvula* at the first and (d) third monthly harvest in a replacement series.

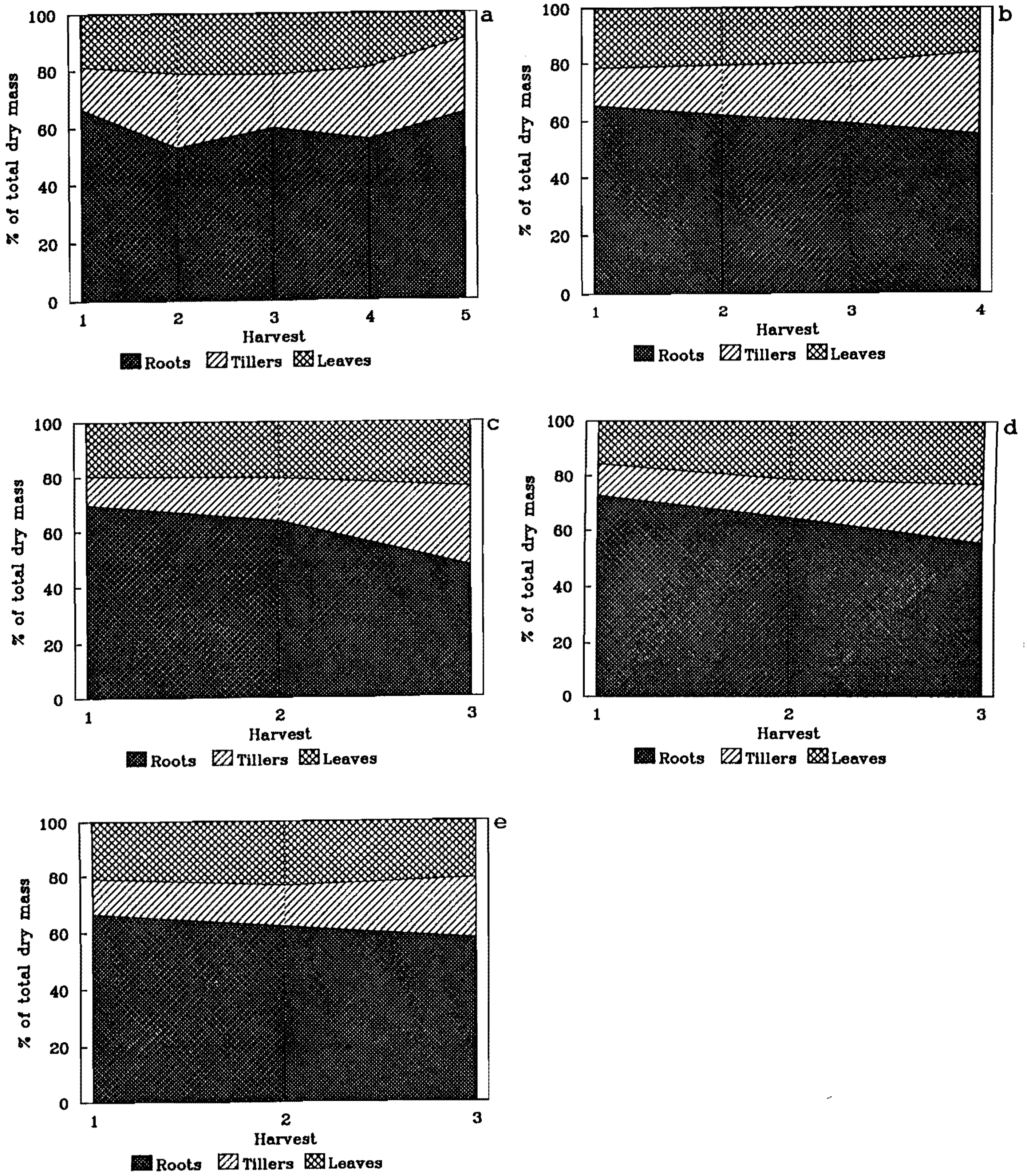

Figure 4 The biomass allocation of Anthephora pubescens to vegetative structures over the growing season at a (a) one - (b) four - (c) eight - (d) twelve - and (e) sixteen - plants per pot density.

exhibited, increasing the root system. This occurrence suggests a possible "investment strategy" - an increase in reserves to ensure occupation and survival as the environment becomes more unfavourable.

Unfortunately the allocation pattern of A. pubescens could not be monitored in the fourth and fifth month due to a high mortality rate. If one considers the sharp decrease in root allocation in A. pubescens from the first to the third month, one would expect the pattern to continue in the fourth and fifth month. According to this supposition it may therefore be possible that the two species exhibit different strategies over time, which may have direct bearing on the management strategies exercised in growing these two species as crops. Possible differences in root allocation strategies which may have been exhibited by A. pubescens and E. curvula over the growing season therefore warrants further investigation. These possible differences in root allocation strategies may accrue for the superior competitive ability of E. curvula and the inferior competitive ability of A. pubescens.

The lapse of time intensified competition in both species as illustrated in a previous study (Mynhardt et al. 1992). Time did not, however, have a significant affect on the pattern of biomass allocation in either species ($p < 0.05$). The biomass allocation pattern of both species in a pure stand did not vary from the allocation pattern in a mixture, irrespective of the time lapse.

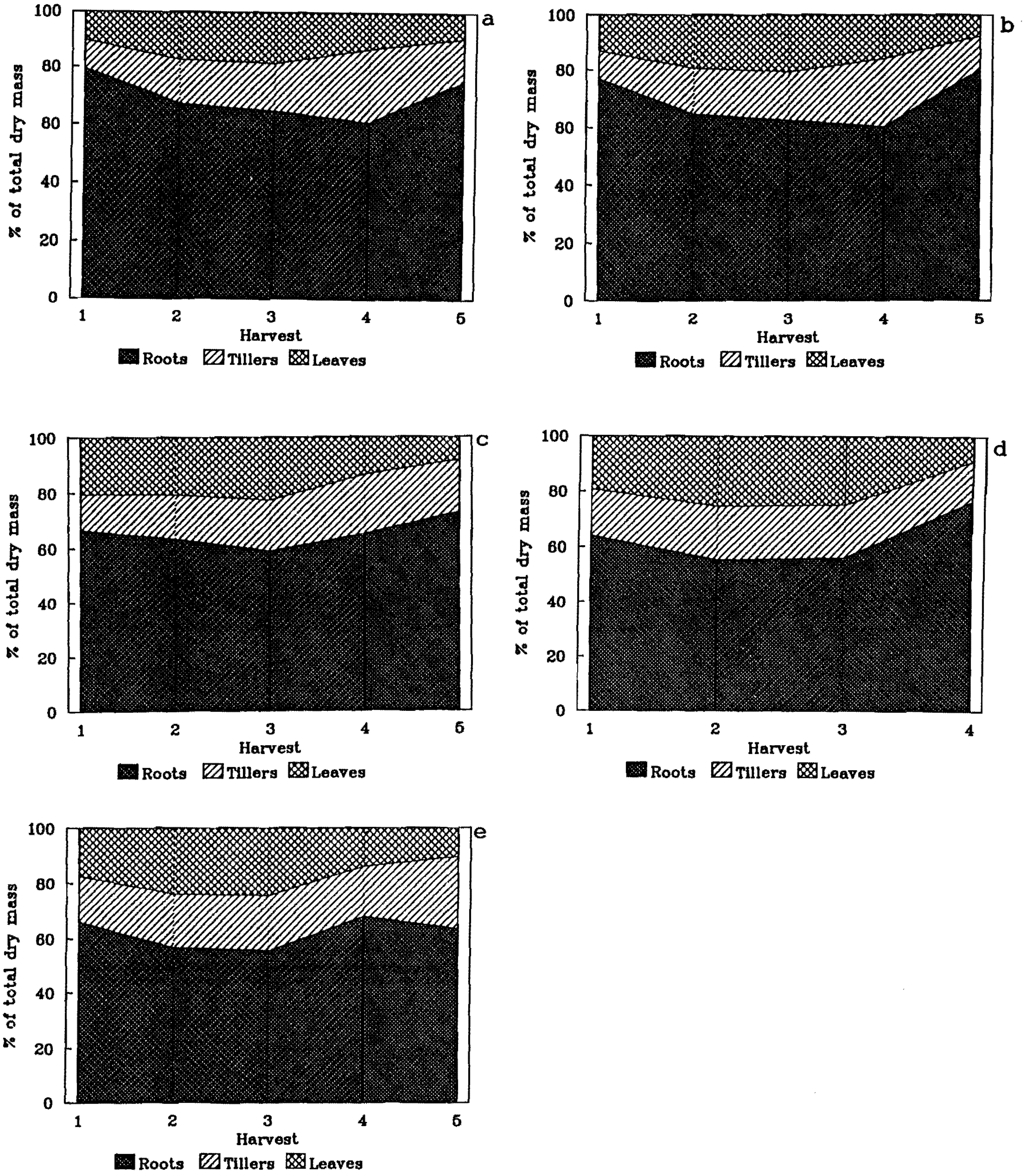

Figure 5 The biomass allocation of *Eragrostis curvula* to vegetative structures over the growing season at a (a) one - (b) four - (c) eight - (d) twelve - and (e) sixteen - plants per pot density.

It is evident in both species that initially an increase in density results in a disproportionate partitioning of biomass to the various plant parts (Table 1). This disproportionate partitioning of biomass was, however, not significant ($p < 0.05$).

Reproductive allocation was absent in both species. An increased shift of dry mass allocation to vegetative reproduction under both intra - and interspecific competition has been reported (Nyahoza 1973; Williams et al. 1977; Fowler 1984). Palmblad (1968) and Harper & Gajic (1961) found evidence that competition modifies growth and reproduction in plants. On the individual level, competition modifies the partitioning of dry mass to vegetative and reproductive structures (Harper 1977). On the population level, competitive interactions result in mortality or in plasticity (Harper 1977). According to the literature the effect of density on reproductive allocation varies from species to species. Some species exhibit a decrease in reproductive allocation with increasing density, while other species remain unchanged (Ogden 1974; Pitelka et al. 1980). It would be expected that annuals would allocate a greater proportion of their resources to seed production, improving colonizing ability, while perennials would allocate a greater proportion of their resources toward vegetative structures enabling persistence on a site. Early reproductive activity would reduce the life span of the individual by lowering the level of stored energy that could be used to maintain tissues as stress increases (Clark & Burk 1980).

The inhibition of reproductive allocation in A. pubescens and E. curvula may be attributed to the size of the pots used in the experiment. A difference in the size of A. pubescens plants planted in the small pots and those planted in larger pots, in a similar experiment, was evident; the plants planted in the larger pots were significantly bigger that those planted in the smaller pots (Figure 6). The limited soil volume of the small pots would have resulted in essential nutrients being lost through leaching and may have failed to provide sufficient moisture resulting in a drought situation. Donaldson et al. (1972) recorded that in A. pubescens seed production depended on the soil moisture supply; insufficient moisture supply resulted in depressed seed production. Depressed seed production under drought conditions, in A. pubescens and E. curvula, has been reported by Donaldson & Kelk (1970). According to Nursey & Kruger (1973) failure to defoliate or burn A. pubescens, in a field situation, could result in depressed seed production. Kelk (1972) as well as Donaldson (1991; Grassland Research Centre, P/Bag X 05, Lynn East, 0039, Republic of South Africa) cited that a shortage of nitrogen and phosphorus has a negative affect on seed yield.

Growth is dependent on the availability of resources. A change in the availability of resources may have retarded the growth rate of the respective species, preventing the production of inflorescences before the end of the growing season.

Figure 6 The effect of pot size on the size of Anthephora pubescens plants two months after thinning.

Hillman (1962, in Primack 1979) reported that plants must achieve a certain size or nutritional status, a "ripeness - to - flowering", before they are capable of responding to environmental factors which induce the formation of inflorescences. It is therefore evident that both species fix the available energy in vegetative structures to allow persistence on a site.

CONCLUSIONS

The allocation of biomass to the vegetative structures of both species investigated remained relatively unchanged under intra - and interspecific competitive stress throughout the duration of the experiment, with the exception of root allocation. The absence of reproductive allocation in both species suggests plasticity in reaction to stress caused by environmental constraints, i.e. pot size. The allocation theory states that organisms have a restricted amount of time and energy to complete their life cycle. Time *per se* is not allocated, but is important in the gaining of photosynthetic energy and the use of energy for maintenance. As a part of the total energy is allocated to each activity in the life cycle, it may be supposed that reproduction, growth and survival set conflicting demands on the limited pool of resources which is available, so that an increase in one process causes a decrease in another. If one considers the supposed different root allocation patterns exhibited by the two species as being possible strategies, then it would be evident that the increased root system of _E_. _curvula_ later in the growing season would have resulted in more effective nutrient and water uptake - and increased reserves - under conditions of stress, accruing for the superior competitive ability of _E_. _curvula_ in contrast to the smaller root system of _A_. _pubescens_ and resultant inferior competitive ability. This supposition, however, needs to be investigated.

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REFERENCES

Barbour M.G., Burk J.H. & Pitts W.D. 1980. Terrestrial plant ecology. 2nd edn. Benjamin / Cummings Publishing Inc., California, pp. 53-94.

Bazzaz F.A. & Reekie E.G. 1985. The meaning and measurement of reproductive effort in plants. In: White J. (ed.). _Studies in plant demography: a Festschrift for John L. Harper_. Academic Press, London, pp. 373-387.

Bleasdale J.K.A. 1966. Plant growth and crop yield. _Ann. appl. Biol_. 57: 173-182.

Bleasdale J.K.A. 1967. The relationship between the weight of a plant part and the total weight as affected by plant density. J. Hort. Sci. 42: 51-58.

Chandrasena J.P.N.R. & Peiris H.C.P. 1989. Studies on the biology of *Panicum repens* L. II. Intraspecific competition and resource - allocation. Trop. Pest Manage. 35: 316-320.

Clark D.D. & Burk J.H. 1980. Resource allocation patterns of two California - Sonoran Desert ephemerals. Oecologia (Berl.) 46: 86-91.

De Wit C.T. 1960. On competition. Versl. Landbouwk. Onderz. 66: 1-82.

Donaldson C.H. & Kelk D.M. 1970. An investigation of the veld problems of the Molopo area. I. Early findings. Proc. Grassld. Soc. sth. Afr. 5: 50-57.

Donaldson C.H., Kelk D.M. & West K.N. 1972. *Anthephora pubescens* Nees. Proc. Grassld. Soc. sth. Afr. 7: 112-116.

Fowler N.L. 1984. The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in *Linum*. J. Ecol. 72: 307-318.

Gadgil M. & Solbrig O.T. 1972. The concept of r - and K - selection. Evidence from wild flowers and some theoretical considerations. Am. Nat. 106: 14-31.

Harper J.L. 1977. Population biology of plants. Academic Press, London.

Harper J.L. & Gajic D. 1961. Experimental studies of the mortality and plasticity of a weed. Weed Res. 1: 91-106.

Harper J.L. & Ogden J. 1970. The reproductive strategy of higher plants. 1. The concept of strategy with special reference to *Senecio vulgaris* L. Ecol. 58: 681-698.

Kelk D.M. 1972. Phosphorus and Nitrogen nutrition of seedlings of *Cenchrus ciliaris* and *Anthephora pubescens*. M.Sc. Agric. thesis, Univ. Natal, Pietermaritzburg.

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992. The effect of intra - and interspecific competition on the dry matter production of *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. J Grassl. Soc. South Afr. (Submitted).

Nursey W.R.E. & Kruger A.H.G. 1973. The effect of spring mowing and burning on seed and dry matter production of Anthephora pubescens Nees. Proc. Grassld. Soc. sth. Afr. 8: 123-127.

Nyahoza F. 1973. Studies on the biology of Cyperus rotundus L. Early growth and vegetative reproduction strategy. East Afr. Agric. For. J. 39: 120-130.

Ogden J. 1974. The reproductive strategy of higher plants. 2. The reproductive strategy of Tussilago farfara L. J. Ecol. 62: 291-324.

Palmblad I.G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of plant population size. Ecol. 49: 26-34.

Pitelka L.F., Stanton D.S. & Peckenham M.O. 1980. Effects of light and density on resource allocation in a forest herb, Aster acuminatus (Compositae). Am. J. Bot. 67: 942-948.

Primack R.B. 1979. Reproductive effort in annual and perennial species of Plantago (Plantaginaceae). Am. Nat. 114: 51-62.

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Schoener T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Van Rooyen Margaretha.W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. PhD. dissertation, University of Pretoria, Pretoria.

Williams R.D., Quimby P.C. & Frick K.E. 1977. Intraspecific competition of Purple Nutsedge (Cyperus rotundus) under greenhouse conditions. Weed Sci. 25: 477-481.

CHAPTER 5

THE EFFECT OF INTRA - AND INTERSPECIFIC COMPETITION ON THE GROWTH OF ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

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The effect of competitive interference on the growth characteristics of *Anthephora pubescens* Nees (wool grass) and *Eragrostis curvula* (Schrad.) Nees (weeping love grass) was examined in a density as well as a replacement series. An increase in density resulted in a decrease in the average number of leaves per plant and the average leaf area per plant and per leaf in both species. This affect on the average number of leaves and average leaf area per plant was more prominent in *E. curvula* than in

A. pubescens. The average number of leaves per plant and average leaf area of A. pubescens in a mixture did not differ significantly from a monoculture. The growth characteristics of E. curvula were, however, favoured in a mixture. The relative growth rate (RGR), crop growth rate (CGR) and leaf area index (LAI) progressively decreased over the growing season in both species, peaking mid - season. It was evident that intraspecific competition had a greater negative affect on the growth characteristics of E. curvula than on the growth characteristics of A. pubescens, while interspecific competition favoured E. curvula to the detriment of A. pubescens.

Die invloed van kompeterende interaksies op die groeikenmerke van Anthephora pubescens Nees (borseltjiegras) en Eragrostis curvula (Schrad.) Nees (oulandsgras) is in 'n digtheids - sowel as 'n vervangingsreeks ondersoek. 'n Toename in digtheid het gelei tot 'n afname in die gemiddelde getal blare per plant en die gemiddelde blaaroppervlakte per plant in beide spesies. Dié invloed op die gemiddelde getal blare en die gemiddelde blaaroppervlakte per plant en per blaar was meer prominent in E. curvula as in A. pubescens. Die gemiddelde getal blare per plant en gemiddelde blaaroppervlakte per plant van A. pubescens, in 'n mengsel, het nie betekenisvol van dié in 'n suiwer stand

verskil nie. Eragrostis curvula se groeikenmerke was egter in 'n mengsel bevoordeel. Die relatiewe groeitempo, oes - groeitempo en blaaroppervlakte - indeks het in beide spesies oor die groeiseisoen afgeneem, met 'n piek in die middel van die seisoen. Dit was duidelik dat intraspesifieke kompetisie 'n groter negatiewe invloed op die groeikenmerke van E. curvula as A. pubescens gehad het, terwyl interspesifieke kompetisie E. curvula bevoordeel het tot die nadeel van A. pubescens.

Additional index words: Density, growth analysis, weeping love grass, wool grass

INTRODUCTION

Growth analysis is the first step in the analysis of primary production. It is a link between recording plant production and analysing it by means of physiological methods. According to Kvet et al. (1971) growth analysis is useful to analyse net photosynthetic production by plants, net production being defined as the net result of the assimilatory activities taking place in a plant during a certain period of time. Plant communities tend to be dominated by their most productive component species. According to Boysen - Jensen (1949, in Kvet et al. 1971) a plant can only thrive in a certain habitat if its long term dry matter balance is positive. Growth characteristics of individual species in a community are therefore useful indicators of the actual equilibrium between the plant community and its habitat. Akey _et al_. (1991) state that growth analysis can help identify plant characteristics that influence the competitive ability of a species. Relative growth rate (RGR), leaf area ratio (LAR) and net assimilation rate (NAR) are three growth analysis parameters that are useful in evaluating the response of plants to irradiance during growth (Patterson 1982).

The objective of the present study was to determine the effect of competition on the growth of _Anthephora pubescens_ Nees and _Eragrostis curvula_ (Schrad.) Nees. The De Wit (1960) replacement series was used to examine the development of _A. pubescens_ and _E. curvula_ separately in monocultures and together in mixtures over the growing season. Such series have been widely used to interpret competitive interactions between two species in mixed populations (Hall 1974; Trenbath 1974). The replacement series design has been criticized because it cannot discriminate between intra - and interspecific competition (Jolliffe _et al_. 1984), it confines attention to a single population density (Firbank & Watkinson 1985), it tends to favour larger species in mixtures, and it may give qualitatively different conclusions about relative competitiveness depending on the series used (Connolly 1986). To compensate for these problems, multiple harvests were used, growth characteristics were calculated over time and species were compared across all mixtures. This approach was considered adequate because the objective was to determine the effect of competition on the growth of two species rather than to determine the relative importance of intra - and interspecific competition. In this study it was aimed to follow the general trend of the growth characteristics rather than their short term fluctuations.

PROCEDURE

The experiment was conducted in a greenhouse at the Grassland Research Centre, Roodeplaat. Anthephora pubescens Nees spikelets and Eragrostis curvula (Schrad.) Nees seeds were planted separately in monocultures and together in mixtures. The A. pubescens ecotype VH20 spikelets were obtained from the Biesiesvlakte Research Station, Vryburg (24° 28" E; 25° 57" S). These spikelets were harvested April 1989 from plants which had been planted in March 1976. Certified E. curvula cultivar Ermelo seeds were obtained from a local seed dealer. The two species were planted in 150 mm deep 170 x 170 mm plastic pots with perforated bases in November 1990. The pots were filled with a 10 mm layer of gravel and topped with a sandy - loam soil. The soil consisted of 82.8 % sand, 8.7 % loam, 8.5 % clay and had a pH of 5.3. In the monocultures the planting densities were 1, 4, 8, 12 and 16 plants per pot respectively. In the mixtures, however, the total planting density was kept constant at 16 plants per pot, whilst the ratio's of A. pubescens to E. curvula were varied at 4:12, 8:8 and 12:4 plants per pot. An excess spikelets and seeds were sown and seedlings were thinned to desired densities within 4 weeks after emergence. Each pot received 500 ml tap water every second day and 100 ml nutrient solution, commercially produced UAN 32, at monthly intervals.

The pots were arranged in five replicate blocks, on trolleys. The trolleys were rotated fortnightly. Each block had six replicates per treatment, which were harvested at the end of each consecutive month, commencing January 1991 and terminating in May 1991. Each plant of each treatment, and species, was harvested separately by clipping at the soil surface and divided into separate plant parts (roots, tillers and leaves). The roots were washed over a fine sieve using a fine spray nozzle. In the case of the mixtures, however, the roots of the two species were intertwined and were therefore not harvested. The separate plant parts of each treatment, and species, were placed in brown paper bags and dried at 90°C for 48 h and weighed. The leaves were clipped at the ligule and the leaf areas (cm^2) determined with a LICOR 3100 Leaf Area Meter. All of the above mentioned values were determined on a per plant and per pot basis for each species. The harvest dates commenced four weeks after thinning.

ANALYSIS

The growth analysis of Hunt (1982) was used to analyse the data. Certain growth characteristics were determined for the monocultures only, whereas specific growth characteristics were determined for the mixtures. Definitions and clarification of the formulae used can be found in Hunt (1982).

The following growth characteristics were determined for the monocultures:

a. Relative growth rate of the whole plant (RGR_W)
b. Relative growth rate of the tillers (RGR_T)
c. Relative growth rate of the leaves (RGR_L)
d. Relative growth rate of the roots (RGR_R)
e. Relative growth rate of leaf area (RGR_{LA})
f. Relative growth rate of leaf area ratio (RGR_{LAR})
g. Crop growth rate (CGR)
h. Leaf area ratio (LAR)
i. Leaf weight ratio (LWR)
j. Specific leaf area (SLA)
k. Leaf area index (LAI)
l. Leaf area duration (LAD).

Specific growth characteristics determined for the mixtures were leaf area ratio (LAR), leaf weight ratio (LWR) and specific leaf area (SLA).

At harvest, only those pots which still had the full number of plants (i.e. initial density) were used. If one plant in a pot died the pot was discarded. A minimum of four replicates were used for data analysis. Due to unequal number of replicates the regression analysis approach was used to analyse the data. The "student's" t - test was used to determine statistical significance at a level of $p < 0.05$ (Rayner 1969).

RESULTS AND DISCUSSION

Due to the high mortality rate of *A. pubescens* under competitive stress, values of only the first three harvest dates could be used. *Eragrostis curvula* did not suffer significant mortality and could be harvested throughout the duration of the experiment, but for the purpose of comparison only the values of the first three harvest dates were used.

INTRASPECIFIC COMPETITION

The average number of leaves per plant and per pot, LA per plant, per pot and per leaf, LAR, LWR and SLA values of *A. pubescens* and *E. curvula* are given in Table 1. The average number of leaves per plant and the average LA per plant decreased with an increase in density. This effect intensified over the growing season. The difference between these values for 1 plant per pot and the higher densities was significant at the second and third harvests ($p < 0.05$). The LAR, LWR and SLA did not exhibit a significant trend with changing density ($p < 0.05$). An increase in density resulted in competition for the limited pool of resources. The greater the number of individuals per unit area the less the amount of resources per individual, resulting in a lesser number of leaves produced per individual and a resultant smaller LA per individual. The total number of leaves per pot increased with

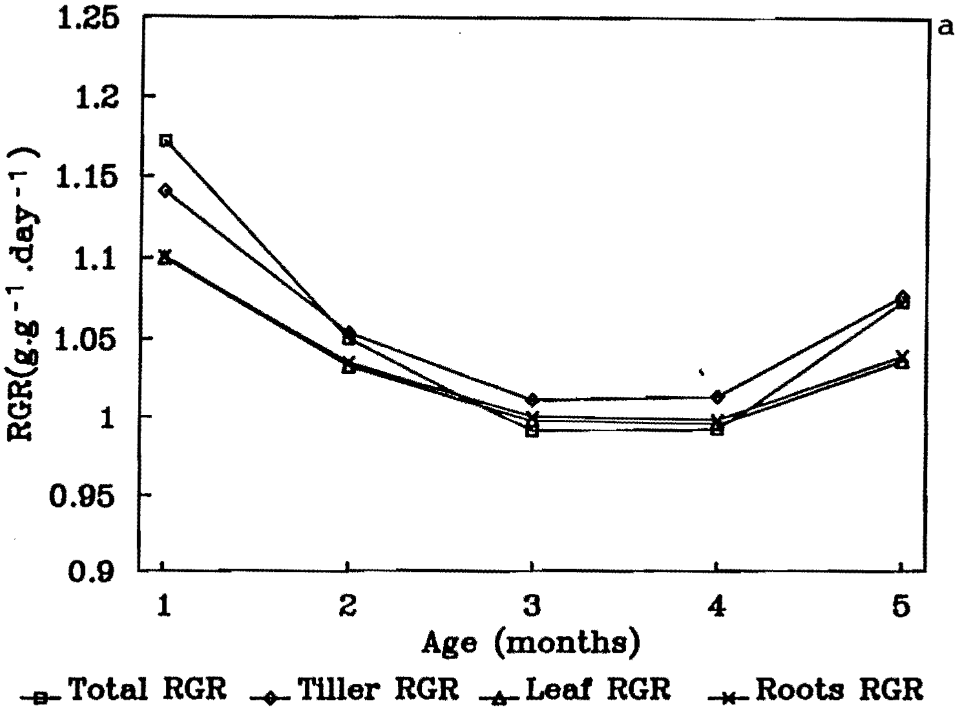
Table 1 The average number of leaves per plant and per pot, average leaf area (LA) per plant, per pot and per leaf, leaf area ratio (LAR), leaf weight ratio (LWR) and specific leaf area (SLA) of Anthephora pubescens and Eragrostis curvula in monocultures at monthly harvests with their respective standard deviations ( )

Harvest	Density (pl/pot)	Number of leaves per plant	Number of leaves per pot	LA per plant	LA per pot	LA per leaf	LAR	LWR	SLA
Anthephora pubescens									
1	1	10.67 (5.96)	10.67	13.06 (11.60)	13.06	1.22	21.24 (13.02)	0.19 (0.07)	112.76 (50.95)
	4	8.75 (5.26)	35.00	15.13 (12.81)	60.52	1.73	41.85 (24.52)	0.25 (0.11)	161.06 (41.41)
	8	10.16 (6.41)	81.28	19.14 (17.06)	153.12	1.88	34.23 (23.60)	0.20 (0.11)	162.60 (47.99)
	12	6.42 (3.48)	77.04	10.38 (10.39)	124.56	1.62	26.68 (21.10)	0.15 (0.09)	162.30 (73.21)
	16	4.77 (2.21)	76.32	6.67 (4.67)	106.72	1.40	32.10 (21.50)	0.22 (0.12)	151.24 (61.22)
2	1	56.00 (27.90)	56.00	199.87 (81.97)	199.87	3.57	26.15 (13.05)	0.18 (0.09)	123.32 (56.87)
	4	24.50 (15.19)	98.00	69.09 (55.52)	276.36	2.82	38.42 (24.56)	0.28 (0.18)	138.35 (31.27)
	8	14.53 (11.14)	116.24	40.75 (37.00)	326.00	2.80	31.47 (18.14)	0.21 (0.13)	177.14 (56.73)
	12	10.47 (5.39)	125.64	25.87 (19.65)	310.44	2.47	33.52 (19.91)	0.21 (0.12)	175.11 (54.11)
	16	8.92 (4.98)	142.72	21.27 (15.14)	340.32	2.38	32.73 (16.17)	0.24 (0.11)	138.41 (30.40)
3	1	73.50 (28.58)	73.50	277.78 (96.66)	277.78	3.78	31.05 (3.98)	0.22 (0.03)	144.62 (16.56)
	4	27.35 (18.32)	109.40	77.20 (59.63)	308.80	2.82	26.31 (12.02)	0.20 (0.09)	133.86 (17.13)
	8	19.47 (9.51)	155.76	53.02 (32.36)	424.16	2.72	48.39 (7.86)	0.30 (0.11)	145.01 (44.26)
	12	14.50 (9.10)	174.00	33.89 (25.01)	406.68	2.34	29.64 (11.56)	0.23 (0.09)	133.61 (40.85)
	16	8.98 (5.55)	143.68	20.53 (19.36)	328.48	2.29	30.04 (15.67)	0.21 (0.11)	170.79 (52.75)
Eragrostis curvula									
1	1	42.67 (17.56)	42.67	39.68 (17.58)	39.68	0.93	19.75 (4.16)	0.10 (0.05)	438.83 (96.71)
	4	28.00 (12.09)	112.00	29.07 (17.52)	116.28	1.04	20.81 (5.64)	0.13 (0.05)	154.33 (43.77)
	8	20.63 (6.90)	165.04	17.46 (9.08)	139.68	0.85	25.05 (9.80)	0.21 (0.06)	122.53 (27.89)
	12	20.69 (7.07)	248.28	17.38 (8.85)	213.96	0.86	29.87 (11.16)	0.19 (0.07)	156.36 (32.30)
	16	16.32 (5.05)	259.68	18.49 (10.20)	295.80	1.14	39.38 (18.98)	0.20 (0.11)	222.23 (83.18)
2	1	152.50 (14.58)	152.50	398.85 (99.75)	398.85	2.62	21.84 (6.12)	0.17 (0.03)	128.24 (34.41)
	4	64.80 (24.59)	259.20	153.92 (96.34)	615.68	2.37	26.98 (12.88)	0.20 (0.09)	142.38 (39.24)
	8	41.63 (12.99)	333.04	44.66 (25.38)	357.28	1.07	17.12 (7.51)	0.21 (0.07)	85.49 (41.67)
	12	31.35 (11.32)	376.20	30.49 (14.07)	365.88	0.97	22.14 (8.10)	0.25 (0.07)	89.74 (31.86)
	16	24.20 (12.06)	387.20	15.68 (9.97)	250.88	0.65	12.56 (6.29)	0.24 (0.10)	51.18 (14.51)
3	1	223.50 (29.06)	223.50	515.28 (61.10)	515.28	2.31	21.31 (4.19)	0.19 (0.03)	114.08 (6.39)
	4	91.75 (38.01)	367.00	164.85 (95.07)	659.40	1.80	22.36 (8.82)	0.21 (0.08)	109.50 (14.66)
	8	63.65 (24.39)	509.20	64.53 (38.82)	516.24	1.01	16.84 (7.49)	0.23 (0.08)	72.02 (22.01)
	12	41.08 (14.55)	492.96	27.08 (13.93)	324.96	0.66	10.37 (4.11)	0.25 (0.07)	40.32 (12.44)
	16	36.41 (14.37)	582.56	25.44 (12.84)	407.04	0.70	13.98 (7.54)	0.25 (0.08)	53.54 (19.97)

increasing density in both species, while the LA per pot did not. The LA per leaf, however, decreased with increasing density. Intraspecific competition had a greater affect on the LA per plant of _E_. _curvula_ than _A_. _pubescens_.

Due to the high mortality rate of _A_. _pubescens_ under competitive stress, the data of only the two lowest densities, 1 and 4 plants per pot, could be used for growth analysis. This occurrence alone was already indicative of the poor competitive ability of _A_. _pubescens_, as an increase in competitive stress resulted in increased mortality rate. This phenomena has been reported by Smith (1983) for _Floerkia_ _proserpinacoides_, while Donaldson & Kelk (1970) reported that establishment by _A_. _pubescens_ in a field situation was only successful under low competitive stress.

The RGR of the whole plant and the respective plant parts of _A_. _pubescens_ progressively decreased over the growing season at both densities (Figures 1a & b). It is interesting to note that both densities exhibited an insignificant increase in RGR in the fifth month of the growing season ($p < 0.05$). Tiller allocation may have been increased to produce inflorescences. There were, however, no inflorescences produced during the duration of the experiment. This retardation in reproductive activity was brought about _inter_ _alia_ by the size of the pots used. A detailed discussion of this occurrence has been given by Mynhardt _et_ _al_. (1992). The RGR of the LA, of 1 plant per pot, progressively decreased over the growing season up to the fourth month, but the RGR of the LAR, of 1 plant per pot, was highest mid - season



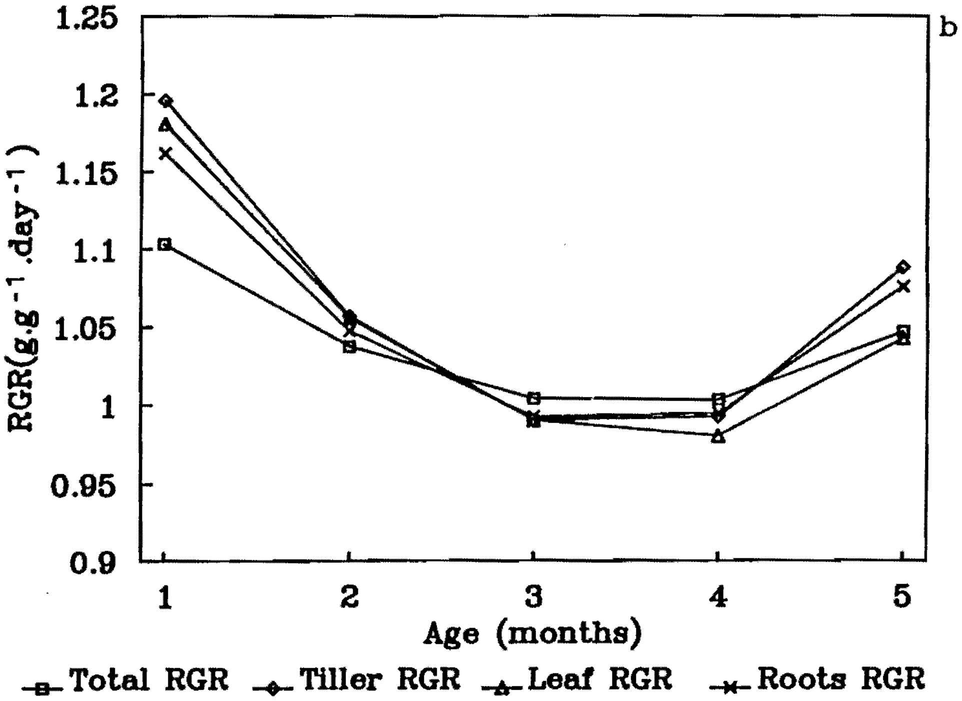


Figure 1 The relative growth rate (RGR) of the whole plant and the respective plant parts of Anthephora pubescens over the growing season at a (a) one - and (b) four - plants per pot density.

(Figures 2a & b). In the case of 4 plants per pot there was a general decrease in the RGR of the LA and LAR over the growing season (Figures 2a & b). The CGR of 1 plant per pot exhibited an initial decrease, but reached a turning point mid - season (Figure 2c). The CGR of 4 plants per pot exhibited an initial increase, but decreased after the second month (Figure 2c). The LAI of 1 plant per pot and 4 plants per pot exhibited a parabolic trend; the highest values being attained in the third and fourth months respectively (Figure 2d). The RGR of the LA and LAR, as well as the CGR and LAI of 1 and 4 plants per pot did, however, not differ significantly ($p < 0.05$). The LAD of 1 and 4 plants per pot progressively increased over the growing season, peaking in the third and fourth month respectively (Figure 2e). The LAD of 1 and 4 plants per pot did not differ significantly ($p < 0.05$).

The RGR of the whole plant and the respective plant parts of E. curvula progressively decreased over the growing season at all densities (Figures 3a - e). The RGR of 1 plant per pot was significantly higher than the other densities ($p < 0.05$). Eragrostis curvula exhibited a similar increase in RGR in the fifth month of the growing season to A. pubescens. The RGR of the LA showed a general decrease at all densities (Figure 4a). The RGR of the LAR of 1 and 4 plants per pot exhibited an initial increase peaking in the second month, while the higher densities decreased throughout the entire experimental period (Figure 4b). A significant CGR in the first month of the growing season was only exhibited by 1 plant per pot; the higher densities exhibited

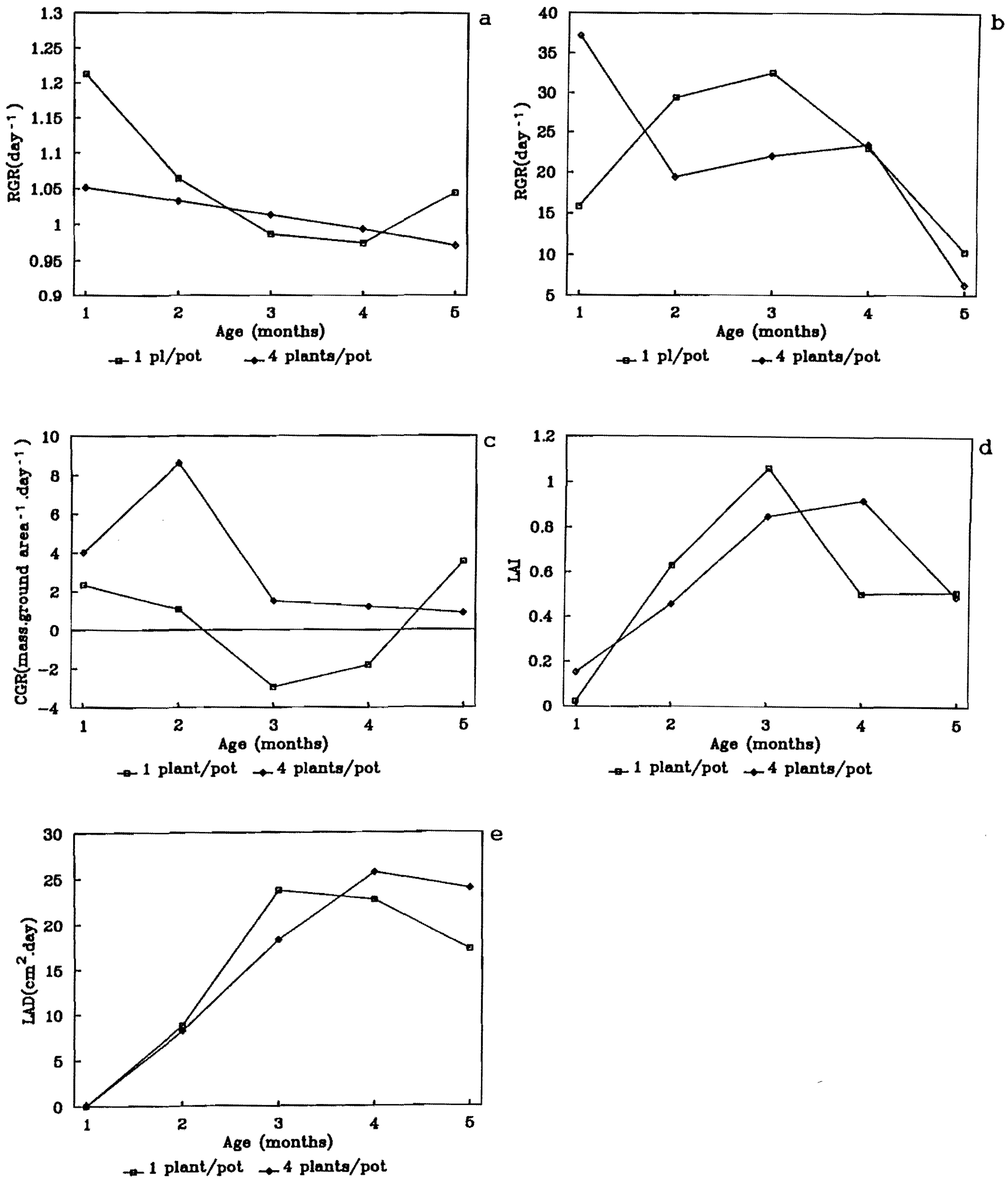


Figure 2 The relative growth rate (RGR) of the (a) leaf area (LA) and (b) leaf area ratio (LAR) of Anthephora pubescens at a one - and four - plants per pot density as well as the (c) crop growth rate (CGR) (d) leaf area index and (e) leaf area duration (LAD) over the growing season.

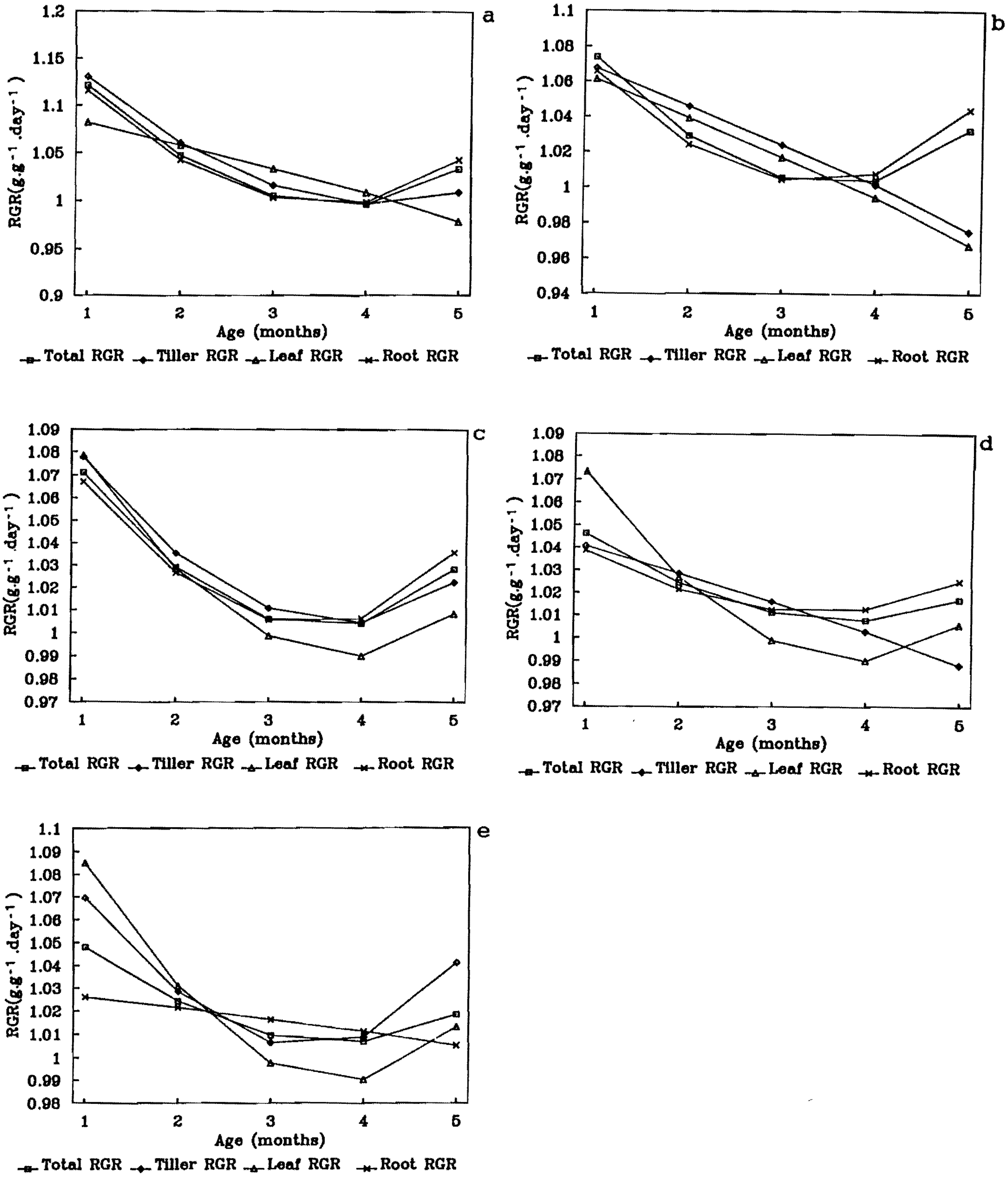


Figure 3 The relative growth rate (RGR) of the whole plant and the respective plant parts of <u>Eragrostis curvula</u> over the growing season at a (a) one - (b) four - (c) eight - (d) twelve - and (e) sixteen - plants per pot density.

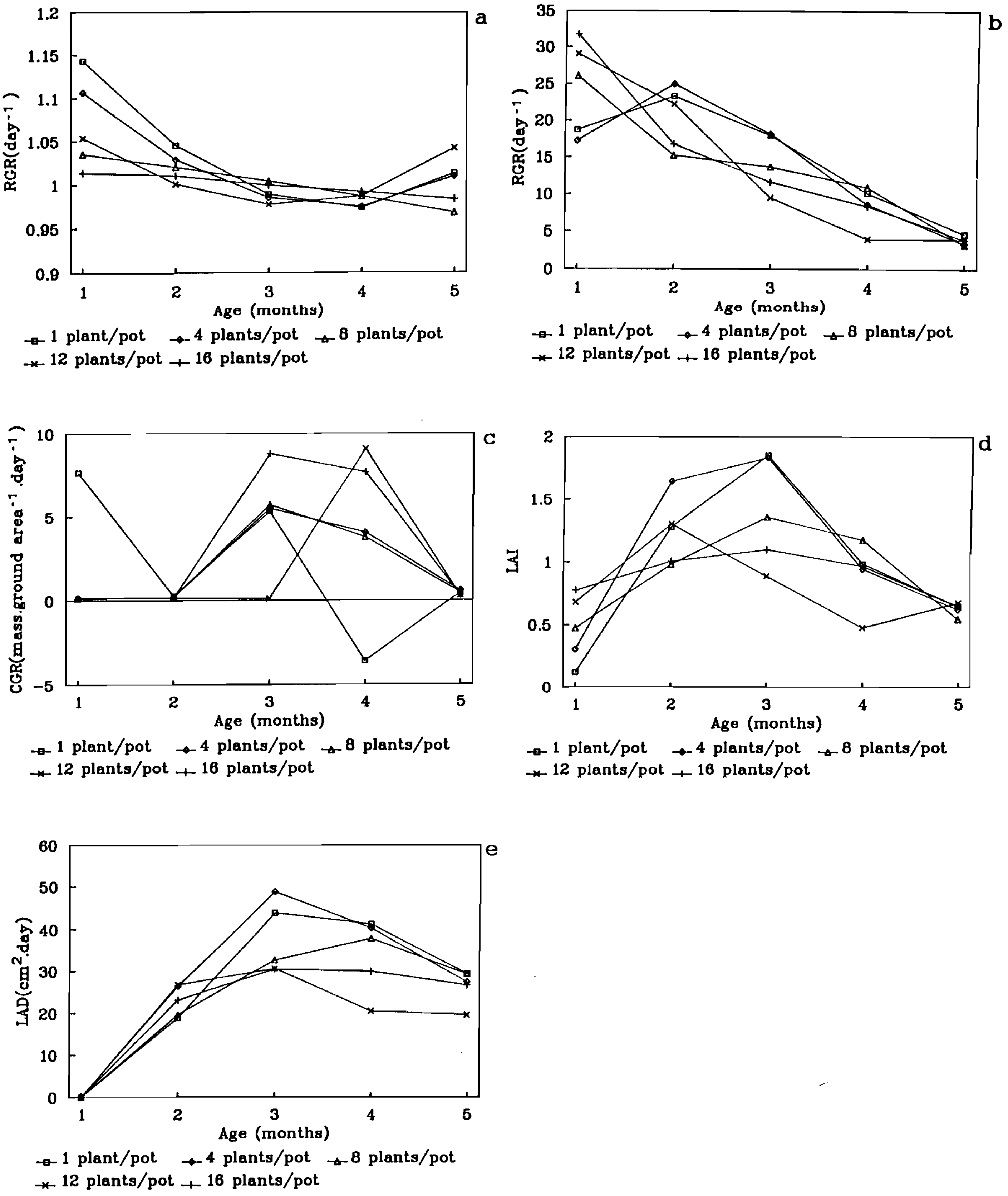


Figure 4 The relative growth rate (RGR) of the (a) leaf area (LA) and (b) leaf area ratio (LAR) of *Eragrostis curvula* at varying densities as well as the (c) crop growth rate (CGR) (d) leaf area index (LAI) and (e) leaf area duration (LAD) over the growing season.

a significant CGR only after the second and third month (Figure 4c; $p < 0.05$). The LAI and LAD of all densities exhibited a parabolic trend, peaking mid - season (Figures 4d & e). The total LAD, however, decreased with increasing density.

Leaf area index is the primary factor that determines the rate of dry matter production (CGR) in a closed stand (Kvet et al. 1971). The maximum LAI can therefore be controlled by stand density. The optimum LAI decreased with an increase in density. The individual plant was able to utilize the available resources effectively and as a result produce more assimilatory apparatus, while at higher densities competition for resources resulted in less assimilatory apparatus being produced. Greatest efficiency was attained at lower densities due to maximal interception of radiation; increased density resulted in a decrease in interception of radiation due to shading. Kvet et al. (1971) recorded optimal LAI values of 6 to 11 in grass and fodder crops. Anthephora pubescens and E. curvula produced optimum LAI values of only 1.06 and 1.86, in a 1 plant per pot stand, respectively. These low LAI values can be accrued to the limited soil volume in which the plants grew - a small soil volume caused a loss in effective retention ability and resultant leaching and loss of resources. Thus a limited supply of water, nutrients and space retarded the absolute growth rate of both species. Eragrostis curvula exhibited higher LAI values, generally grew taller and had more tillers than A. pubescens. Colvill & Marshall (1981) recorded a 50 % reduction in the RGR of Lolium perenne with increasing density. This effect of density on the growth and development of the individual plant has been shown in a number of experiments with grasses and cereals (Puckridge & Donald 1967; Kirby & Faris 1972; Kays & Harper 1974).

INTERSPECIFIC COMPETITION

The average number of leaves produced by *A. pubescens* and the average LA in a mixture did not differ significantly from that in a pure stand (Figures 5a & b; $p < 0.05$). *Eragrostis curvula*, however, produced significantly more leaves per plant and had a concomitant greater LA in a mixture than in a pure stand ($p < 0.05$); a 12 *A. pubescens* : 4 *E. curvula* ratio producing the highest values (Figures 5a & b). In the mixtures an increase in the ratio of *E. curvula* to *A. pubescens* resulted in a decrease in the average number of leaves per plant and the concomitant LA per plant of *E. curvula*. In a mixture the minority species therefore faces predominantly interspecific interference, whereas the majority species faces predominantly intraspecific interference. An increase in the ratio of the concerned species resulted in an increase in the LAR and SLA. The LAR and SLA of both species were, however, significantly smaller in a mixture than in a pure stand (Figures 5c & d), while the LWR values were unaffected by intra - and interspecific competition (Figure 5e; $p < 0.05$).

The effect of interspecific competition on the average number of leaves and LA per plant of *A. pubescens* did not differ significantly from the effect of intraspecific competition on these values ($p < 0.05$). The average number of leaves and LA per

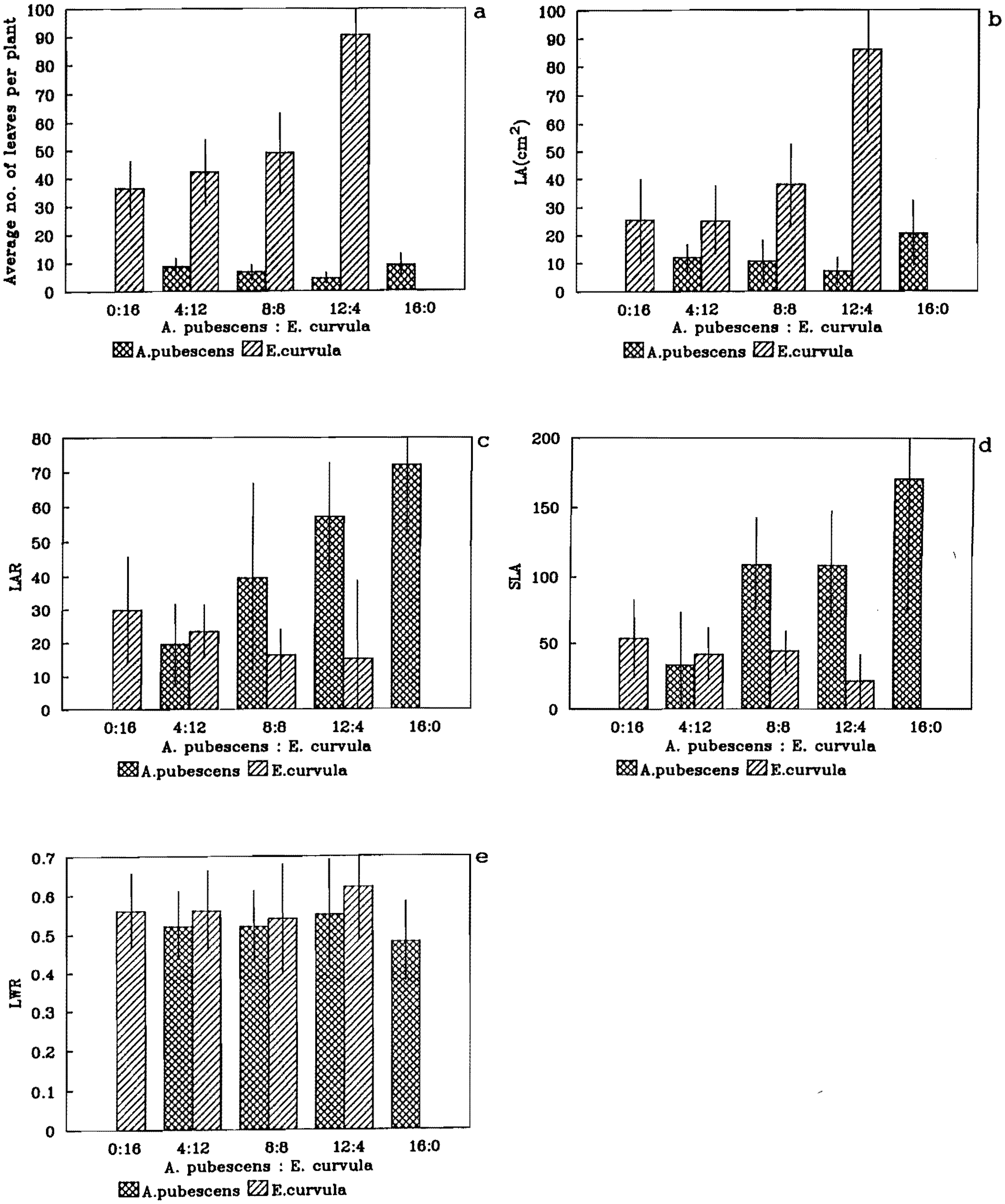


Figure 5 The effect of competition on the (a) average number of leaves per plant (b) leaf area per plant (LA) (c) leaf area ratio (LAR) (d) specific leaf area (SLA) and (e) leaf weight ratio (LWR) of Anthephora pubescens and Eragrostis curvula in a replacement series at the third monthly harvest.

plant of E. curvula was, however, affected less by interspecific competition than intraspecific competition. Leaf production and the resultant LA of E. curvula was favoured in a mixture; 4 plants of E. curvula in a 12 A. pubescens : 4 E. curvula mixture produced on average 90 leaves per plant and had a LA of 85 cm^2 per plant in contrast to the 39 leaves produced by 16 plants of E. curvula which had a LA of 25 cm^2 per plant; a significant difference ($p < 0.05$). The presence of individuals of A. pubescens therefore had less effect on the growth of E. curvula than the presence of individuals of E. curvula. Akey et al. (1991) recorded similar results in soybean and velvetleaf.

CONCLUSIONS

Competition evidently placed constraints on the growth of both species. A decrease in the growth characteristics of E. curvula in a monoculture suggests that intraspecific competition had a greater affect on the growth of E. curvula than on the growth of A. pubescens. In contrast, A. pubescens grew better in a monoculture than a mixture, suggesting that interspecific competition was more detrimental than intraspecific competition. This effect of competition on the growth characteristics of both species intensified over the growing season. The higher LAI and LAD values of E. curvula in comparison to A. pubescens, gave E. curvula a greater carbon assimilation capacity and a greater potential yielding capacity than A. pubescens. The CGR decreased when the optimum LAI was surpassed. The competitive advantage of

E. curvula resulted in interference with the vegetative growth of A. pubescens. The greater height of E. curvula lead to larger plant size and increased shading of A. pubescens later in the season. Eragrostis curvula therefore gained resources at the expense of A. pubescens, diminishing the vegetative growth of A. pubescens.

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REFERENCES

Akey W.C., Jurik T.W. & Dekker J. 1991. A replacement series evaluation of competition between velvetleaf (Abutilon theophrasti) and soybean (Glycine max). Weed Res. 31: 63-72.

Colvill Kay E. & Marshall C. 1981. The patterns of growth, assimilation of $^{14}CO_2$ and distribution of ^{14}C - assimilate within vegetative plants of Lolium perenne at low and high density. Ann. appl. Biol. 99: 179-190.

Connolly J. 1986. On difficulties with replacement series methodology in mixture experiments. J. appl. Ecol. 23: 125-137.

De Wit C.T. 1960. On competition. Versl. Landbouwkd. Onderz. 66: 1-82.

Donaldson C.H. & Kelk D.M. 1970. An investigation of the veld problems of the Molopo area: I. Early findings. Proc. Grassld. Soc. sth. Afr. 5: 50-57.

Firbank G. & Watkinson A.R. 1985. On the analysis of competition. J. appl. Ecol. 22: 503-517.

Hall R.L. 1974. Analysis of the nature of interference between plants of different species. I. Concepts and extension of the De Wit analysis to examine effects. Aust. J. Agric. Res. 25: 739-747.

Hunt R. 1982. Plant growth curves. The functional approach to plant growth analysis. Edward Arnold, London, pp. 1-246.

Jolliffe P.A., Minjas A.N. & Runeckles V.C. 1984. A reinterpretation of yield relationships in replacement series experiments. J. appl. Ecol. 21: 227-243.

Kays S. & Harper J.L. 1974. The regulation of plant and tiller density in a grass sward. J. Ecol. 62: 97-105.

Kirby E.J.M. & Faris D.G. 1972. The effect of plant density on tiller growth and morphology in barley. J. agric. Sci. Camb. 78: 281-288.

Kvet J., Ondok J.P., Necas J. & Jarvis P.G. 1971. Methods of growth analysis. In: Sestak J., Catsky J. & Jarvis P.G. (eds). Plant photosynthetic production: Manual of methods. The Hague, Junk, pp. 343-385.

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992. The effect of intra - and interspecific competition on the pattern of biomass allocation in Anthephora pubescens Nees and Eragrostis curvula (Schrad.) Nees. J. Grassl. Soc. South. Afr. (Submitted).

Patterson D.T. 1982. Effects of light and temperature on weed/ crop growth and competition. In: Hatfield J.L. & Thomason I.J. (eds). Biometeorology in Integrated Pest Management. Academic Press, New York, pp. 407-420.

Puckridge D.W. & Donald C.M. 1967. Competition among wheat plants sown at a wide range of densities. Aust. J. Agric. Res. 18: 193-211.

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Smith 1983. Demography of *Floerkia proserpinacoides*, a forest floor annual. 1. Density - dependent growth and mortality. *J. Ecol*. 71: 391-404.

Trenbath B.R. 1974. Biomass productivity of mixtures. *Adv. Agron*. 26: 177-210.

CHAPTER 6

THE EFFECT OF INTRA - AND INTERSPECIFIC COMPETITION ON THE MORPHOLOGICAL DEVELOPMENT OF *ANTHEPHORA PUBESCENS* NEES AND *ERAGROSTIS CURVULA* (SCHRAD.) NEES

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Anthephora pubescens Nees (wool grass) and *Eragrostis curvula* (Schrad.) Nees (weeping love grass) were grown in a greenhouse in monocultures at densities of 1, 4, 8, 12 and 16 plants per pot and in mixed cultures where the ratio's of *A. pubescens* to *E. curvula* were varied at 4:12, 8:8 and 12:4 plants per pot. Morphological development was monitored fortnightly over a period of 18 weeks. An increase in density resulted in decreased lateral tiller production and tuft height in both species. Intraspecific competition had a greater negative effect on the lateral tiller production of E. curvula than A. pubescens. The lateral tiller production of E. curvula was favoured in a mixture, while that of A. pubescens was favoured in a monoculture. Eragrostis curvula was evidently the superior competitor, to the detriment of A. pubescens.

Anthephora pubescens Nees (borseltjiegras) en Eragrostis curvula (Schrad.) Nees (oulandsgras) is in suiwer stande by digthede van 1, 4, 8, 12 and 16 plante per pot en in gemengde stande, waar die verhouding van A. pubescens tot E. curvula gevariëer het by 4:12, 8:8 en 12:4 plante per pot, in 'n kweekhuis geplant. Morfologiese ontwikkeling is elke twee weke oor 'n periode van 18 weke gemonitor. Toenemende digtheid het gelei tot 'n afname in die produksie van laterale lote en 'n afname in polhoogte in beide spesies. Intraspesifieke kompetisie het 'n groter negatiewe invloed op E. curvula se laterale lootproduksie as op A. pubescens se laterale lootproduksie gehad. Eragrostis curvula se laterale lootproduksie was in 'n mengsel bevoordeel, terwyl dié van A. pubescens in 'n monokultuur bevoordeel was. Dit was duidelik dat E. curvula die sterker kompeteerder was tot die nadeel van A. pubescens.

Additional index words: Density, morphology, weeping love grass, wool grass

INTRODUCTION

Reports on many experiments to compare the growth in a mixture of pairs of species which commonly cohabit in nature exist (Sagar & Harper 1961; Harper & McNaughton 1962; Harper & Clatworthy 1963). The mutual interference of species that do not occur together naturally, however, may nevertheless be of considerable ecological significance. A failure of two species to cohabit in nature may be because the effect of each species in its own habitat is to exclude the other. It is therefore interesting to bring the two species together in a mixture and examine the performance of each species in the presence of the other. According to Tripathi & Harper (1973) biological differences that have survival value are more likely to be exposed under density stress, than when the plants grow as isolated individuals. Kirby (1967) reported that competition is a factor which markedly affects tillering.

Populations of higher plants may vary in growth rate or mortality in reaction to stress. Mortality tends to be a continuing process throughout the life of dense populations and Yoda _et_ _al_. (1963) showed that there was a relationship between the mean size of the surviving plants and the residual density at various stages in the development of a population. The exploitation of resources by plants in a community depends on their ability to make rapid changes in the environment. The hierarchy in a grass population is largely determined by small differences in emergence time of simultaneously sown seed resulting in differing success of the various genets in the capture of space (resources) as shown by Ross & Harper (1972). Thomas & Steppler (1971) have shown that in Dactylis glomerata and Phleum pratense there is a relationship between the density at which grass is sown and the rate at which its ramets multiply and grow in size.

The objective of this study was to determine the effect of intra - and interspecific competition on the morphological development of two key grass species, Anthephora pubescens Nees and Eragrostis curvula (Schrad.) Nees. These two grasses do not normally occur together under natural conditions, but a major part of the present study was, however, to look at interactions between the species when allowed to grow in pure stands and mixtures, at varying densities, and to compare their performance. There is a large amount of evidence (Bleasdale 1967; White & Harper 1970) to show that individual features of a plant's vegetative growth, as well as the proportional relationships between various organs, can be varied by changes in environmental conditions. It is clear that studies of the inter - relationships of various species within a complex association such as a pasture must be based on a knowledge of the effect of changes in external conditions on the pattern of morphological development of individual species. Both A. pubescens and E. curvula are tufted grasses which grow erect. Interference would therefore be expected if these two grasses were grown separately or together in dense stands.

PROCEDURE

Pure and mixed stands of Anthephora pubescens Nees ecotype VH20 and Eragrostis curvula (Schrad.) Nees cultivar Ermelo were sown in 150 mm deep 170 x 170 mm plastic pots with perforated bases in November 1990. The pots were filled with a 10 mm layer of gravel and topped with a sandy - loam soil (82.8 % sand, 8.7 % loam, 8.5 % clay and a pH of 5.3). These pots were kept in a greenhouse at the Grassland Research Centre, Roodeplaat. The A. pubescens spikelets were obtained from the Biesiesvlakte Research Station, Vryburg (24° 28" E; 25° 57" S). The spikelets were harvested in April 1989 from plants which had been planted in March 1976. Certified E. curvula seeds were obtained from a local seed dealer. The two species were sown separately in pure stands at varying densities of 1, 4, 8, 12 and 16 plants per pot respectively. In the mixed stands, in which case the two species were sown together, the total planting density was kept constant at 16 plants per pot, but the ratio's of A. pubescens to E. curvula were varied at 4:12, 8:8 and 12:4 plants per pot (De Wit 1960). A surplus spikelets and seeds were sown and thinned to the desired density 4 weeks after emergence. The pots received 500 ml tap water every second day and 100 ml nutrient solution, commercially produced UAN 32, at monthly intervals.

The pots were placed on trolleys which were rotated fortnightly. There were six replicates per treatment. In the treatments where there were more than one plant per pot, four plants in the center of each pot, of each treatment and species, were marked with pigeon rings. A colour code was used, i.e. four different coloured pigeon rings (red, green, yellow and blue) to ensure that the same plant was measured at each monitoring date. These pigeon rings were placed on the primary tiller of each plant. The four marked plants in each pot were considered as being representative of the whole population in each pot. The morphological development was monitored at fortnightly intervals, commencing January 1991 and terminating in May 1991. At each monitoring date the following were determined :

a. total number of leaves on the primary tiller
b. average number of lateral tillers per plant
c. average tuft height (mm).

The seedling shoot was counted as the primary tiller and secondary and subsequent tillers were counted as soon as they reached the two - leaf stage. The tuft height was measured to the highest living part. Monitoring commenced 4 weeks after thinning. At each monitoring date, only those pots which still had the full number of plants (i.e. initial density) were used. A minimum of four replicates were used. If one plant in a pot died the pot was discarded. Due to unequal number of replicates the regression analysis approach was used to analyse the data. The "student's" t - test was used to determine statistical significance at a level of $p < 0.05$ (Rayner 1969).

RESULTS AND DISCUSSION

1. TOTAL NUMBER OF LEAVES ON THE PRIMARY TILLER

The total number of leaves produced on the primary tiller remained unaffected by increasing density in both A. pubescens and E. curvula. The pattern of leaf death was not affected by density; first deaths were recorded when the primary tiller had produced five or six leaves. The number of live leaves on the primary tiller remained more or less constant over the growing season as the appearance of a new leaf was accompanied by the death of the oldest leaf. This corresponds with the results recorded by Colvill & Marshall (1981) in Lolium perenne.

2. NUMBER OF LATERAL TILLERS PER PLANT

Anthephora pubescens suffered a high rate of mortality under competitive stress. Due to the loss of plants with increasing density, the morphological development of A. pubescens at higher densities could only be monitored for 8 weeks. Eragrostis curvula did not suffer loss under competitive stress and as a result the morphological development of E. curvula could be monitored for the duration of the experiment (18 weeks). In discussing the effect of density on morphological development, however, data of only the first 8 weeks of E. curvula were used for the purpose of comparison.

The average number of lateral tillers per plant of A. pubescens increased over the growing season, peaked and then decreased at all densities (Figure 1a). The increase in tiller number was, however, only significant in the one plant per pot density ($p < 0.05$). A decrease was observed in 4, 8, 12 and 16 plants per pot after the fourth week. The increase in the eighth week was insignificant and may be accrued to experimental variation ($p < 0.05$). In E. curvula the number of lateral tillers per plant increased over the growing season at all densities (Figure 1b). A significant increase in tiller number on a fortnightly basis was only exhibited by the one plant per pot density ($p < 0.05$). Although the dense stands did not exhibit a significant increase on a fortnightly basis, the total increase over the experimental period was significant ($p < 0.05$).

According to Mitchell (1953) the number of tillers on plants of equal leaf appearance gives a direct comparison of the extent to which the potentialities for tiller formation have been utilized, i.e. whether lateral buds have developed or remained dormant. It is an index of fresh active meristematic centres. Since each tiller is capable of rooting and assuming virtually independent existence it is, within definite limits, an index of the rate of vegetative reproduction. The maximum number of lateral tillers produced by A. pubescens at the lowest and highest densities, at the eighth week of monitoring, differed significantly

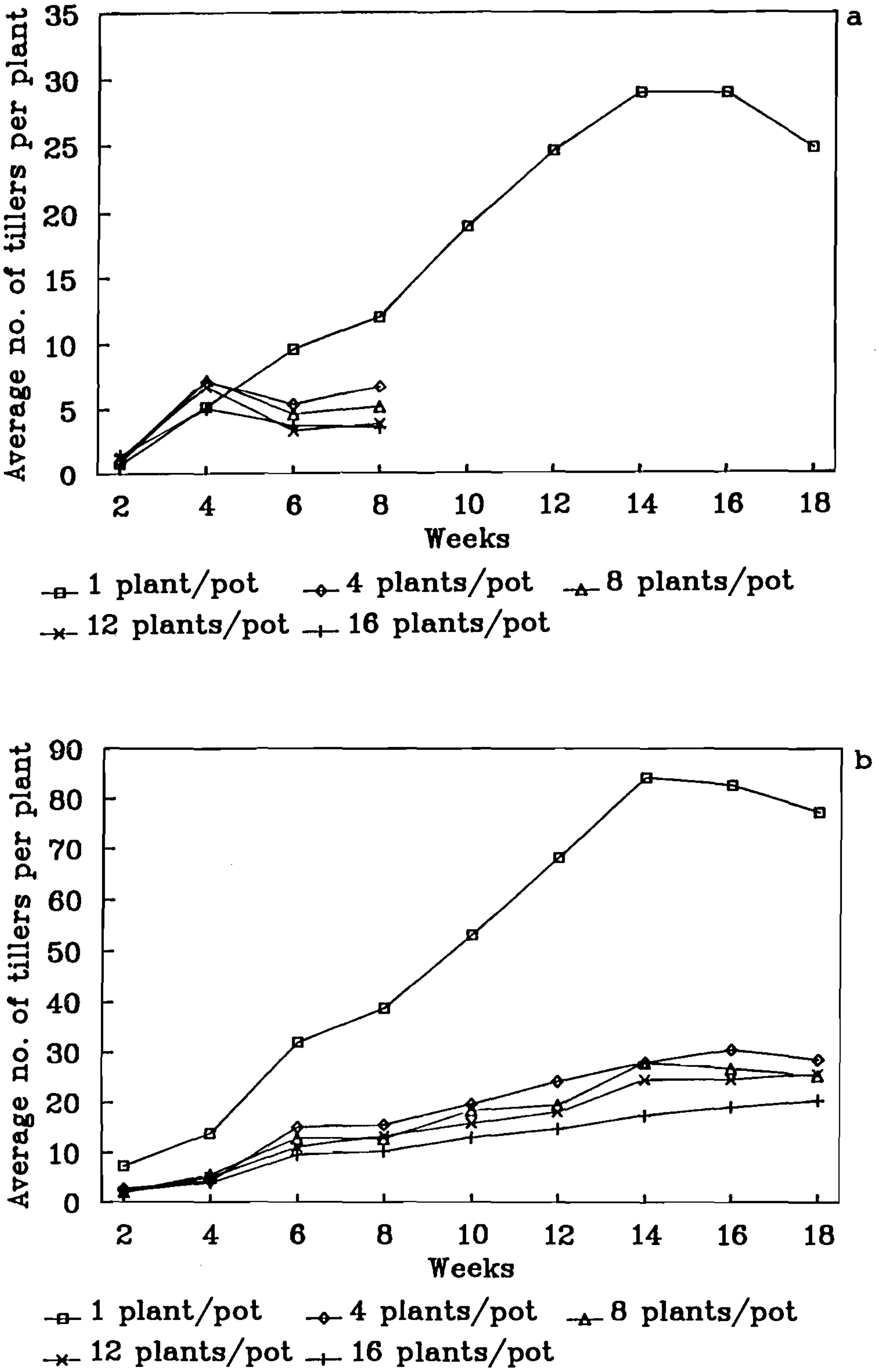

Figure 1 The effect of various densities on the average lateral tiller production of (a) Anthephora pubescens and (b) Eragrostis curvula over the growing season.

($p < 0.05$). Anthephora pubescens, however, attained maximum tiller production sooner in the growing season at higher densities than at the lowest density, suggesting suppression of tiller production with increasing density and earlier tiller initiation. Kirby & Faris (1972) found that in barley, tillers started growth earlier in the growing season at higher densities. In E. curvula, however, the maximum number of tillers produced per plant was attained from the fourteenth to eighteenth week at all densities. In A. pubescens the single spaced plants produced on average 10 to 15 lateral tillers per plant, while the higher densities produced on average 3 to 7 lateral tillers per plant at the eighth week of monitoring; a significant difference ($p < 0.05$). In E. curvula, however, the number of lateral tillers was still increasing after 18 weeks of monitoring at higher densities. The single spaced plants produced on average 75 to 80 lateral tillers per plant, while the higher densities produced on average 15 to 30 lateral tillers per plant at the eighteenth week of monitoring; a significant difference ($p < 0.05$). It was evident that intraspecific competition had intervened, limiting the amount of resources available to each individual plant and therefore limiting the maximum number of lateral tillers produced by both species. It appears that peak lateral tiller production was attained early in the growing season in A. pubescens at higher densities, while E. curvula did not exhibit a peak at higher densities. Colvill & Marshall (1981) recorded a 50 % reduction in the relative growth rate of Lolium perenne due to the production of fewer tillers with increasing density.

Harper & Ogden (1970) state: "the life history of an organism is to some extent pre - determined; it is a function of the organism's genotype." The genotypic programme may follow a range of possible developmental pathways and the one followed depends upon the environmental conditions to which the organism is exposed. The basic genotypic programme or strategy may be modified and expressed in a range of phenotypes representing varied tactics. Growth is dependent upon the availability of resources to the growing organs and correlations between the growth of different structures may therefore be a function of competition for resources. A change in the environment, affecting the availability of resources, may therefore change the relative growth rate of different organs to different extents. Such developmental plasticity represents a change in tactics by the plant. Survival of an adverse period, referred to as the perennation strategy, is encountered in most perennial plants (Harper & Ogden 1970). Anthephora pubescens and E. curvula exhibited different perennation strategies in terms of morphological development, under competitive stress. At high densities A. pubescens exhibited earlier lateral tiller initiation in the growing season, while E. curvula exhibited retarded lateral tiller initiation. The earlier lateral tiller initiation of A. pubescens under competitive stress may be viewed as an "emergency strategy". The purpose of earlier lateral tiller initiation may have been to gear towards reproduction; the production of inflorescences would ensure propagation. This strategy was, however, inhibited due to competition for limited resources (Mynhardt et al. 1992b). Eragrostis curvula did not exhibit a similar strategy, probably due to intense competition for limited resources resulting in retarded lateral tiller production; intraspecific competition had a greater negative affect on E. curvula than on A. pubescens (Mynhardt et al. 1992a).

The effect of density on the average number of lateral tillers produced per plant by A. pubescens is illustrated in Figure 2a. An increase in density resulted in an initial increase in the average number of lateral tillers produced per plant in the second week of monitoring. The differences between densities were, however, not significant at this early stage ($p < 0.05$) nor at the fourth week of monitoring. At the sixth and eighth week, however, an increase in density resulted in a decrease in the average number of lateral tillers per plant. The effect of varying density on the average number of lateral tillers produced per plant by E. curvula is represented in Figure 2b. An increase in density resulted in a significant decrease in the average number of lateral tillers produced per plant ($p < 0.05$). It has been shown in many experiments with grasses and cereals that density has a major affect on the growth and morphological development of the individual plant (Puckridge & Donald 1967; Kirby & Faris 1972; Kays & Harper 1974). Initially the average number of lateral tillers produced per plant remained unaffected by increasing density in A. pubescens. Intraspecific competition did, however, become effective from the fourth week of

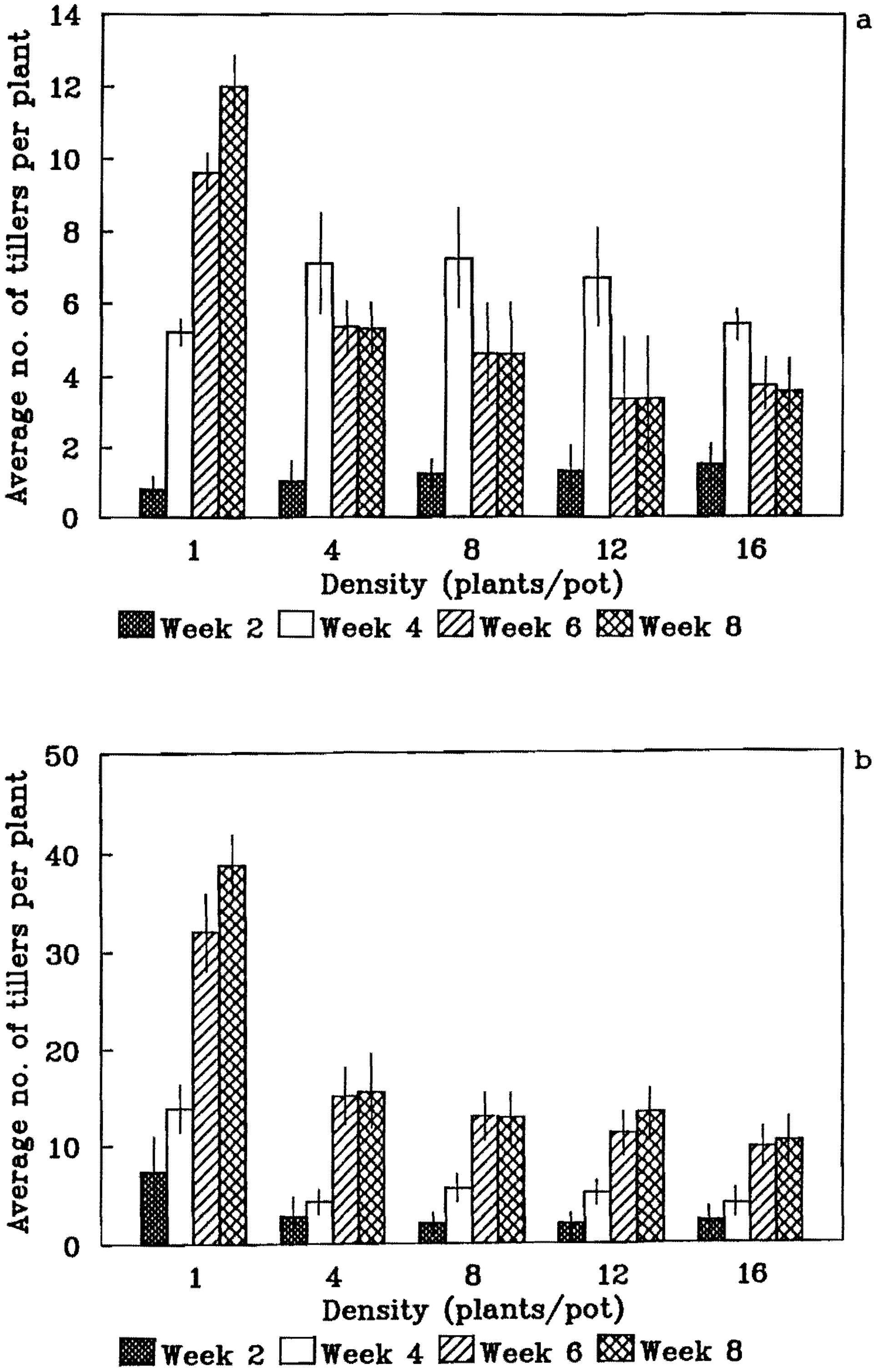

Figure 2 The effect of increasing density on the average lateral tiller production of (a) Anthephora pubescens and (b) Eragrostis curvula over the growing season.

monitoring. Lateral tiller production in E. curvula was, however, affected from day one. Increased intraspecific competition resulted in decreased lateral tiller production per plant. It was therefore evident that intraspecific competition intervened sooner in E. curvula than in A. pubescens and had a greater effect on E. curvula than on A. pubescens.

Due to the high mortality rate of A. pubescens in the mixtures, data of only the first six weeks of monitoring could be used. This was already indicative of the high sensitivity of A. pubescens to interspecific competitive stress. The effect of interspecific competition on the average number of lateral tillers per plant is illustrated in Figures 3a, b & c for both species. Within the replacement series an increase in the density of the respective species did not result in a significant increase in the average number of lateral tillers produced per plant at the second, fourth or sixth week of monitoring ($p < 0.05$). Eragrostis curvula did, however, produce significantly more lateral tillers per plant than A. pubescens in every species combination and at each monitoring date ($p < 0.05$).

3. TUFT HEIGHT

The average tuft height of A. pubescens increased and then decreased over the growing season at all densities (Figure 4a). The decrease in tuft height was as a result of tissue death which commenced at the tips of the respective plant parts. Plants grown at the lowest density reached maximum height in the twelfth week

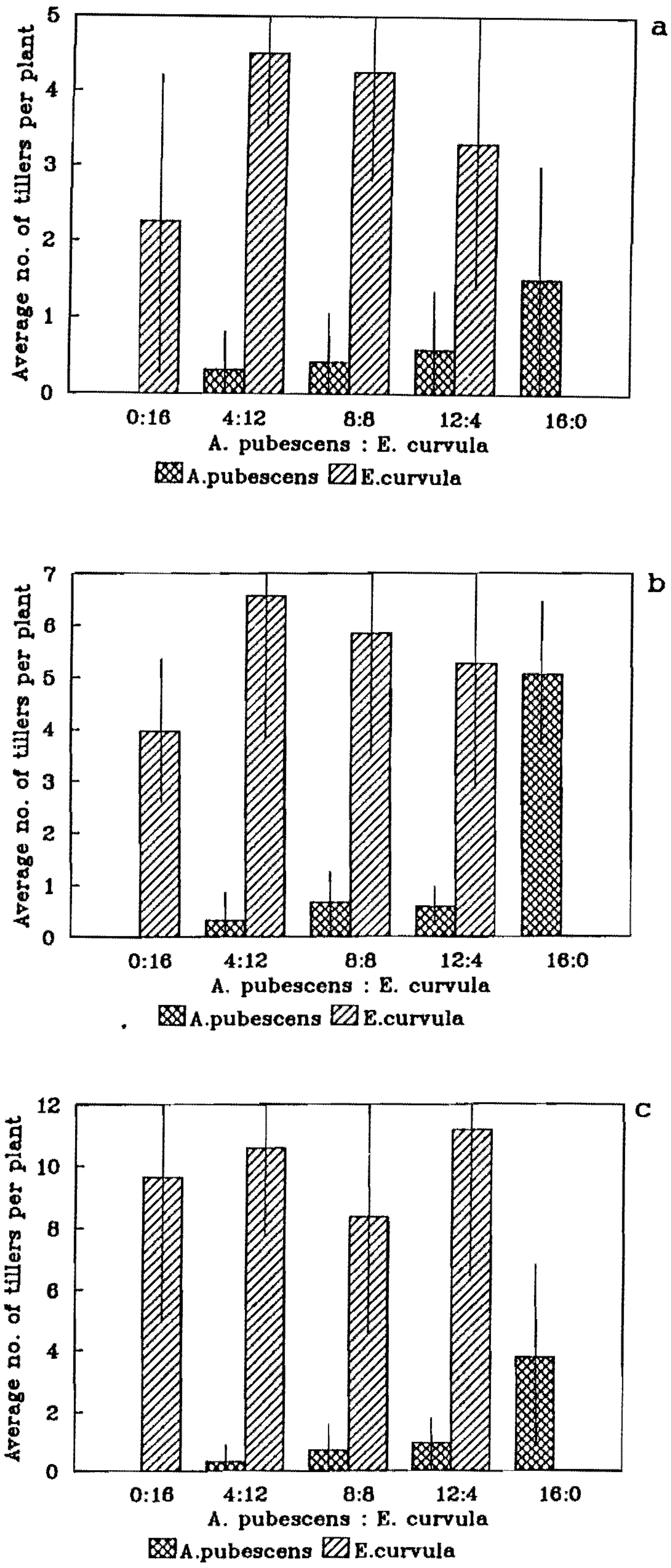

Figure 3 The effect of competition on the average lateral tiller production of Anthephora pubescens and Eragrostis curvula in the (a) second (b) fourth and (c) sixth week of monitoring.

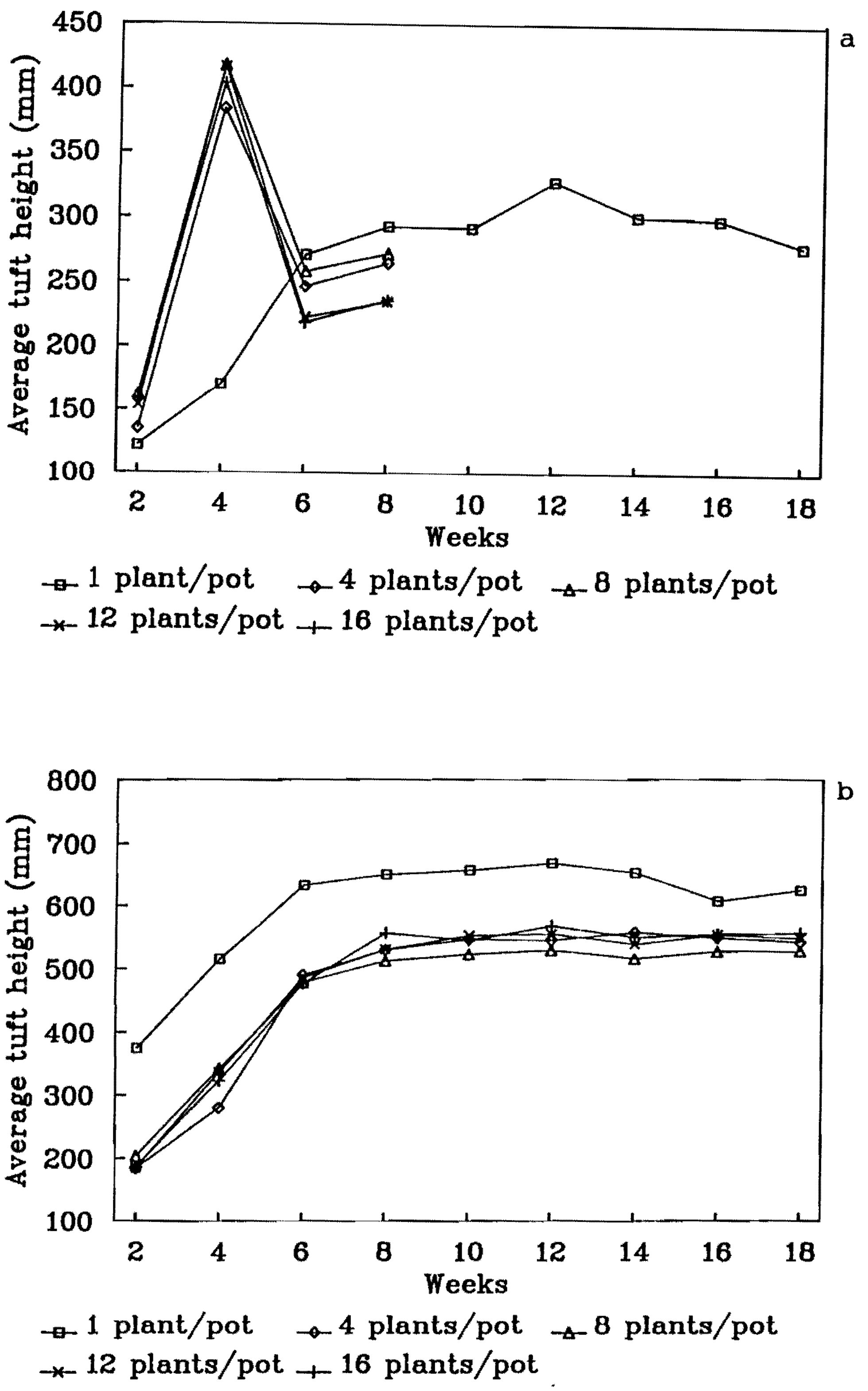

Figure 4 The effect of various densities on the average tuft height of (a) <u>Anthephora pubescens</u> and (b) <u>Eragrostis curvula</u> over the growing season.

of monitoring, while those of the higher densities peaked in the fourth week. The differences in plant height at the different densities were, however, not significant ($p < 0.05$), with the exception of the fourth week of monitoring. The average tuft height of E. curvula increased significantly over the growing season at all densities (Figure 4b; $p < 0.05$). After eight weeks, however, a significant increase in tuft height was not evident ($p < 0.05$). Increasing density resulted in an increase in the average tuft height of A. pubescens at the second and fourth week of monitoring, peaking at 8 plants per pot. From the sixth week, however, an increase in density resulted in a decrease in average tuft height. A significant difference in the average tuft height of E. curvula, with increasing density, was exhibited between 1 plant per pot and the higher densities from the second week of monitoring ($p < 0.05$).

The effect of interspecific competition on average tuft height is illustrated in Figures 5a, b & c for both species. The average tuft height of the respective species exhibited a similar trend to the average number of lateral tillers with increasing density.

Anthephora pubescens produced more lateral tillers per plant and attained a greater tuft height in a pure stand than in a mixture at each monitoring date. Eragrostis curvula, however, produced more lateral tillers per plant and attained a greater tuft height in a mixture. The differences in tuft height in both species were, however, not significant with the exception of

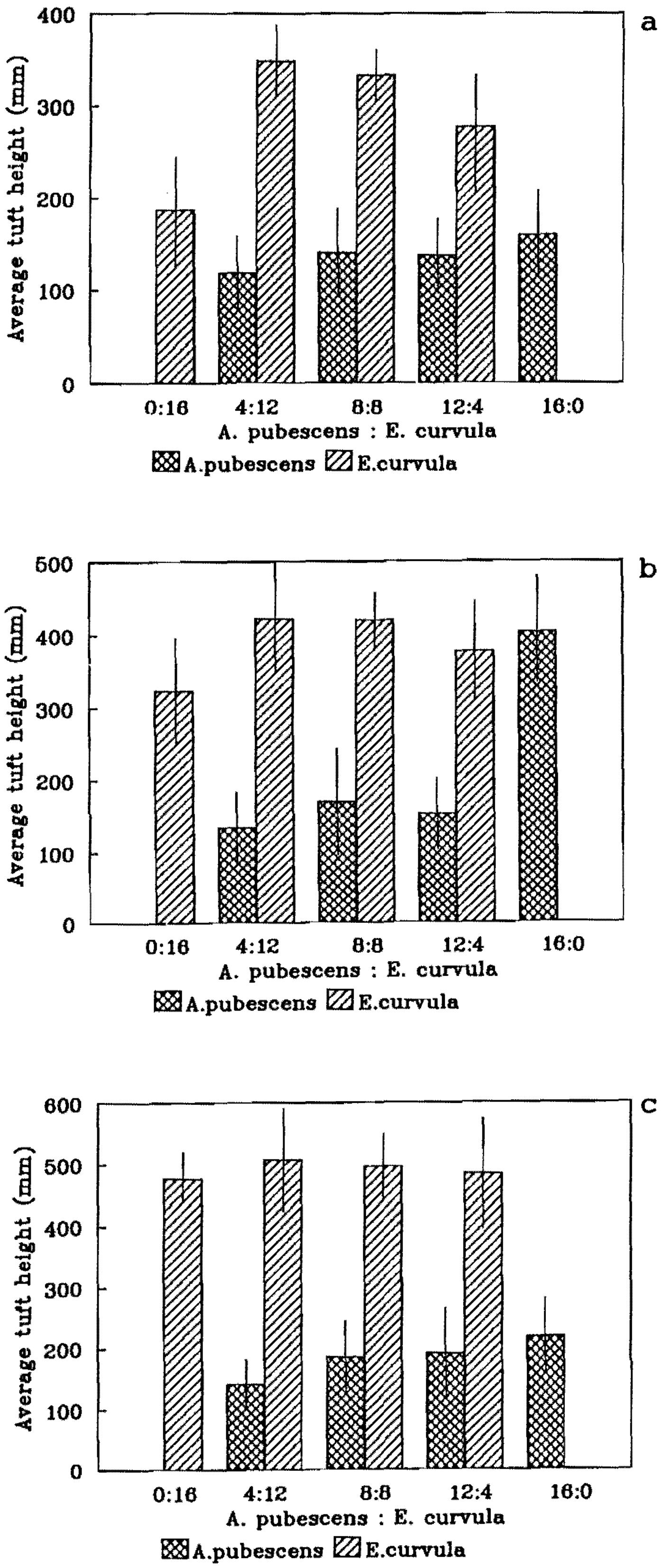

Figure 5 The effect of competition on the average tuft height of <u>Anthephora pubescens</u> and <u>Eragrostis curvula</u> in the (a) second (b) fourth and (c) sixth week of monitoring.

A. pubescens in the fourth week of monitoring ($p < 0.05$). It was evident that lateral tiller production and tuft height was favoured in a pure stand in *A. pubescens*, while in *E. curvula* it was favoured in a mixture.

High density plants were characterised by the production of fewer tillers and decreased tuft height. These features closely correspond to those described by Kirby & Faris (1970, 1972) in barley grown at high densities. Overall changes in morphology therefore reflect the differences in light relationships within stands at low and high densities. The pattern of assimilation by the leaves is modified due to shading. These changes can be attributed to the altered light relationships at high densities. Firstly, photosynthetic effects arise due to reduced total irradiance and different patterns of light interception by the plant. Secondly, it is likely that the altered spectral energy distribution could exert a major influence in modifying the pattern of development. Mitchell (1953) found that the quantity of light energy available appeared to be the chief determinant of the number of tillers produced in ryegrass; reducing the light tended to inhibit development from the basal nodes. The capacity of an individual tiller to assimilate CO_2 depends on its photosynthetic potential and the light it receives *in situ* within the stand.

CONCLUSIONS

It can be concluded that the growth of an individual plant is modified at high densities. Tillering is restricted and therefore the primary tiller plays a greater role in the overall carbon economy of the plant compared with its relative importance at low densities. *Eragrostis curvula* generally grew taller than *A. pubescens*, produced more lateral tillers and therefore had a greater light utilization than *A. pubescens*. These characteristics in combination may accrue for the competitive superiority of *E. curvula*. The height advantage of *E. curvula* enhanced its interception of light energy at the expense of *A. pubescens*. Under the conditions present in the experiment reported, and probably under most agricultural environments tillering is a valuable mechanism to enable the crop to exploit fully the environment.

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REFERENCES

Bleasdale J.K.A. 1967. The relationship between the weight of a plant part and the total weight as affected by plant density. J. Hort. Sci. 42: 51-58.

Colvill Kay E. & Marshall C. 1981. The patterns of growth, assimilation of $^{14}CO_2$ and distribution of ^{14}C - assimilate within vegetative plants of *Lolium perenne* at low and high density. Ann. appl. Biol. 99: 179-190.

De Wit C.T. 1960. On competition. Versl. Landbouwkd. Onderz. 66: 1-82.

Harper J.L. & Clatworthy J.N. 1963. The comparative biology of closely related species. VI. Analysis of the growth of *Trifolium repens* and *T. fragiferum* in pure and mixed populations. J. Exp. Bot. 14: 172-190.

Harper J.L. & Mcnaughton I.H. 1962. The comparative biology of closely related species living in the same area. VII. Inter - ference between individuals in pure and mixed populations of *Papaver* species. New Phytol. 61: 175-188.

Harper J.L. & Ogden J. 1970. The reproductive strategy of higher plants. 1. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol*. 58: 681-698.

Kays S. & Harper J.L. 1974. The regulation of plant and tiller density in a grass sward. *J. Ecol*. 62: 97-105.

Kirby E.J.M. 1967. The effect of plant density upon the growth and yield of barley. *J. agric. Sci. Camb*. 68: 317-324.

Kirby E.J.M. & Faris D.G. 1970. Plant population induced growth correlations in the barley plant main shoot and possible hormonal mechanisms. *J. Exp. Bot*. 21: 787-798.

Kirby E.J.M. & Faris D.G. 1972. The effect of plant density on tiller growth and morphology in barley. *J. agric. Sci. Camb*. 78: 281-288.

Mitchell K.J. 1953. Influence of light and temperature on the growth of ryegrass (*Lolium* spp.). 1. Pattern of vegetative development. *Physiol. Plant*. 6: 21-46.

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992a. The effect of intra - and interspecific competition on the dry matter production of *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992b. The effect of intra - and interspecific competition on the pattern of biomass allocation in *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Puckridge D.W. & Donald C.M. 1967. Competition among wheat plants sown at a wide range of densities. *Aust. J. Agric. Res*. 18: 193-211.

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Ross M.A. & Harper J.L. 1972. Occupation of biological space during seedling establishment. *J. Ecol*. 60: 77-88.

Sagar G.R. & Harper J.L. 1961. Controlled interference with natural populations of *Plantago lanceolata*, *P. major* and *P. media*. *Weed Res*. 1: 163-176.

Thomas N. & Steppler H.A. 1971. A density yield relationship in *Phleum pratense* L. and *Dactylis glomerata* L. *J. Br. Grassld. Soc*. 26: 143-144.

Tripathi R.S. & Harper J.L. 1973. The comparative biology of *Agropyron repens* (L.) Beauv. and *A. caninum* (L.) Beauv. I. The growth of mixed populations established from tillers and seeds. *J. Ecol*. 61: 353-368.

White J. & Harper J.L. 1970. Correlated changes in plant size and number in plant populations. *J. Ecol*. 58: 467-485.

Yoda K., Kira T., Ogawa H. & Hozumi H. 1963. Intraspecific competition among higher plants. XI. Self - thinning in over - crowded pure stands under cultivated and natural conditions. *J. Inst. Poltech. Osaka Cy Univ. Ser. D*. 14: 107-129.

CHAPTER 7

THE EFFECT OF INTRASPECIFIC COMPETITION ON THE NET CO_2 UPTAKE OF ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

INTRODUCTION

Plants of the same species or of different species differ in their ability to draw their requirements from the environment or their requirements differ, resulting in differences in their ability to survive periods of stress. Two plants compete with each other when demand exceeds supply, i.e. when such factors as water supply, nutrient supply, oxygen, CO_2, light and heat become limiting. Harper (1964) did, however, point out that competition itself is only one facet of interference between plants, although at times it may be a dominating one. In the case where light is the limiting factor, certain plants may be photosynthetically or morphologically better adapted than other plants to intercept sufficient light. Plants which are not as well adapted may be denied their light energy requirements by more competitive neighbours and therefore grow slower than what they would have in the absence of competition. It is generally accepted that the more similar the needs of the two organisms, the more intense the contest.

Most of the radiation intercepted by a field crop is absorbed by leaf laminae. The architecture of the leaf canopy is therefore fundamental to light interception by plants. Competition for light is unique as there is no common pool from which plants continue to draw their supplies until it is depleted. Incoming light energy is instantaneously available, it must be used or be lost. According to Donald (1963) competition for light may occur whenever one plant casts a shadow on another or when one leaf shades another. Physical and dependent physiological variables must be measured in order to understand the interaction between the environment and a crop. The separation of the complex physiological system of grasses into components which respond to discrete elements of the physical environment is, however, not simple. There are several techniques which can be used to assess the influence of the environment on CO_2 uptake. One of these involves the use of infra - red gas analysis to determine the influence of an environmental factor on the net uptake of carbon dioxide by the crop (Biscoe _et_ _al_. 1975). Another is the use of $^{14}CO_2$ to examine the influence of the environment on the distribution of labelled assimilates between the different growth centres of the crop (Ryle 1970; Singh & Coleman 1973).

The aim of this study was to examine the influence of intraspecific competition, on the net uptake of carbon dioxide by two key grass species, _Anthephora_ _pubescens_ Nees and _Eragrostis curvula_ (Schrad.) Nees. It has been demonstrated in a previous investigation that competition had a significant affect on the yield of the respective species (Mynhardt *et al*. 1992), and it would therefore be interesting to determine whether intraspecific competition also affected the rate of photosynthesis.

MATERIALS AND METHODS

The experiment was carried out in a greenhouse at the Grassland Research Centre, Roodeplaat. Monocultures of *Anthephora pubescens* Nees of the VH20 ecotype and *Eragrostis curvula* (Schrad.) Nees cultivar Ermelo were planted in 150 mm deep 170 x 170 mm plastic pots with perforated bases in November 1990. The pots were filled with a 10 mm layer of gravel and topped with a sandy - loam soil, which consisted of 82.8 % sand, 8.7 % loam, 8.5 % clay and had a pH of 5.3. The planting densities were 1, 4, 8, 12 and 16 plants per pot respectively. A surplus spikelets and seeds were sown and thinned to the desired density 4 weeks after emergence. Each pot received 500 ml tap water every second day and 100 ml nutrient solution, commercially produced UAN 32, at monthly intervals.

The pots were laid out on trolleys which were rotated fortnightly. Each treatment had six replicates. The net carbon dioxide uptake was an once - only determination which was monitored at the third harvest date; three months after thinning. A portable LICOR LI 6250 IRGA (infra - red gas analyser) was used to determine the net carbon dioxide uptake. A complete description of the IRGA can be found in Field *et al*. (1989).

Ten leaves were monitored per treatment and a mean was calculated for each treatment. The leaves sampled were similar in their position on the plant and in age. Measurements were made on a sunny cloudless day between 10:00 and 13:00. The light intensity was measured using a LICOR quantum sensor which was held at the same angle as that of the leaf. The Least Significant Difference (LSD) statistical test was used to test for significant difference at a level of $p < 0.05$ (Rayner 1969).

RESULTS AND DISCUSSION

The effect of changing density on net rate of CO_2 uptake per unit leaf area of A. pubescens is represented in Figure 1a. The net CO_2 uptake rate per unit leaf area increased and then decreased; peaking at 4 plants per pot. The net CO_2 uptake rate per unit leaf area of 4 plants per pot was significantly higher than that of the other densities ($p < 0.05$). The effect of increasing density on stomatal conductance and stomatal resistance is represented in Figure 1b. It was evident that when stomatal conductance was highest and stomatal resistance was lowest, optimum CO_2 uptake occurred. The optimum net CO_2 uptake rate per unit leaf area at a density of 4 plants per pot did not correspond with an optimum in leaf production per plant, leaf area (LA) per plant or per leaf, leaf area index (LAI) or yield per pot at that density (Table 1). The calculated net CO_2 uptake

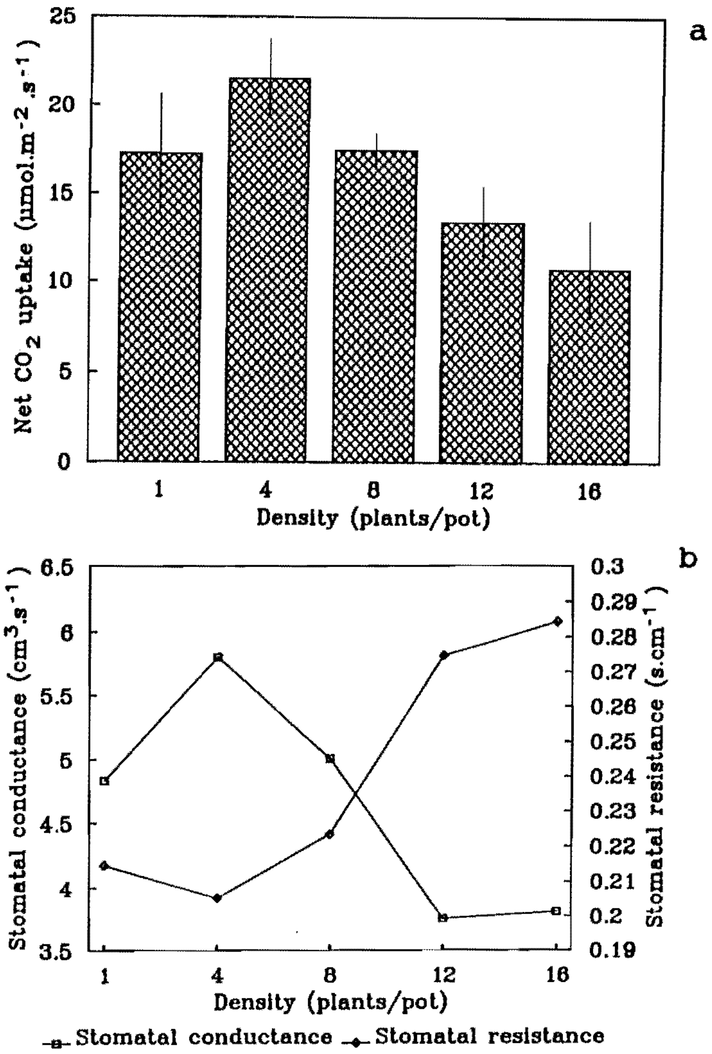

Figure 1 The effect of intraspecific competition on (a) the net CO_2 uptake rate per unit leaf area (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 1 8 4) and (b) the stomatal conductance and stomatal resistance of Anthephora pubescens at the third monthly harvest (stomatal conductance: 12 16 1 8 4; stomatal resistance: 4 1 8 12 16).

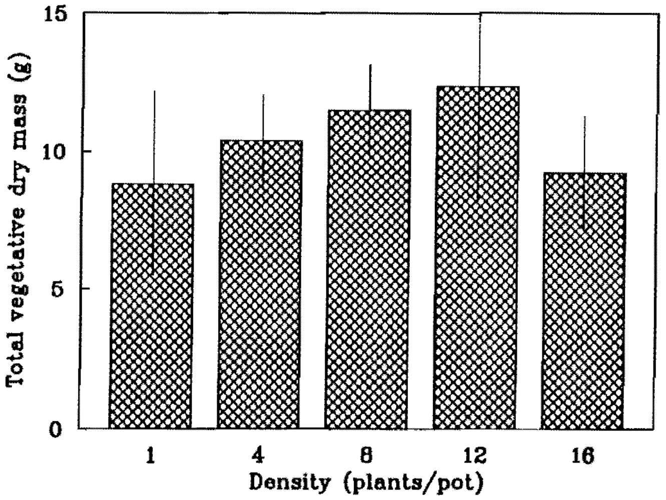

Figure 2 The effect of intraspecific competition on the average vegetative dry mass per pot of Anthephora pubescens at the third monthly harvest (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 8 4 1).

per pot (net CO_2 uptake per unit leaf area x leaf area per pot) reached a maximum at 8 plants per pot, whereas the yield per pot reached a maximum at 12 plants per pot (Figure 2).

The effect of changing density on net rate of CO_2 uptake per unit leaf area in E. curvula is represented in Figure 3a. An increase in density resulted in a progressive non - significant decrease in net CO_2 uptake rate per unit leaf area ($p < 0.05$). The effect of changing density on stomatal conductance and stomatal resistance is illustrated in Figure 3b. Maximal CO_2 uptake rate per unit leaf area was attained when stomatal conductance was highest and stomatal resistance was lowest. The calculated net CO_2 uptake per pot reached a maximum at 4 plants per pot, whereas the yield per pot reached a maximum at 12 plants per pot (Figure 4).

Increasing the level of intraspecific competition lead to a reduction in the rate of leaf production per plant as well as a reduction in the LA per plant (Table 1). Black (1958) recorded similar results in subterranean clover. By resolving the LA per plant into it's two components, it can be seen that the reduction can be attributed to a decrease in the number of leaves per plant as well as a decrease in the mean leaf area per leaf (Table 1). High LAI values at lower densities resulted in effective light utilization, while increasing density resulted in increased shading therefore limiting carbon assimilation. The difference in LAI values between densities may reflect changes in the leaves

Table 1 The average number of leaves per plant, average leaf area (LA) per plant and per leaf and leaf area index (LAI) of Anthephora pubescens and Eragrostis curvula at the third monthly harvest as extracted from Coetsee et al. (1992)

Harvest	Density (pl/pot)	Number of leaves per plant	LA per plant	LA per leaf	LAI
Anthephora pubescens					
3	1	73.50	277.78	3.78	1.06
	4	27.40	77.20	2.82	0.84
	8	19.50	53.02	2.72	*
	12	14.50	33.89	2.34	*
	16	8.90	20.58	2.29	*
Eragrostis curvula					
3	1	223.50	515.28	2.31	1.86
	4	91.80	164.85	1.80	1.84
	8	63.70	64.53	1.01	1.35
	12	41.10	27.08	0.66	0.89
	16	36.40	25.44	0.70	1.10

* Insufficient replicates to determine growth characteristics

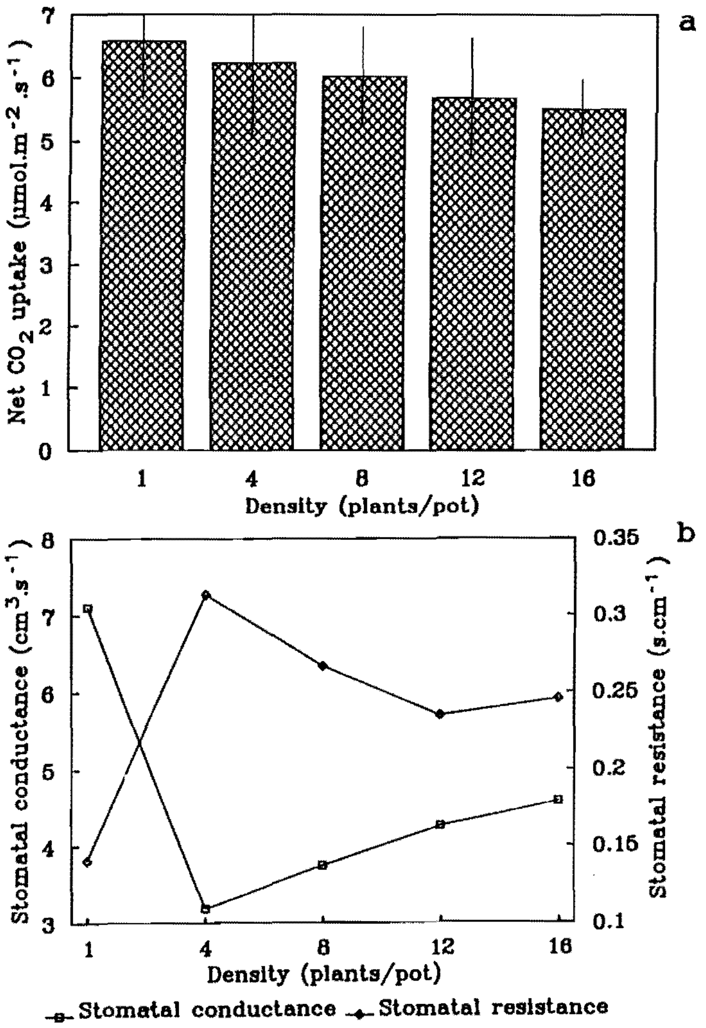

Figure 3 The effect of intraspecific competition on (a) the net CO_2 uptake rate per unit leaf area (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 8 4 1) and (b) the stomatal conductance and stomatal resistance of *Eragrostis curvula* at the third monthly harvest (stomatal conductance: 4 8 12 16 1; stomatal resistance: 1 12 16 8 4).

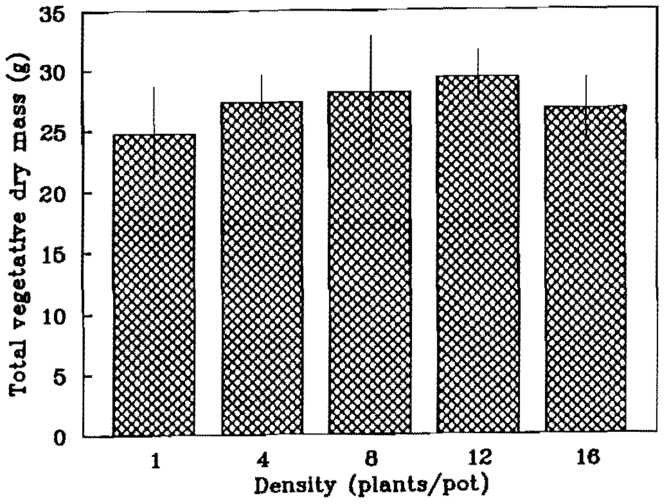

Figure 4 The effect of intraspecific competition on the average vegetative dry mass per pot of *Eragrostis curvula* at the third monthly harvest (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 8 4 1).

themselves, as each leaf develops under conditions of increasing shade, and may take on some of the attributes of "shade" leaves, transmitting more of the incident light. This suggestion is supported by the data of Burnside & Bohning (1957), who showed that saturation light intensity of leaves which develop in shade was less than those which developed under higher light intensities. Differences in the pattern of growth and quantity of tissue produced as a result of variations in light was demonstrated by Mitchell (1953) in ryegrass. Shaded plants produced less leaves and a lower leaf dry mass than unshaded plants.

The last decade researchers have referred to the "paradox" that no relationship exists between the rate of net CO_2 uptake per unit of leaf area and crop yield (Evans 1975; Moss 1976; Elmore 1980). Evans (1975) stated that there is no instance where selection for certain photosynthetic rates increased yield. Moss (1976) wrote that it is difficult to document that economic yield and photosynthesis are related in any direct way, and Elmore (1980) called attention to the "paradox" that no correlation exists between rates of CO_2 exchange per unit of leaf area and crop yield; in spite of the fact that it seems obvious that higher rates of photosynthesis should lead to higher yields. Good & Bell (1980) believe that this often - claimed "paradox" is a semantic problem.

Biological yield ultimately depends on whether the products of photosynthesis are used to increase photosynthetic capacity or are mainly stored. The former process would result in increased leaf area and perhaps more chloroplasts and hence a more efficient conversion of photosynthate into dry matter. Light is the paramount factor in the vitality and productivity of plants, as it ensures the energy basis of photosynthesis. The major biogenic elements assimilated from CO_2 and H_2O in photosynthesis comprise 90 - 95 % of the biomass of daily final increments. This, however, only accounts for that portion which remains after metabolism of the primary organic products of photosynthesis. According to Kramer (1981) growth and yield depend on many factors in addition to rate of photosynthesis, such as dark respiration, nitrogen metabolism, translocation and the partitioning of photosynthate to the various organs of plants. Plant growth is also affected by environmental factors such as water, mineral nutrients, temperature and light, and these affect growth through other processes in addition to photosynthesis. It must also be kept in mind that the CO_2 uptake measurements made in this experiment were instantaneous - a single occasion - and on a specific leaf position at a single stage of development, at constant temperature and under greenhouse conditions. Such an assay may reflect maximum or potential photosynthesis, but need have no relation to net seasonal assimilation of CO_2 by the entire plant and its translocation to the harvested plant organ, upon which yield is ultimately based.

CONCLUSIONS

It can be concluded that an increase in density results in shading and concomitant competition for light. Increasing density affects the rate of leaf production as well as the size of the leaves produced per plant. Maximal CO_2 uptake per unit leaf area was favoured under low competitive stress in both species. The effect of intraspecific competition on the net CO_2 uptake rate of A. pubescens and E. curvula differed significantly in that A. pubescens exhibited a peak in net CO_2 uptake rate per unit leaf area at 4 plants per pot, while E. curvula exhibited a decrease in net CO_2 uptake rate per unit leaf area with increasing density. It is evident that in A. pubescens and E. curvula, growth and increase in dry mass are not necessarily closely correlated with the rate of photosynthesis measured over short periods of time; instantaneous measurements of photosynthesis may therefore be misleading.

REFERENCES

Biscoe P.V., Scott R.K. & Monteith J.L. 1975. Barley and its environment. III. Carbon balance of the crop. J. appl. Ecol. 12: 269-293.

Black J.N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (Trifolium subterraneum L.) with particular reference to leaf area and the light microclimate. Aust. J. Agric. Res. 9: 299-318.

Burnside C.A. & Bohning R.H. 1957. The effect of prolonged shading on the light saturation curves of apparent photo - synthesis in sun plants. Plant Physiol. 32: 61-78.

Donald C.M. 1963. Competition among crop and pasture plants. Adv. Agron. 15: 1-118.

Elmore C.D. 1980. The paradox of no correlation between leaf photosynthetic rates and crop yields. In: Hesketh J.D. & Jones J.W. (eds). Predicting Photosynthesis for Ecosystem Models. Vol II. CRC Press, Boca Raton, FL, pp. 155-167.

Evans L.T. 1975. The physiological basis of crop yield. In: Evans L.T. (ed.). Crop physiology. Cambridge University Press, Cambridge, UK, pp. 327-335.

Field C.B., Ball T. & Berry J.A. 1989. Photosynthesis: principles and field techniques. In: Pearcy R.W., Ehleringer J.R., Mooney H.A. & Rundel P.W. (eds). Plant physiological ecology: Field methods and instrumentation. Chapman and Hall Ltd, London, pp. 209-248.

Good N.E. & Bell D.H. 1980. Photosynthesis, plant productivity, and crop yield. In: Carlson P.S. (ed.). The Biology of Crop productivity. Academic Press, New York, pp. 3-51.

Harper J.L. 1964. The nature and consequences of interference among plants. Proc. 11th international conference on genetics, The Hague, 1963, pp. 465-481.

Kramer P.J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. BioScience 31: 29-33.

Mitchell K.J. 1953. Influence of light and temperature on the growth of ryegrass (Lolium spp.). I. Pattern of vegetative development. Physiol. Plant. 6: 21-46.

Moss D.N. 1976. Studies on increasing photosynthesis in crop plants. In: Burris R.H. & Black C.C. (eds). CO_2 Metabolism and Plant Productivity. University Park Press, Baltimore, MD, pp. 31-41.

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992. The effect of intra - and interspecific competition on the growth of Anthephora pubescens Nees and Eragrostis curvula (Schrad.) Nees. J. Grassl. Soc. South. Afr. (Submitted).

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Ryle G.J.A. 1970. Distribution patterns of assimilated ^{14}C in vegetative and reproductive shoots of *Lolium perenne* and *L. temulentum*. *Ann. appl. Biol*. 66: 155-167.

Singh J.S. & Coleman D.C. 1973. A technique for evaluating functional root biomass in grassland ecosystems. *Can. J. Bot*. 51: 1967-1970.

CHAPTER 8

AN ANALYSIS OF THE COMPETITIVE INTERFERENCE IN *ANTHEPHORA PUBESCENS* NEES IN A NATURAL PLANT COMMUNITY

INTRODUCTION

An understanding of the response of desired and undesired key species, to the separate and combined pressures of a variable physical environment, is essential to the manipulation of rangeland vegetation to achieve a given objective. Such knowledge includes the conditions required for a species to establish from seed, to reach maturity and to produce seed, or the conditions that are likely to lead to large - scale mortality. In addition to such knowledge, an understanding of how management can affect the competition is necessary.

According to Teague (1989) results of direct gradient analysis, ordination and classification suggest that a given environment, mainly due to its physical characteristics, disposes a relatively predictable species association. A given species occurring in a predictable association may quite likely occur with another group of species under different conditions in another environment. Such a state will arise as long as individuals have tolerance limits which encompass a range of conditions, individuals within a species differ ecologically from each other, different species differ in their tolerance levels, and conditions vary as gradients in space (Teague 1989). Just as the relative importance of species vary in space, their patterns of abundance change in time. In either case the species will only occur if it is capable of reaching a location, the resources and conditions are appropriate, and predators and competitors do not preclude it. Noble & Slatyer (1981) attempted to formulate the role of different features, of different species, which determines their place in succession. The two most important features relate to the method of recovery and the ability of individuals to reproduce in the absence of competitors. According to Harper (1977) species react to selection pressure and develop features which enable them to survive for a longer period in the succession or they may develop more effective mechanisms of escape.

A species' ecological features, abiotic tolerance, maximum relative growth rate, phenology, receptiveness to various enemies and relative competitive ability can be summarised by the niche concept. The behaviour of a plant growing in isolation differs greatly from its behaviour in the presence of other plants and enemies. The competitive ability of a species is therefore not only a feature of the genetic potential of the species itself, but also depends on the environmental conditions, other plants and the consumers involved. For every combination of soil, climate, altitude, slope and aspect there will be one species that grows better than another species, so that it produces more seeds or occupies more space by vegetative spread. In a spatially uniform and temporally constant world this single species would dominate the community to the exclusion of all others (Teague 1989). Most plant communities do, however, consist of many species, and the environment is not spatially uniform nor temporally constant.

Anthephora pubescens Nees is an important component of permanent pastures in the Cape Province north of the Orange River. In its natural state *A. pubescens* is prevalent on sandy soil with a neutral pH (Donaldson *et al*. 1972). A valuable attribute of *A. pubescens* is its relatively low sensitivity to poor soil nutritional conditions (Fourie *et al*. 1987). Little study has, however, been done to examine the competitive ability of *A. pubescens* in a natural population. The objective of this study was therefore to examine the occurence frequency of *A. pubescens* in the presence of other species, in a natural plant community.

MATERIALS AND METHODS

The study area is located at the Biesiesvlakte Research Station, Vryburg (24° 28" E; 25° 57" S). The research station lies 1 208 m above sea level and has a mean annual rainfall of 475 mm. The soil is characterised by 92.7 % sand, 4.9 % loam and 2.4 % clay and has a pH of 6.64. The survey was conducted in a natural plant community in April 1991. A sample of two hundred points was taken using the nearest - neighbour method (Yeaton & Cody 1976). At each point, A. pubescens was used as the reference tuft from which measurements were made. Four sets of measurements were made in the field. Firstly, nearest - neighbour distances, i.e. the distance between the reference A. pubescens tuft and the nearest neighbour. Secondly, the diameter of each tuft was measured (mm). Thirdly, the nearest neighbour was identified. Lastly, the percentage occurrence of the different species in the plant community was determined.

It is of importance in studies of spacing and competition to choose sites in which the limiting resource is evenly distributed. For example, on slopes where the ground surface shows run - off channels, water is unevenly distributed. Studies carried out on such sites therefore must take in account the considerable variations in water availability (Barbour 1973). For this reason a level site was selected for the present study, where the substrate was uniform and coarse and where run - off channels were not visible on the surface; situations at the feet of slopes, where run - off water might be directed on to the site, were avoided.

The nearest - neighbour distances and the sizes of the nearest neighbours were analysed as follows: nearest - neighbour distances were regressed against the sums of the size indices for each pair. The question as to whether the distance between neighbours may be less if they belong to different species than if they belong to the same species, was approached as follows: the larger of the two individuals, of the nearest - neighbour pair, was regarded as determining the size of the other. Since the latter could vary according to distance from the larger individual, the ratio of the size of the smaller individual to the distance from its neighbour was calculated. These ratio's are referred to as arbitrary size index values (ASIV). Ratio's for intraspecific pairs were compared to those for interspecific pairs. Regression analyses were applied and statistical significance was tested at a level of $p < 0.05$ (Rayner 1969).

RESULTS AND DISCUSSION

It must be kept in mind that in the interpretation of all the results, *A. pubescens* is used as the vantage point; none of the other grass species or forb species were analysed to determine their respective competitive abilities.

1. PERCENTAGE OCCURRENCE

The species recorded for the plant community surveyed is represented in Table 1. It was evident that *A. pubescens* was the dominant species; *A. pubescens* constituted almost 80 % of the plant community, while the rest was mainly constituted by other grass species, *Stachys spathulata*, a forb, being the exception.

Table 1 The total number of individuals of grass species recorded (nomenclature follows Gibbs Russel et al. 1990) and their relative percentage frequency in an Anthephora pubescens community at Biesiesvlakte Research Station (24° 28" E; 25° 57" S)

Plant species	Total number recorded	Relative percentage frequency
Anthephora pubescens Nees	159	79.5
Schmidtia pappophoroides Steud.	23	11.5
Eragrostis lehmanniana Nees	4	2.0
*Stachys spathulata Burch. ex Benth.	4	2.0
Aristida meridionalis Henr.	2	1.0
Pogonarthria squarrosa (Roem. & Schult.) Pilg.	2	1.0
Stipagrostis uniplumis (Licht.) De Winter	2	1.0
Aristida species	1	0.5
Hemarthria altissima (Poir.) Stapf & C.E. Hubb.	1	0.5
Themeda triandra Forssk.	1	0.5
Tragus koelerioides Aschers.	1	0.5

* Forb

Besides A. pubescens, Schmidtia pappophoroides was the most frequent species occurring significantly more often than the other species in this particular plant community ($p < 0.05$). Anthephora pubescens rarely occurred in the vicinity of other dominant grass species.

2. REGRESSION ANALYSES

On basis of the above results, the data were divided into two groups: (a) regressions between A. pubescens pairs (intraspecific competition) and (b) regressions between A. pubescens and S. pappophoroides pairs (interspecific competition).

a) Intraspecific competition

The relationship between nearest - neighbour distances and the sums of the size indices of A. pubescens pairs is illustrated in Figure 1. A regression could not be fitted, i.e. a significant relationship was not exhibited ($p < 0.05$). Neither was a significant relationship between the ASIV and nearest - neighbour distances of A. pubescens pairs exhibited (Figure 2).

b) Interspecific competition

The relationship between nearest - neighbour distances and the sums of the size indices of *A. pubescens* and *S. pappophoroides* pairs is illustrated in Figure 3. A significant relationship was not evident in the interspecific pairs ($p < 0.05$). Neither was a significant relationship exhibited between the ASIV and nearest - neighbour distances of *A. pubescens* and *S. pappophoroides* pairs (Figure 4; $p < 0.05$).

It was evident from the percentage occurrence survey that *A. pubescens* occurred most often in the vicinity of other *A. pubescens* tufts, while other grass species virtually failed to occur in the vicinity of *A. pubescens* tufts. In the interpretation of these results one is faced with two possible reasonings. If *A. pubescens* is considered a pioneer species in the evolutionary pathway of plant succession, then *A. pubescens* could be classed as a species belonging to the facilitation or tolerance models (Connell & Slatyer 1977); i.e. *A. pubescens* is an early coloniser but dies out due to competition from invading superior competitors. If this be the case, then according to Harper's (1977) view *A. pubescens* should be a good coloniser but may be a poor competitor. *Anthephora pubescens* is known to establish well on nutrient poor soil (Fourie *et al*. 1987). This characteristic may clarify the good colonizing ability of

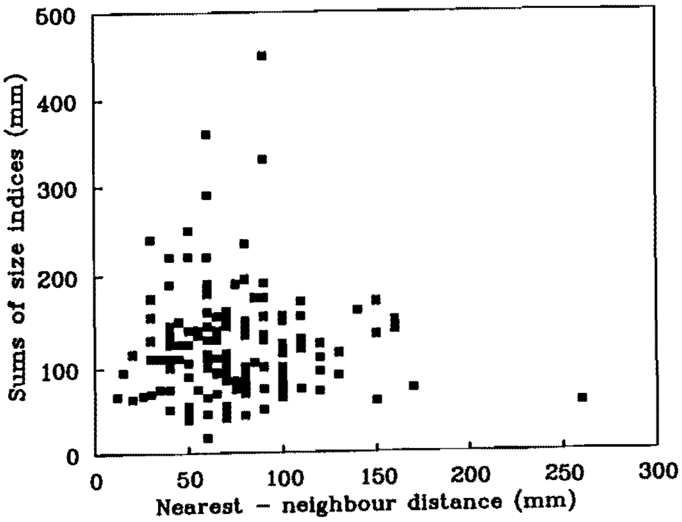

Figure 1 The relationship between the nearest - neighbour distances and the sums of the size indices of <u>Anthephora pubescens</u> pairs in a natural plant community ($y = 117.39x + 0.001$; $r = 0.184$; $p < 0.05$).

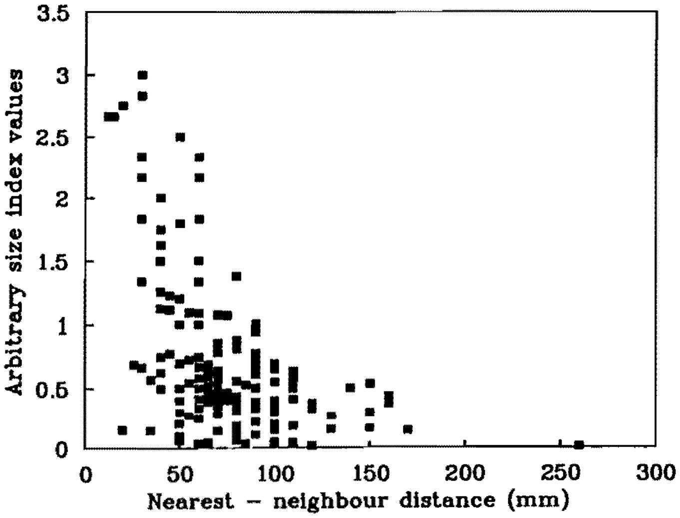

Figure 2 The relationship between the nearest - neighbour distances and the arbitrary size index values (ASIV) of <u>Anthephora pubescens</u> pairs in a natural plant community ($y = 1.465x - 0.015$; $r = 0.182$; $p < 0.05$).

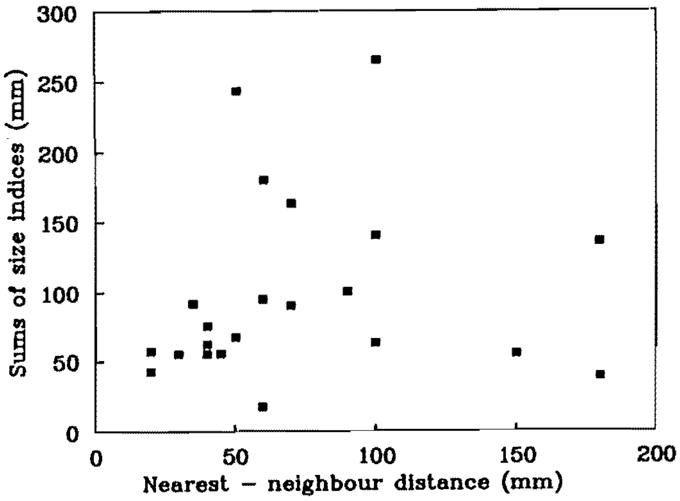

Figure 3 The relationship between the nearest - neighbour distances and the sums of the size indices of <u>Anthephora pubescens</u> and <u>Schmidtia pappophoroides</u> pairs in a natural plant community ($y = 81.6x + 0.198$; $r = 0.106$; $p < 0.05$).

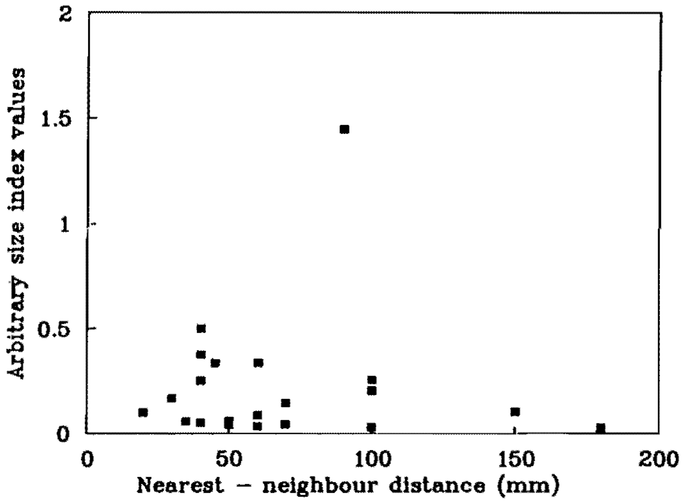

Figure 4 The relationship between the nearest - neighbour distances and the arbitrary size index values (ASIV) of <u>Anthephora pubescens</u> and <u>Schmidtia pappophoroides</u> pairs in a natural plant community ($y = 0.230x - 0.003$; $r = 0.108$; $p < 0.05$).

A. pubescens, and the poor competitive ability of A. pubescens has been illustrated by Mynhardt et al. (1992).

If one considers this reasoning to be the appropriate one, then the population surveyed must be in an early successional stage and one would expect S. pappophoroides to increase in number to the detriment of A. pubescens and become the dominant species.

If A. pubescens is, however, considered to be a decreaser in a plant community - according to Dankwert's (1989) classification of a decreaser where the species decreases in abundance when the pasture is overgrazed or undergrazed - then A. pubescens occurs later in the successional sequence. It could therefore be that A. pubescens is a strong competitor which resists invasion from other grass species. It is therefore apparent that a verdict cannot be given pertaining to the competitive ability of A. pubescens in a natural plant community based on the given results.

The reason as to why a significant relationship was not exhibited between nearest - neighbour distances and the sums of the size indices and ASIV of both intraspecific and interspecific pairs is not evident. It may be accrued to the method used in the present survey. A mature A. pubescens tuft is characterised by tissue death from the center of the tuft outwards. An originally single tuft therefore becomes divided forming separate smaller tufts with time. In the present survey the smaller tufts were considered as separate tufts and neighbours, as they form their own root system and are able to grow independently, allowing other species to establish in the areas between the small tufts. The results may therefore have been confounded due to these complexities which are prominent in a mature A. pubescens tuft.

CONCLUSIONS

It may only be concluded that competitive interactions were prevalent in the particular plant community. It must, however, be kept in mind that the results presented are from a single survey and can not be considered as representative of all natural plant communities. The method used is evidently not suitable to determine potential competitive ability in a natural plant community and should therefore be revised. Further investigation is evidently necessary, where the relationships between A. pubescens and the other dominant grass species in the particular community, must be determined before any conclusions can be made of the competitive ability of A. pubescens in a natural plant community or any management strategy be devised. Essential characteristics which determine the ecology of a species can only be determined by studying the reactions of individuals to neighbouring individuals. The behaviour of an individual in isolation may therefore be irrelevant to understanding the individuals behaviour in a community.

REFERENCES

Barbour M.G. 1973. Desert dogma re-examined: root/shoot productivity and plant spacing. Am. Midl. Nat. 89: 41-57.

Connell J.H. & Slatyer R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organisation. Am. Nat. 111: 1119-1144.

Dankwerts J.E. 1989. Plant growth and responses to defoliation. In: Dankwerts J.E. & Teague W.R. (eds). Veld management in the Eastern Cape. Government Printer, Pretoria, pp. 8-19.

Donaldson C.H., Kelk D.M. & West K.N. 1972. *Anthephora pubescens* Nees. Proc. Grassld. Soc. sth. Afr. 7: 111-116.

Fourie J.H., Du Pisani L.G. & Donaldson C.H. 1987. Fertilizer requirements and production of *Anthephora pubescens* Nees on a soil of the Mangano series in the Northern Cape. J. Grassld. Soc. South. Afr. 4: 109-112.

Gibbs Russel G.E., Watson L., Koekemoer M., Smook L., Barker N.P., Anderson H.M. & Dallwitz M.J. 1990. Grasses of Southern Africa. Gutenburg Book Printers, Pretoria West.

Harper J.L. 1977. The population biology of plants. Academic Press, London.

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992. The effect of intra - and interspecific competition on the dry matter production of *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Noble I.R. & Slatyer R.O. 1981. Concepts and models of succession in vascular plant communities subject to recurrent fire. In: Gill A.M., Groves R.H. & Noble I.R. (eds). *Fire and the Australian biota*. Australian Academy of Science, Canberra.

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Teague W.R. 1989. Responses of communities to environmental and management gradients. In: Dankwerts J.E. & Teague W.R. (eds). *Veld management in the Eastern Cape*. Government Printer, Pretoria, pp. 31-36.

Yeaton R.I. & Cody M.L. 1976. Competition and spacing in plant communities: The Northern Mohave Desert. *J. Ecol*. 64: 689-696.

CHAPTER 9

GENERAL CONCLUSIONS

i) POT TRIALS

Intraspecific competition, in which individual development is restricted due to interference from neighbours, has been studied as an agronomic problem - what is the optimal density of plants per unit area to achieve maximal dry matter production per area, or economic yield per unit area? Plants may not interfere with each other at low densities, but as density increases the growth of the population becomes limited by a shortage of environmental factors - such as light, water and nutrients - and the growth of the population becomes a function of the availability of supplies rather than the number of individuals. The effect of intra - and interspecific competition was conclusive in both species investigated. Increasing density (intraspecific competition) resulted in decreased total vegetative yield per plant. The total vegetative yield per pot initially increased and then decreased; 12 plants per pot being the optimum density yielding maximal dry matter in both _A_. _pubescens_ and _E_. _curvula_ at the third harvest date. The effect of competition intensified over the growing season, limiting the total vegetative yield per plant. Data analysis affirmed the superior competitive ability of E. curvula, in contrast to the inferior competitive ability of A. pubescens.

In a monoculture intraspecific competition intensifies the expression of small differences between individuals, while in a mixture interspecific competition exaggerates interspecific differences. The differential effects of both intra - and interspecific competition were evident; the total vegetative yield of A. pubescens was favoured in a monoculture (intraspecific competition), while that of E. curvula was favoured in a mixture (interspecific competition).

The biomass allocated to the separate vegetative plant parts remained relatively unaltered under intra - and interspecific competition. Supposed differences in the pattern of root allocation over the growing season between the two species suggest that A. pubescens and E. curvula possibly exhibit different root allocation strategies over the growing season, which may accrue for their differing competitive abilities. This supposition, however, needs to be tested. Biomass allocation to reproductive structures was absent in both species. The absence of the production of inflorescences under conditions of limited space, signifies the importance of the role played by environmental constraints - stress, on plant growth and production. According to Harper (1967) self - thinning is absent in many agronomic experiments, so that all density stress is absorbed in the plastic development of the individuals, which was applicable to E. curvula, but not A. pubescens.

It appears that under conditions of density stress not only is there a forced sharing of limited resources with a compensating plastic reduction in individual development, but that a hierarchy emerges amongst individuals in the population. This hierarchy consists of a few large individuals and a number of small individuals. The RGR of the total plant and respective plant parts, leaf production per plant, LA per plant and per leaf and LAI of A. pubescens and E. curvula was retarded by the intense competition for the limited resources that were available to both species. Intraspecific competition had a greater negative affect on the growth characteristics of E. curvula, while interspecific competition had a greater negative affect on A. pubescens. The constraints placed on the growth of the two species by density stress intensified over the growing season. Increased density resulted in possible shading and resultant competition for light. Maximal net CO_2 uptake rate per unit leaf area and the concomitant carbon assimilation was favoured under low competitive stress. Eragrostis curvula attained greater height and produced more lateral tillers than A. pubescens under both intra - and interspecific competition. The height advantage of E. curvula enhanced its interception of light energy, possibly explaining it's competitive superiority at the expense of

A. pubescens.

ii) FIELD TRIAL

According to Harper (1967) the direct consequences of density stress on a plant population are three - fold: (i) a plastic response as the individuals adjust to share limiting resources, (ii) increased mortality, and (iii) exaggeration of differences within the population which encourages a hierarchy of exploitation. The inferior competitive ability of *A. pubescens* in the pot trials was not affirmed by the field survey conducted. *Anthephora pubescens* appeared to be prevalent only in an intraspecific situation in a natural plant community. An explanation for this occurrence was, however, indecisive. The experiments of Pimental *et al*. (1965) and of Seaton & Antonovics (1967) illustrate three evolutionary solutions to the problem of inter - group competition for limited resources: (i) extinction of one group, (ii) mutual oscillating inter - group selection leading to increased stability of the mixture, and (iii) mutual divergence in behaviour leading to the avoidance of inter - group competition. Results of the field survey suggest that *A. pubescens* may follow the latter evolutionary solution, leading to virtually pure populations of *A. pubescens* in a natural plant community.

Darwin (1859) wrote: "It has been experimentally proved that if a plot of ground be sown with one species of grass, and a plot be sown with several distinct genera of grasses, a greater number of plants and a greater dry weight of herbage can be raised in the latter than in the former case." The present study conclusively supports Darwin's finding in the case of *E. curvula*, but not in the case of *A. pubescens*. It may therefore be suggested that *E. curvula* should be used for intercropping, as a management strategy, if the aim is to obtain a productive pasture. Further investigation is, however, essential pertaining to *A. pubescens*, as successful management of *A. pubescens* will only be possible once clarity is found on the reaction of this species to competitive interactions in a natural plant community.

SUMMARY

AN ECOPHYSIOLOGICAL STUDY OF TWO KEY GRASS SPECIES, ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

by

JENNIFER ELIZABETH MYNHARDT

Supervisor : Prof. G.K. Theron
Co - supervisor: Dr. Margaretha W. van Rooyen

DEPARTMENT OF BOTANY

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The objective of the study was to determine the competitive abilities of A. pubescens and E. curvula, and to examine the differential effects of both intra - and interspecific competition.

Both species investigated proved to be highly plastic in their ability to regulate their size under prevailing conditions of density stress; intra - and interspecific competitive stress. Intraspecific competition proved to have a greater negative affect on the total vegetative yield per plant and per pot of

E. curvula, while interspecific competition had a greater negative affect on the total vegetative yield of A. pubescens.

The relationship between density and the above - ground dry mass, for both species investigated, could be described by the reciprocal yield law.

Results of the competition experiments indicate that E. curvula has a clear advantage over A. pubescens. In most of the replacement series the relative yield total exceeded one, which indicates a degree of niche differentiation between species.

The detrimental effect of intra - and interspecific competition on the growth of both species was illustrated by the constraints placed on the net CO_2 uptake rate per unit leaf area and resultant retarded growth rate and restricted morphological development. In addition to the height advantage of E. curvula, resulting in improved light utilisation, the increased root system of E. curvula over the growing season may have resulted in more effective uptake at the expense of A. pubescens. A combination of these characteristics may accrue for the competitive superiority of E. curvula, in comparison to the competitive inferiority of A. pubescens. The poor competitive ability of A. pubescens under conditions of interspecific competition could, however, not be supported by the field survey conducted in a natural plant community.

OPSOMMING

'N EKOFISIOLOGIESE STUDIE VAN TWEE SLEUTEL - GRASSPESIES, *ANTHEPHORA PUBESCENS* NEES EN *ERAGROSTIS CURVULA* (SCHRAD.) NEES

deur

JENNIFER ELIZABETH MYNHARDT

Leier : Prof. G.K. Theron
Mede - leier: Dr. Margaretha W. van Rooyen

DEPARTEMENT PLANTKUNDE

MAGISTER SCIENTIAE

Die doel van die studie was om die kompeterende vermoëns van *A. pubescens* en *E. curvula* te bepaal, en om die verskeie invloede van intra - en interspesifieke kompetisie te ondersoek.

Beide spesies het 'n groot mate van plastisiteit getoon in hulle vermoë om hul grootte te reguleer onder heersende toestande van digtheidspanning; intra - sowel as interspesifieke kompetisie. In die geval van *E. curvula* het intraspesifieke kompetisie 'n groter

nadelige invloed op die totale vegetatiewe opbrengs per plant en per pot gehad, terwyl interspesifieke kompetisie 'n groter nadelige invloed op die totale vegetatiewe opbrengs van A. pubescens gehad het.

By beide spesies is 'n goeie passing tussen die bogrondse droëmassa per plant en digtheid met behulp van die resiproke opbrengswet verkry.

Resultate van die kompetisie - eksperimente het aangetoon dat E. curvula 'n duidelike kompeterende voordeel bo A. pubescens het. In die meerderheid van die vervangingsreekse was die totale relatiewe opbrengs meer as een, wat daarop dui dat daar 'n mate van nisdifferensiasie tussen die spesies voorkom.

Die nadelige invloed van intra - en interspesifieke kompetisie op die groei van beide spesies is geïllustreer deur die beperkings wat op die netto CO_2 - opnametempo per eenheid blaaroppervlakte en gevolglike vertraagde groeitempo en morfologiese ontwikkeling geplaas is. Benewens E. curvula se hoogtevoordeel, wat tot verbeterde ligverbruik gelei het, het E. curvula se wortelstelsel oor die groeiseisoen toegeneem wat moontlik gelei het tot verbeterde opname, tot die nadeel van A. pubescens. Eragrostis curvula se sterker kompeterende vermoë, in vergelyking met

A. *pubescens* se swak kompeterende vermoë, kan moontlik aan 'n kombinasie van dié kenmerke toegskryf word. *Anthephora pubescens* se swak kompeterende vermoë, onder toestande van interspesifieke kompetisie, word egter nie ondersteun deur die veldopname wat in 'n natuurlike plantgemeenskap gemaak is nie.

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REFERENCES

Akey W.C., Jurik T.W. & Dekker J. 1991. A replacement series evaluation of competition between velvetleaf (Abutilon theophrasti) and soybean (Glycine max). Weed Res. 31: 63-72.

Antonovics Janis & Levin D.A. 1980. The ecological and genetic consequences of density - dependent regulation in plants. Ann. Rev. Ecol. Syst. 11: 411-452.

Barbour M.G. 1973. Desert dogma re-examined: root/shoot productivity and plant spacing. Am. Midl. Nat. 89: 41-57.

Barbour M.G., Burk J.H. & Pitts W.D. 1980. Terrestrial plant ecology. 2nd edn. Benjamin / Cummings Publishing Inc., California, pp. 53-94.

Bazzaz F.A. & Reekie E.G. 1985. The meaning and measurement of reproductive effort in plants. In: White J. (ed.). Studies in plant demography: a Festschrift for John L. Harper. Academic Press, London, pp. 373-387.

Berendse F. 1983. Interspecific competition and niche differentiation between Plantago lanceolata and Anthoxanthum odoratum in a natural hayfield. J. Ecol. 71: 379-390.

Bergelson J. & Perry R. 1989. Interspecific competition between seeds: Relative planting date and density affect seedling emergence. Ecol. 70: 1639-1644.

Biscoe P.V., Scott R.K. & Monteith J.L. 1975. Barley and its environment. III. Carbon balance of the crop. J. appl. Ecol. 12: 269-293.

Black J.N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (Trifolium subterraneum L.) with particular reference to leaf area and the light microclimate. Aust. J. Agric. Res. 9: 299-318.

Black J.N. & Wilkinson G.N. 1963. The role of the time of emergence in determining the growth of individual plants in swards of subterranean clover (Trifolium subterraneum L.). Aust. J. Agric. Res. 14: 628-638.

Bleasdale J.K.A. 1966. Plant growth and crop yield. Ann. appl. Biol. 57: 173-182.

Bleasdale J.K.A. 1967. The relationship between the weight of a plant part and the total weight as affected by plant density. J. Hort. Sci. 42: 51-58.

Brown J.H., Davidson D.W. & Reichmann O.J. 1979. An experimental study between seed - eating rodents and ants. Amer. Zool. 19: 1129-1144.

Burnside C.A. & Bohning R.H. 1957. The effect of prolonged shading on the light saturation curves of apparent photosynthesis in sun plants. Plant Physiol. 32: 61-78.

Chandrasena J.P.N.R. & Peiris H.C.P. 1989. Studies on the biology of Panicum repens L. II. Intraspecific competition and resource - allocation. Trop. Pest Manage. 35: 316-320.

Clark D.D. & Burk J.H. 1980. Resource allocation patterns of two California - Sonoran Desert ephemerals. Oecologia (Berl.) 46: 86-91.

Colvill Kay E. & Marshall C. 1981. The patterns of growth, assimilation of $^{14}CO_2$ and distribution of ^{14}C - assimilate within vegetative plants of Lolium perenne at low and high density. Ann. appl. Biol. 99: 179-190.

Connell J.H. & Slatyer R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organisation. Am. Nat. 111: 1119-1144.

Connolly J. 1986. On difficulties with replacement series methodology in mixture experiments. J. appl. Ecol. 23: 125-137.

Dankwerts J.E. 1989. Plant growth and responses to defoliation. In: Dankwerts J.E. & Teague W.R. (eds). Veld management in the Eastern Cape. Government Printer, Pretoria, pp. 8-19.

Darwin C.R. 1859. The origin of species by means of natural selection. John Murray, London.

De Wit C.T. 1960. On competition. Versl. Landbouwkd. Onderz. 66: 1-82.

De Wit C.T. & Ennik G.C. 1958. Over concurrentie. Yearbook I.B.S., Wageningen, pp. 59-73.

De Wit C.T. & Van den Bergh J.P. 1965. Competition between herbage plants. Neth. J. Agric. Sci. 13: 212-221.

Donald C.M. 1958. The interaction of competition for light and nutrients. Aust. J. Agric. Res. 9: 421-435.

Donald C.M. 1963. Competition among crop and pasture plants. Adv. Agron. 15: 1-118.

Donaldson C.H. & Kelk D.M. 1970. An investigation of the veld problems of the Molopo area: I. Early findings. Proc. Grassld. Soc. sth. Afr. 5: 50-57.

Donaldson C.H., Kelk D.M. & West K.N. 1972. Anthephora pubescens Nees. Proc. Grassld. Soc. sth. Afr. 7: 112-116.

Elmore C.D. 1980. The paradox of no correlation between leaf photosynthetic rates and crop yields. In: Hesketh J.D. & Jones J.W. (eds). Predicting Photosynthesis for Ecosystem Models. Vol II. CRC Press, Boca Raton, FL, pp. 155-167.

Evans L.T. 1975. The physiological basis of crop yield. In: Evans L.T. (ed.). Crop physiology. Cambridge University Press, Cambridge, UK, pp. 327-335.

Field C.B., Ball T. & Berry J.A. 1989. Photosynthesis: principles and field techniques. In: Pearcy R.W., Ehleringer J.R., Mooney H.A. & Rundel P.W. (eds). Plant physiological ecology: Field methods and instrumentation. Chapman and Hall Ltd, London, pp. 209-248.

Firbank L.G. & Watkinson A.R. 1985. On the analysis of competition. J. appl. Ecol. 22: 503-517.

Fourie J.H., Du Pisani L.G. & Donaldson C.H. 1987. Fertilizer requirements and production of Anthephora pubescens Nees on a soil of the Mangano series in the Northern Cape. J. Grassld. Soc. South. Afr. 4: 109-112.

Fowler N. 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. J. Ecol. 70: 77-92.

Fowler N.L. 1984. The role of germination date, spatial arrangement, and neighbourhood effects in competitive interactions in Linum. J. Ecol. 72: 307-318.

Gadgil M. & Solbrig O.T. 1972. The concept of r - and K - selection. Evidence from wild flowers and some theoretical considerations. Am. Nat. 106: 14-31.

Gibbs Russel G.E., Watson L., Koekemoer M., Smook L., Barker N.P., Anderson H.M. & Dallwitz M.J. 1990. Grasses of Southern Africa. Gutenburg Book Printers, Pretoria West.

Good N.E. & Bell D.H. 1980. Photosynthesis, plant productivity, and crop yield. In: Carlson P.S. (ed.). The Biology of Crop productivity. Academic Press, New York, pp. 3-51.

Grime J.P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111: 1169-1194.

Hall R.L. 1974. Analysis of the nature of interference between plants of different species. I. Concepts and extension of the De Wit analysis to examine effects. Aust. J. Agric. Res. 25: 739-747.

Hall R.L. 1978. The analysis and significance of competitive interference between species. In: Wilson J.R. (ed.). Plant relations in pastures. Hedges and Bell, Australia, pp. 163-174.

Harper J.L. 1961. Approaches to the study of plant competition. Symp. Soc. Exp. Biol. 15: 1-39.

Harper J.L. 1964. The nature and consequences of interference among plants. Proc. 11th international conference on genetics, The Hague, 1963, pp. 465-481.

Harper J.L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55: 247-270.

Harper J.L. 1977. Population biology of plants. Academic Press, London.

Harper J.L. & Clatworthy J.N. 1963. The comparative biology of closely related species. VI. Analysis of the growth of *Trifolium repens* and *T. fragiferum* in pure and mixed populations. *J. Exp. Bot*. 14: 172-190.

Harper J.L. & Gajic D. 1961. Experimental studies of the mortality and plasticity of a weed. *Weed Res*. 1: 91-106.

Harper J.L. & McNaughton I.H. 1962. The comparative biology of closely related species living in the same area. VII. Interference between individuals in pure and mixed populations of *Papaver* species. *New Phytol*. 61: 175-188.

Harper J.L. & Ogden J. 1970. The reproductive strategy of higher plants. 1. The concept of strategy with special reference to *Senecio vulgaris* L. *J. Ecol*. 58: 681-698.

Hunt R. 1982. Plant growth curves. The functional approach to plant growth analysis. Edward Arnold, London, pp. 1-246.

Inouye R.S. 1980. Density - dependent germination response by seeds of desert annuals. *Oecologia* (Berl.) 46: 235-238.

Jolliffe P.A., Minjas A.N. & Runeckles V.C. 1984. A reinterpretation of yield relations in replacement series experiments. *J. appl. Ecol*. 21: 227-243.

Kays S. & Harper J.L. 1974. The regulation of plant and tiller density in a grass sward. J. Ecol. 62: 97-105.

Kelk D.M. 1972. Phosphorus and Nitrogen nutrition of seedlings of *Cenchrus ciliaris* and *Anthephora pubescens*. M.Sc. Agric. thesis, Univ. Natal, Pietermaritzburg.

Kirby E.J.M. 1967. The effect of plant density upon the growth and yield of barley. J. agric. Sci. Camb. 68: 317-324.

Kirby E.J.M. & Faris D.G. 1970. Plant population induced growth correlations in the barley plant main shoot and possible hormonal mechanisms. J. Exp. Bot. 21: 787-798.

Kirby E.J.M. & Faris D.G. 1972. The effect of plant density on tiller growth and morphology in barley. J. agric. Sci. Camb. 78: 281-288.

Kramer P.J. 1981. Carbon dioxide concentration, photosynthesis, and dry matter production. BioScience 31: 29-33.

Kvet J., Ondok J.P., Necas J. & Jarvis P.G. 1971. Methods of growth analysis. In: Sestak J., Catsky J. & Jarvis P.G. (eds). Plant photosynthetic production: Manual of methods. The Hague, Junk, pp. 343-385.

Martin M.P.L.D. & Snaydon R.W. 1982. Root and shoot interactions between barley and field beans when intercropped. J. appl. Ecol. 19: 263-272.

McGilchrist C.A. & Trenbath B.R. 1971. A revised analysis of plant competition experiments. Biometrics 27: 659-671.

Mead R. & Riley J. 1981. A review of statistical ideas relevant to intercropping research. J. Roy. Sta. A 144: 462-509.

Miller T.E. 1987. Effects of emergence time on survival and growth in an early old - field plant community. Oecologia (Berl.) 72: 272-278.

Mitchell K.J. 1953. Influence of light and temperature on the growth of ryegrass (Lolium spp.). I. Pattern of vegetative development. Physiol. Plant. 6: 21-46.

Moss D.N. 1976. Studies on increasing photosynthesis in crop plants. In: Burris R.H. & Black C.C. (eds). CO_2 Metabolism and Plant Productivity. University Park Press, Baltimore, MD, pp. 31-41.

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992a. The effect of intra - and interspecific competition on the dry matter production of *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992b. The effect of intra - and interspecific competition on the pattern of biomass allocation in *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992c. The effect of intra - and interspecific competition on the growth of *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Mynhardt Jennifer E., Theron G.K. & Van Rooyen Margaretha W. 1992d. The effect of intra - and interspecific competition on the morphological development of *Anthephora pubescens* Nees and *Eragrostis curvula* (Schrad.) Nees. *J. Grassl. Soc. South. Afr*. (Submitted).

Noble I.R. & Slatyer R.O. 1981. Concepts and models of succession in vascular plant communities subject to recurrent fire. In: Gill A.M., Groves R.H. & Noble I.R. (eds). Fire and the Australian biota. Australian Academy of Science, Canberra.

Nursey W.R.E. & Kruger A.H.G. 1973. The effect of spring mowing and burning on seed and dry matter production of Anthephora pubescens Nees. Proc. Grassld. Soc. sth. Afr. 8: 123-127.

Nyahoza F. 1973. Studies on the biology of Cyperus rotundus L. Early growth and vegetative reproduction strategy. East Afr. Agric. For. J. 39: 120-130.

Ogden J. 1974. The reproductive strategy of higher plants. 2. The reproductive strategy of Tussilago farfara L. J. Ecol. 62: 291-324.

Palmblad I.G. 1968. Competition in experimental populations of weeds with emphasis on the regulation of plant population size. Ecol. 49: 26-34.

Patterson D.T. 1982. Effects of light and temperature on weed/ crop growth and competition. In: Hatfield J.L. & Thomason I.J. (eds). Biometeorology in Integrated Pest Management. Academic Press, New York, pp. 407-420.

Patterson D.T. 1990. Effects of density and species proportion on competition between Spurred Anoda (*Anoda cristata*) and Velvetleaf (*Abutilon theophrasti*). *Weed Sci*. 38: 351-357.

Pimental D., Feinberg E.G., Wood P.W. & Hayes J.T. 1965. Selection, spatial distribution, and the coexistence of competing fly species. *Am. Nat*. 94: 97-109.

Pitelka L.F., Stanton D.S. & Peckenham M.O. 1980. Effects of light and density on resource allocation in a forest herb, *Aster acuminatus* (Compositae). *Am. J. Bot*. 67: 942-948.

Primack R.B. 1979. Reproductive effort in annual and perennial species of *Plantago* (Plantaginaceae). *Am. Nat*. 114: 51-62.

Puckridge D.W. & Donald C.M. 1967. Competition among wheat plants sown at a wide range of densities. *Aust. J. Agric. Res*. 18: 193-211.

Rayner A.A. 1969. A first course in biometry for Agriculture students. University of Natal Press, Pietermaritzburg.

Roberts B.R. & Fourie J.H. 1975. Common grasses of the Northern Cape. N.G. Sendingspers, Bloemfontein.

Robinson G.G. & Whalley R.D.B. 1991. Competition between three agronomic types of the Eragrostis curvula (Schrad.) Nees complex and three temperate pasture grasses of the Northern Tablelands of New South Wales. Aust. J. Agric. Res. 42: 309-316.

Ross M. & Harper J.L. 1972. Occupation of biological space during seedling establishment. J. Ecol. 60: 77-88.

Ryle G.J.A. 1970. Distribution patterns of assimilated ^{14}C in vegetative and reproductive shoots of Lolium perenne and L. temulentum. Ann. appl. Biol. 66: 155-167.

Sagar G.R. & Harper J.L. 1961. Controlled interference with natural populations of Plantago lanceolata, P. major and P. media. Weed Res. 1: 163-176.

Schoener T.W. 1974. Resource partitioning in ecological communities. Science 185: 27-39.

Seaton A.J.P. & Antonovics J. 1967. Population inter - relationships. I. Evolution in mixtures of Drosophila mutants. Heredity, Lond. 50: 143-154.

Shinozaki K. & Kira T. 1956. Intraspecific competition among higher plants. 7. Logistic theory of the C - D effect. J. Inst. Polytech. Osaka Cy Univ. 7: 35-72.

Singh J.S. & Coleman D.C. 1973. A technique for evaluating functional root biomass in grassland ecosystems. Can. J. Bot. 51: 1967-1970.

Smith 1983. Demography of Floerkia proserpinacoides, a forest floor annual. 1. Density - dependent growth and mortality. J. Ecol. 71: 391-404.

Taylor D.R. & Aarssen L.W. 1989. On the density dependence of replacement series competition experiments. J. Ecol. 77: 975-988.

Teague W.R. 1989. Responses of communities to environmental and management gradients. In: Dankwerts J.E. & Teague W.R. (eds). Veld management in the Eastern Cape. Government Printer, Pretoria, pp. 31-36.

Thomas N. & Steppler H.A. 1971. A density yield relationship in Phleum pratense L. and Dactylis glomerata L. J. Br. Grassld. Soc. 26: 143-144.

Tow P.G., Ennik G.C. & De Wit C.T. 1966. Competition between legumes and grasses. *Agric. Res. Rep*. 687: 1-30.

Trenbath B.R. 1974. Biomass productivity of mixtures. *Adv. in Agron*. 26: 177-210.

Tripathi R.S. & Harper J.L. 1973. The comparative biology of *Agropyron repens* (L.) Beauv. and *A*. *caninum* (L.) Beauv. I. The growth of mixed populations established from tillers and seeds. *J. Ecol*. 61: 353-368.

Van Rooyen Margaretha W. 1988. Ekofisiologiese studies van die efemere van Namakwaland. PhD. dissertation, University of Pretoria, Pretoria.

Weiner J. & Thomas S.C. 1986. Size variability and competition in plant monocultures. *Oikos* 47: 211-222.

White J. & Harper J.L. 1970. Correlated changes in plant size and number in plant populations. *J. Ecol*. 58: 467-485.

Williams R.D., Quimby P.C. & Frick K.E. 1977. Intraspecific competition of Purple Nutsedge (*Cyperus* *rotundus*) under greenhouse conditions. *Weed Sci*. 25: 477-481.

Wilson J.B. 1988. Shoot competition and root competition. J. appl. Ecol. 25: 279-296.

Yeaton R.I. & Cody M.L. 1976. Competition and spacing in plant communities: The Northern Mohave Desert. J. Ecol. 64: 689-696.

Yoda K., Kira T., Ogawa H. & Hozumi H. 1963. Intraspecific competition among higher plants. XI. Self - thinning in overcrowded pure stands under cultivated and natural conditions. J. Inst. Polytech. Osaka Cy Univ. Ser. D. 14: 107-129.