CHAPTER 3

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

Jennifer E. Mynhardt
Grassland Research Centre, P/Bag X 05, Lynn East, 0039,
Republic of South Africa

G.K. Theron & Margaretha W. van Rooyen
Department of Botany, University of Pretoria, Pretoria, 0002,
Republic of South Africa

Submitted to: Journal of the Grassland Society of southern Africa

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^{o} 28" E; 25^{o} 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).

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

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).

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

Jolliffe _et_ _al_. (1984) calculated various indices :

Let Y_p = projected yield

Y_m = monoculture yield

Y_x = mixture yield

$$Y_p - Y_m = \text{species monoculture reaction}$$

$$(Y_p - Y_m)/Y_p = \text{relative monoculture reaction}$$

$$Y_m - Y_x = \text{species mixture reaction}$$

$$(Y_m - Y_x)/Y_m = \text{relative mixture reaction}$$

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

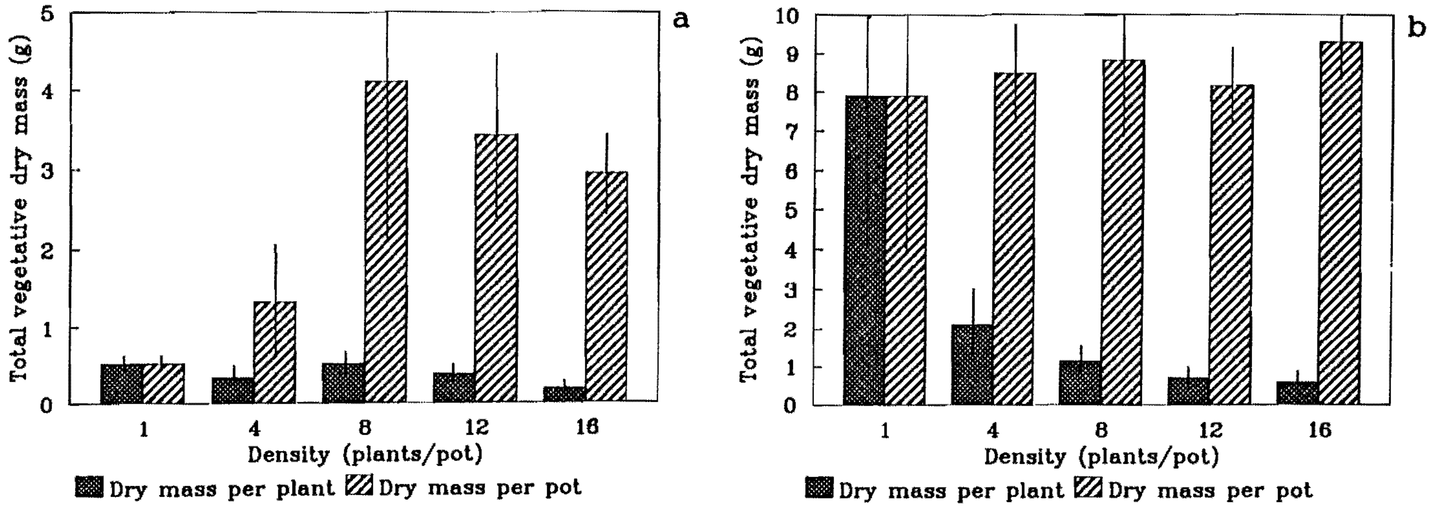
p = density

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.



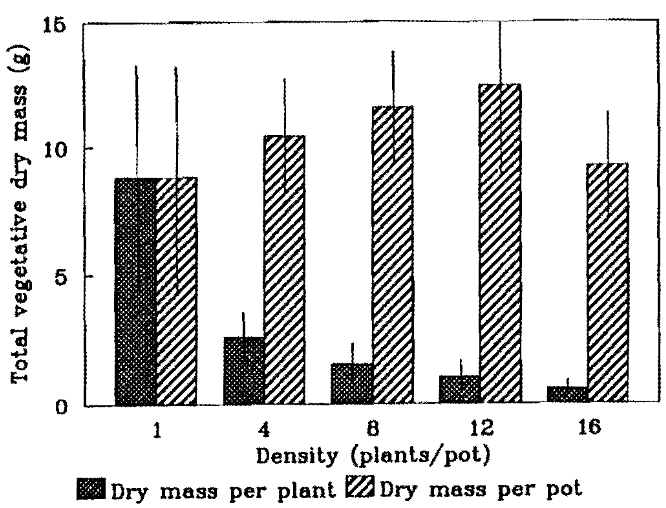


Figure 1 The effect of density on the total vegetative dry mass per plant and per pot of <u>Anthephora</u> <u>pubescens</u> at the (a) first (b) second and (c) third monthly harvests.

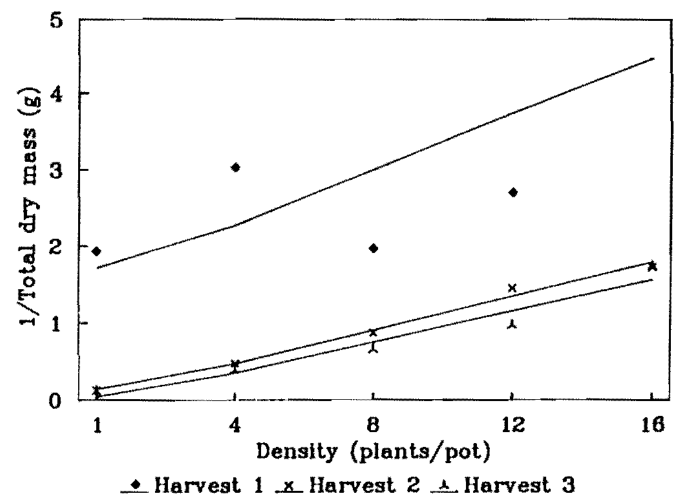
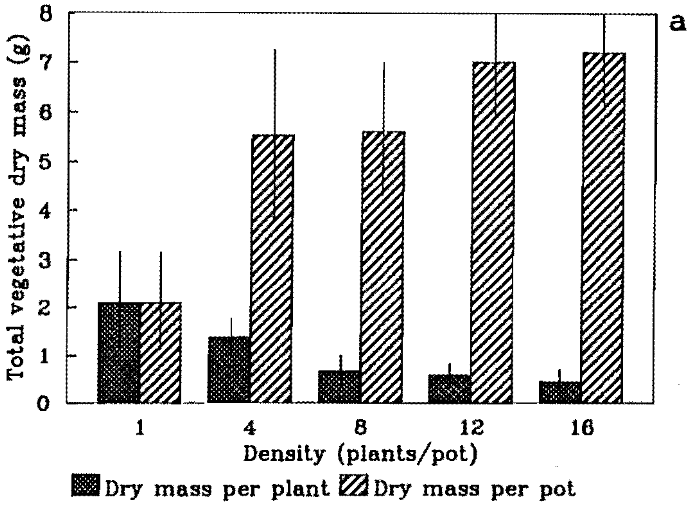


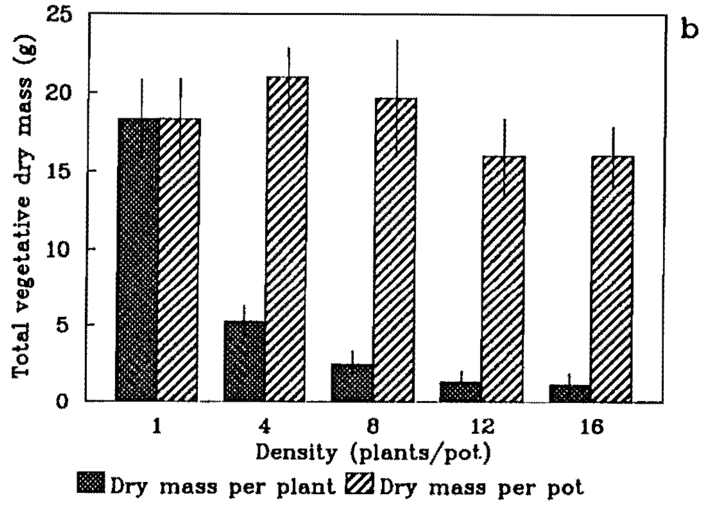
Figure 2 A regression between density and the inverse of the total vegetative dry mass of <u>Anthephora</u> <u>pubescens</u> at all three monthly harvests (harvest 1: y = 0; 0.183x + 1.525; r = 0.553; harvest 2: y = 0; 0.109x + 0.029; r = 0.990; harvest 3: y = 0; 0.101x - 0.058; r = 0.947).

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.





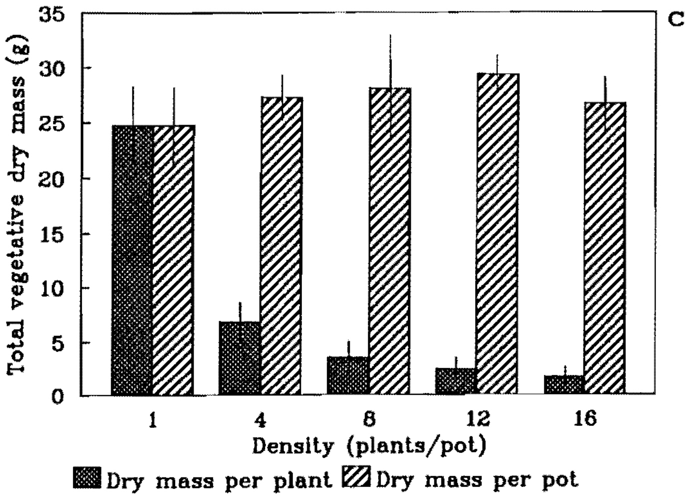


Figure 3 The effect of density on the total vegetative dry mass per plant and per pot of Eragrostis curvula at the (a) first (b) second and (c) third monthly harvests.

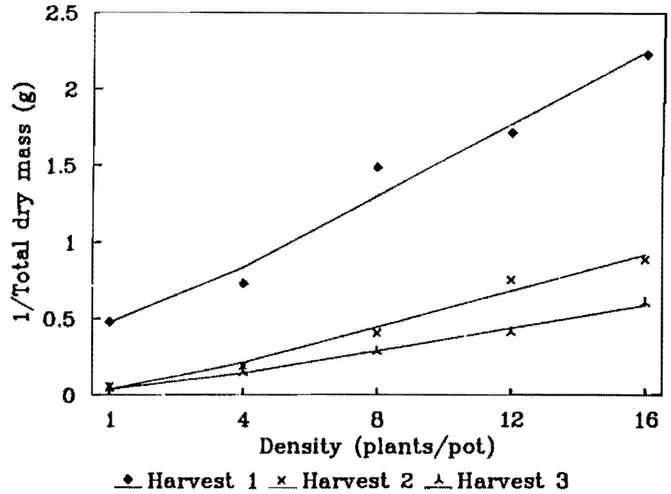


Figure 4 A regression between density and the inverse of the total vegetative dry mass of Eragrostis curvula at all three monthly harvests (harvest 1: y = 0; 0.117x + 0.358; r = 0.976; harvest 2: y = 0; 0.058x + 0.021; r = 0.983; harvest 3: y = 0; 0.036x - 0.002; r = 0.994).

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*.

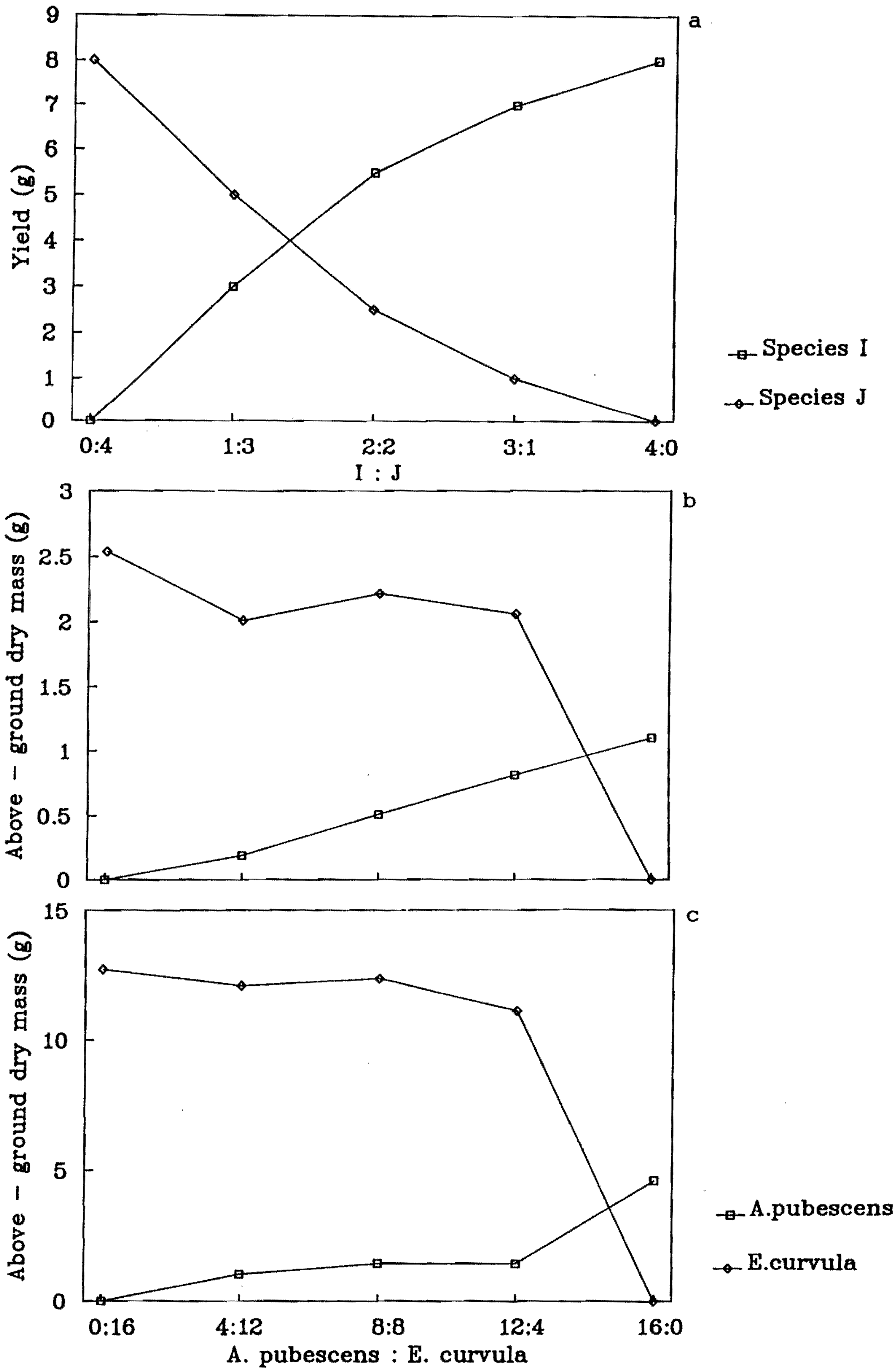


Figure 5 (a) A schematic representation of the relationship between density and yield in a replacement series (De Wit 1960) (b) the effect of competition on the above - ground yield of Anthephora pubescens and Eragrostis curvula in a replacement series at the first and (c) third monthly harvests.

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 Anthephora pubescens (AP) and Eragrostis curvula (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 Anthephora pubescens (AP) and Eragrostis curvula (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

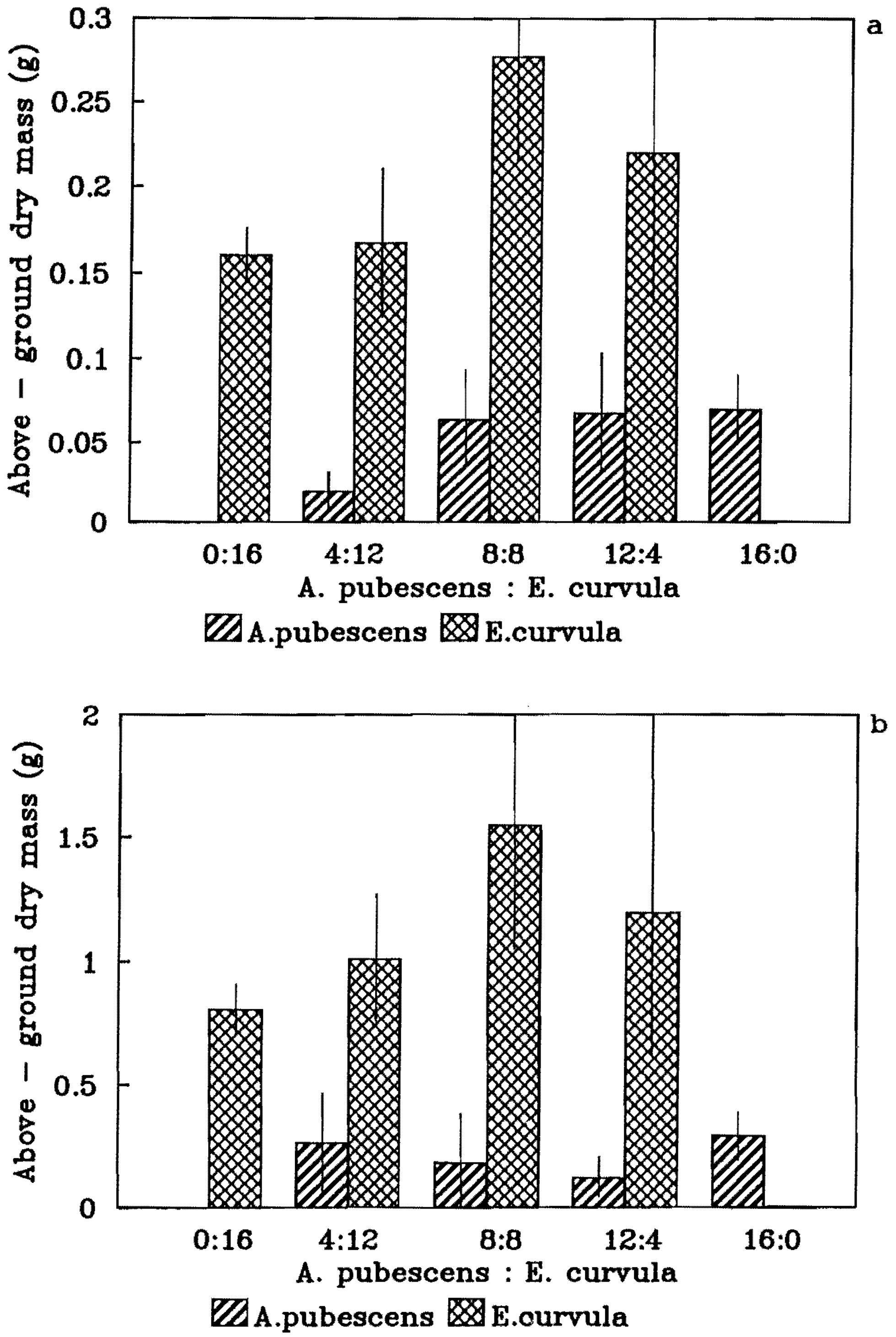


Figure 6 The effect of competition on the above - ground dry mass per plant of Anthephora pubescens and Eragrostis curvula in a replacement series at the (a) first and (b) third monthly harvests.

$K_{ij} \times K_{ji} < 1.0$ 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.

ACKNOWLEDGEMENTS

We wish to thank Carel Moolman and Frans Mashabala for technical assistance as well as the Grassland Research Centre for financial support and provision of facilities.

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.