

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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Submitted to: Journal of the Grassland Society of southern Africa

Antheophora 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.

Antheophora 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 & Stepler (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, Antheophora 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 Anthehora 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

Anthehora 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

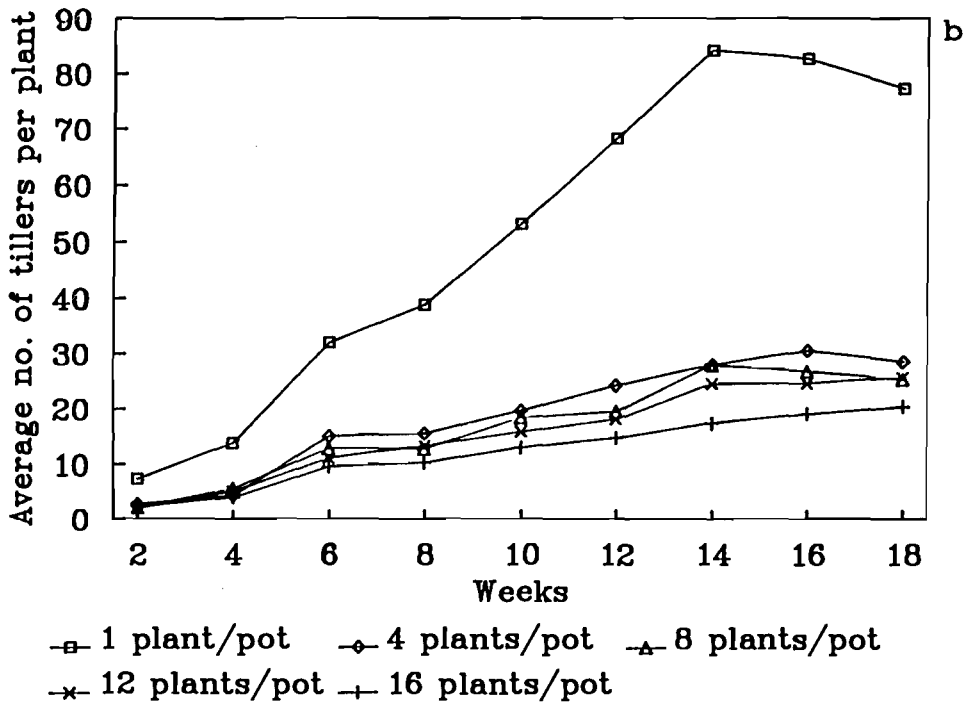
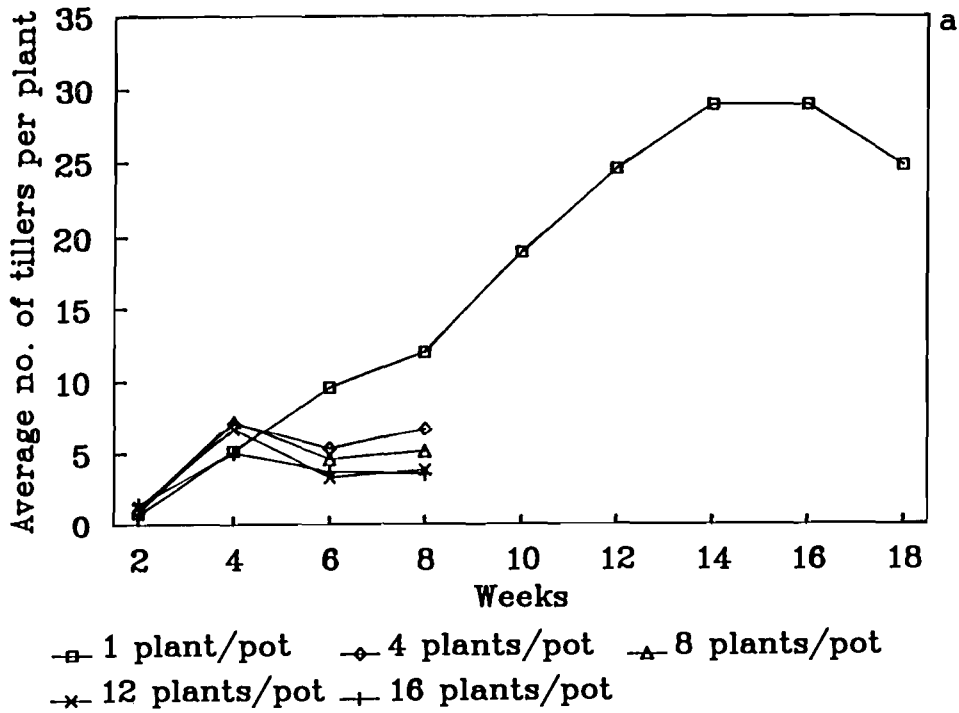


Figure 1 The effect of various densities on the average lateral tiller production of (a) *Anthephora pubescens* and (b) *Eragrostis curvula* over the growing season.

($p < 0.05$). 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). Antheophora 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

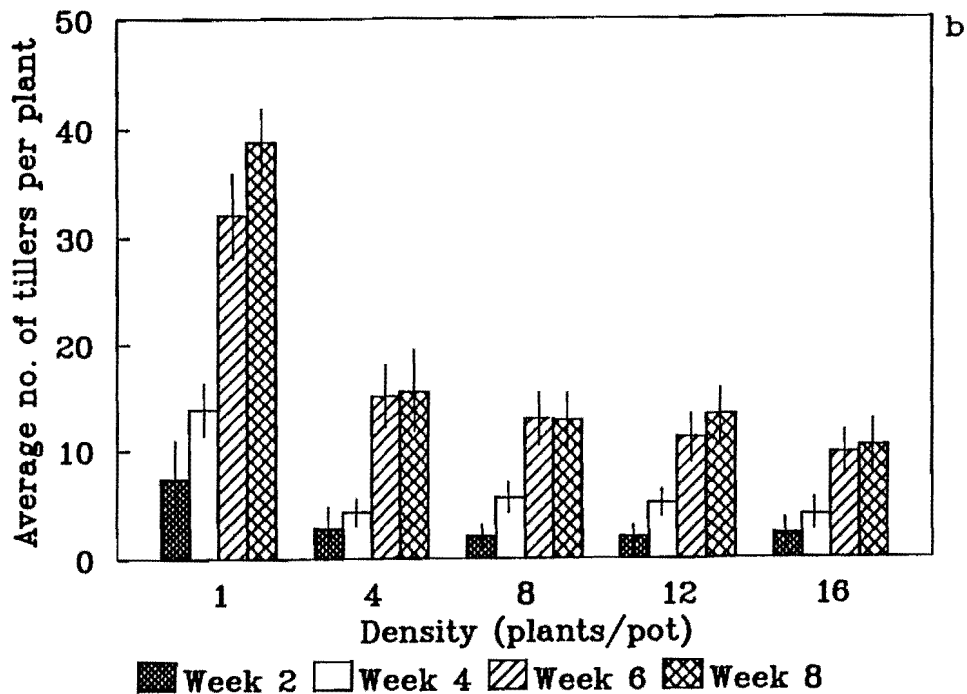
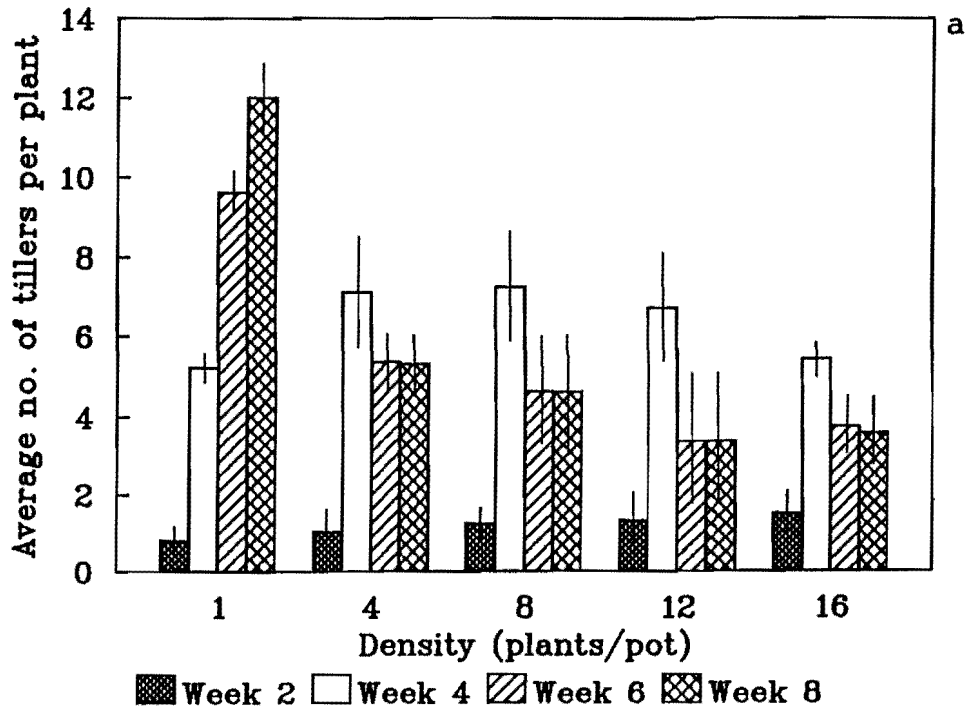


Figure 2 The effect of increasing density on the average lateral tiller production of (a) *Anthephora pubescens* and (b) *Eragrostis curvula* over the growing season.

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

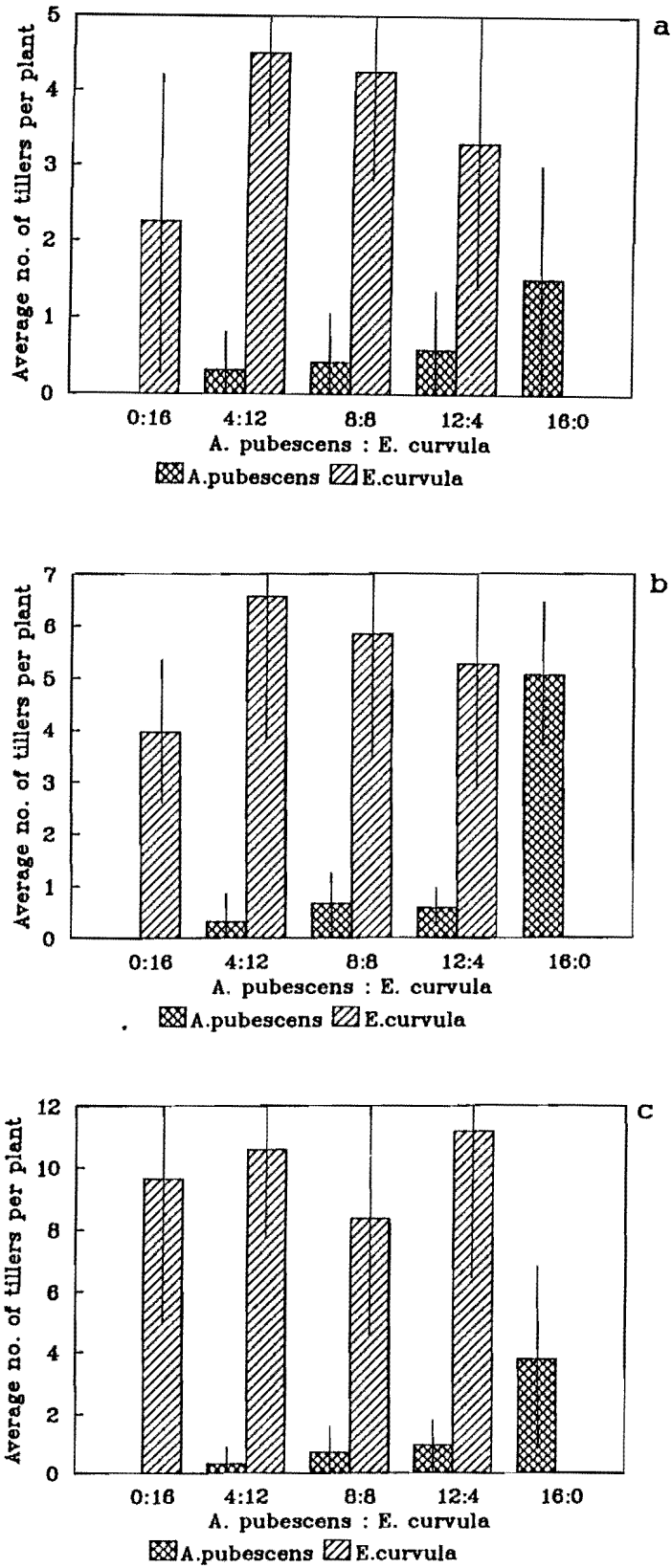


Figure 3 The effect of competition on the average lateral tiller production of *Anthephora pubescens* and *Eragrostis curvula* in the (a) second (b) fourth and (c) sixth week of monitoring.

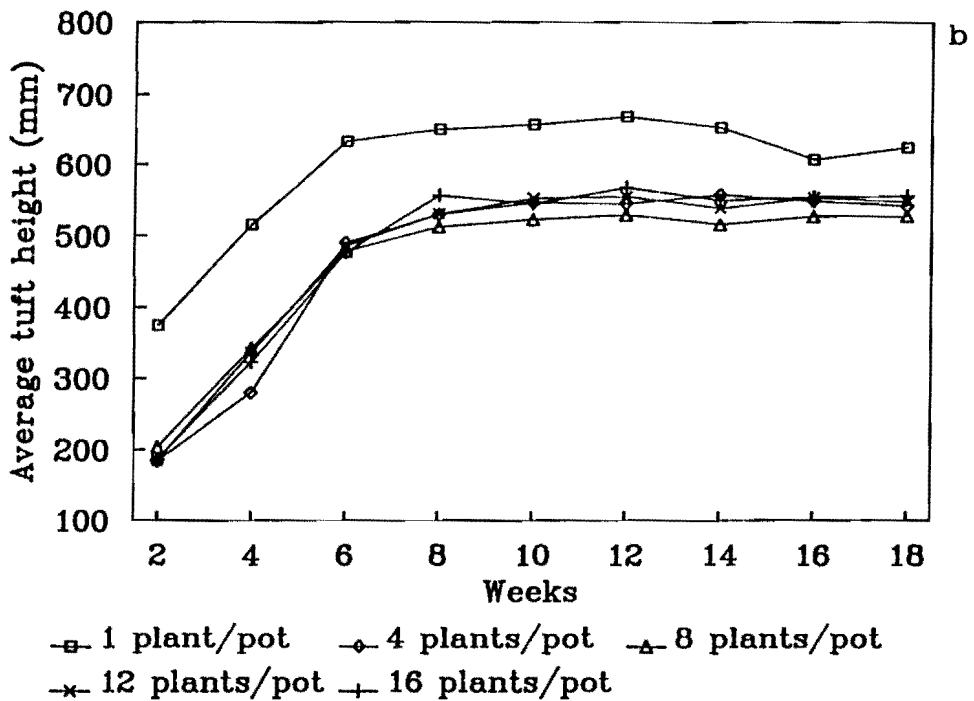
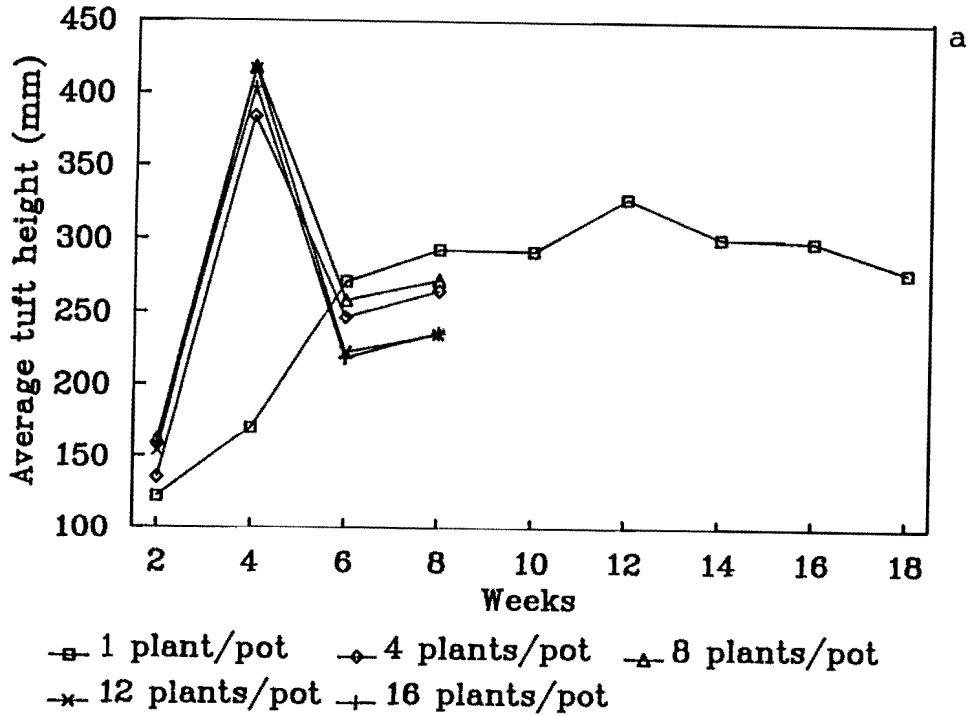


Figure 4 The effect of various densities on the average tuft height of (a) *Anthephora pubescens* and (b) *Eragrostis curvula* over the growing season.

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.

Anthehora 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

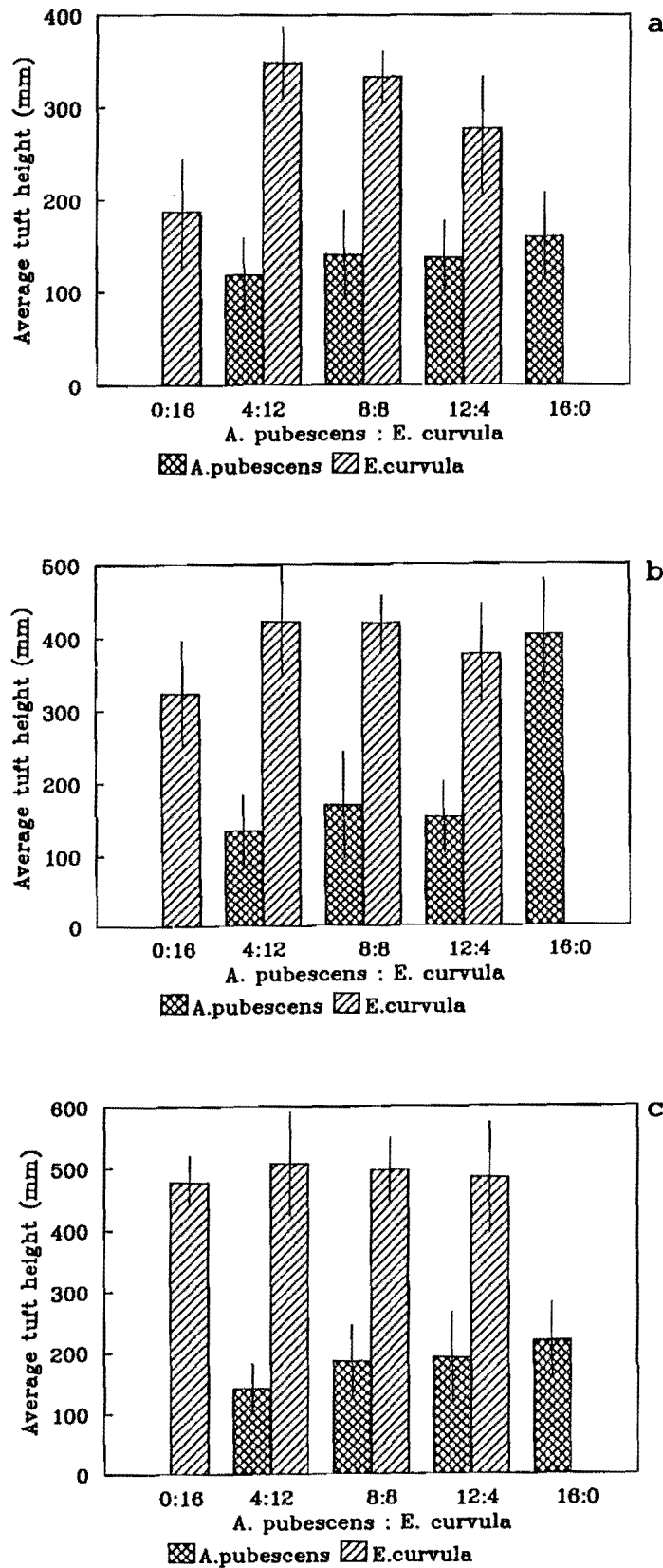


Figure 5 The effect of competition on the average tuft height of *Anthephora pubescens* and *Eragrostis curvula* in the (a) second (b) fourth and (c) sixth week of monitoring.

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.

ACKNOWLEDGEMENTS

We wish to thank Marie Smith for statistical assistance, Carel Moolman for technical assistance and the Grassland Research Centre for financial support and provision of facilities.

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