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

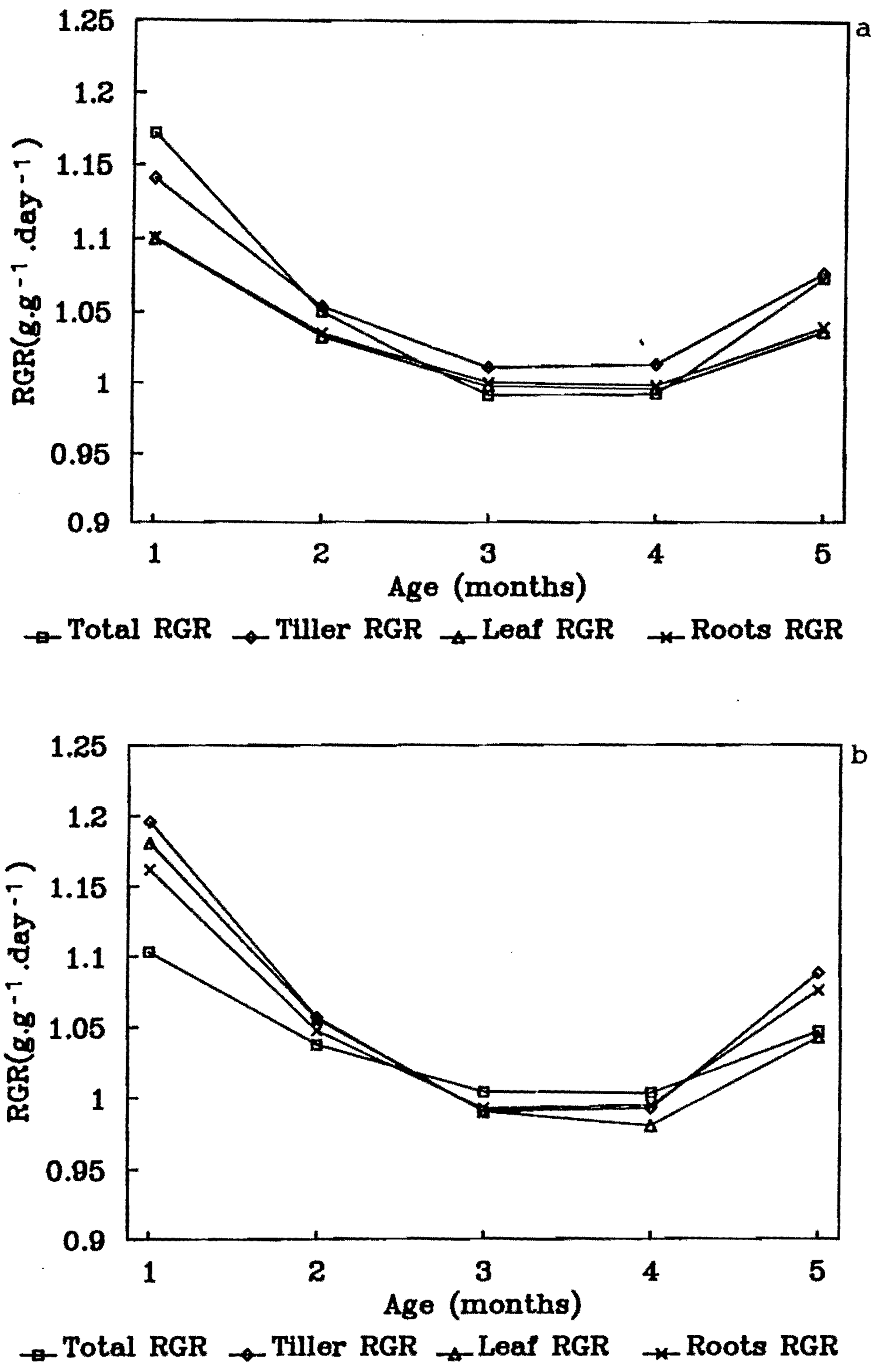

Figure 1 The relative growth rate (RGR) of the whole plant and the respective plant parts of <u>Anthephora pubescens</u> over the growing season at a (a) one - and (b) four - plants per pot density.

(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

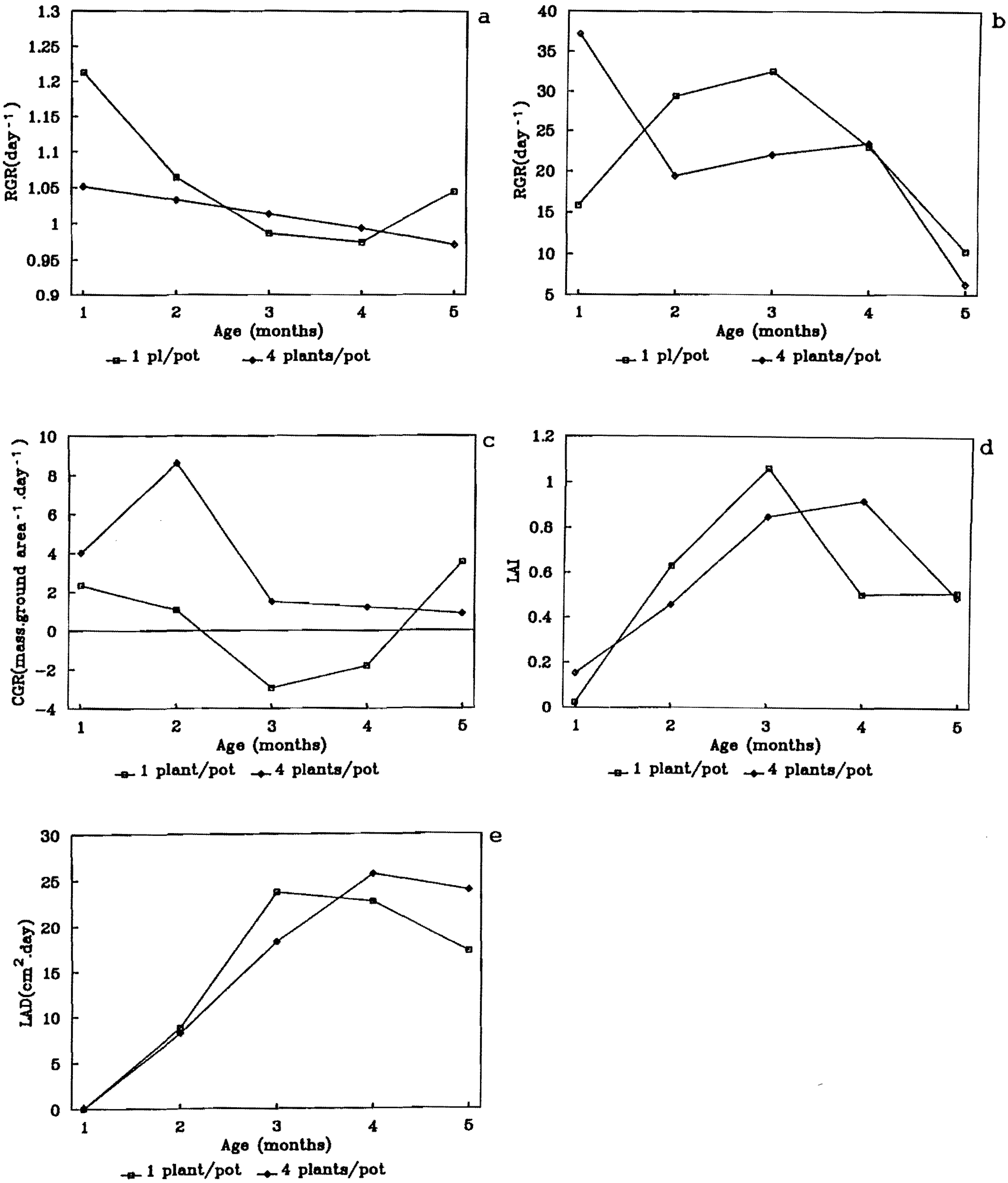

Figure 2 The relative growth rate (RGR) of the (a) leaf area (LA) and (b) leaf area ratio (LAR) of Anthephora pubescens at a one - and four - plants per pot density as well as the (c) crop growth rate (CGR) (d) leaf area index and (e) leaf area duration (LAD) over the growing season.

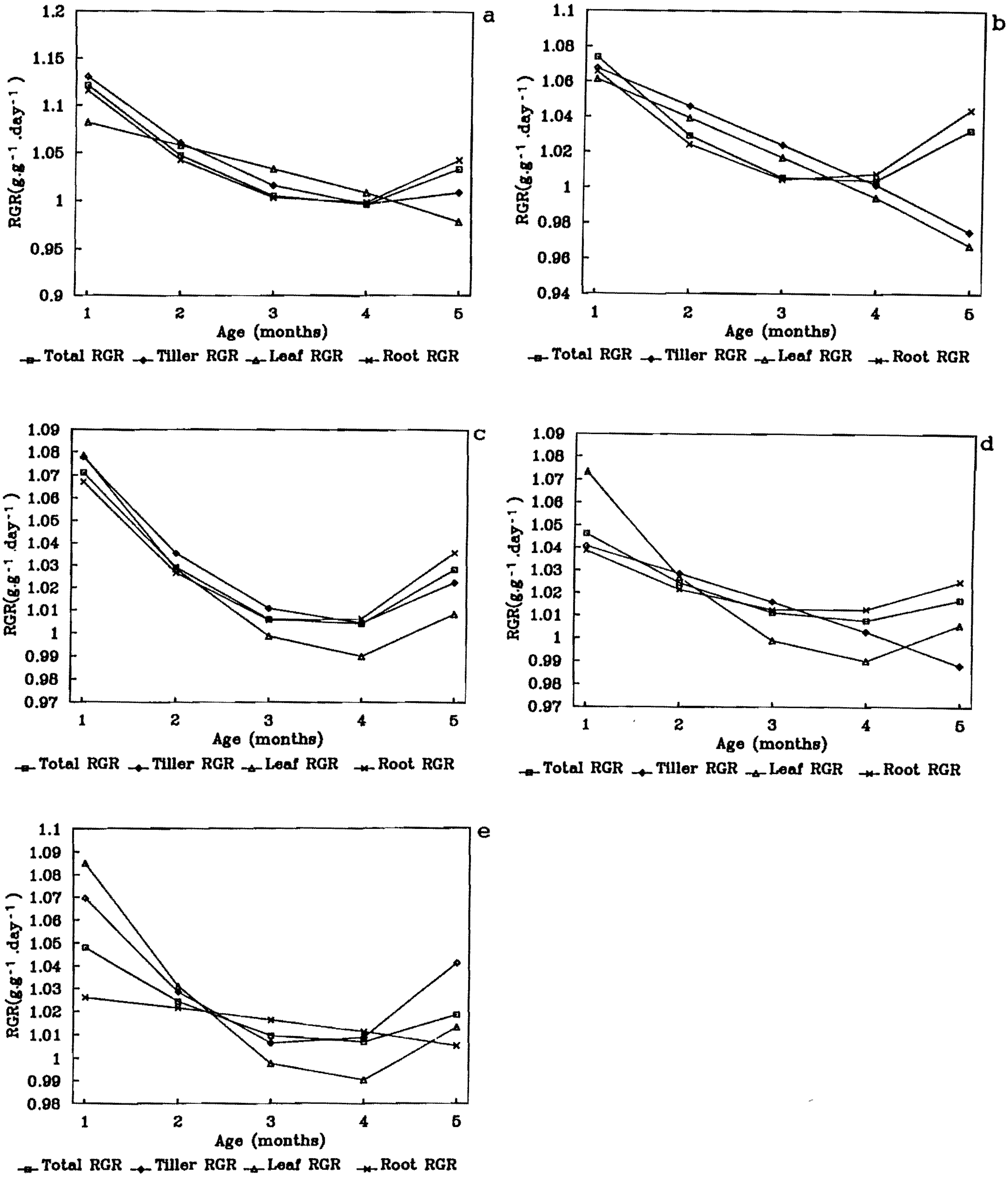

Figure 3 The relative growth rate (RGR) of the whole plant and the respective plant parts of Eragrostis curvula over the growing season at a (a) one - (b) four - (c) eight - (d) twelve - and (e) sixteen - plants per pot density.

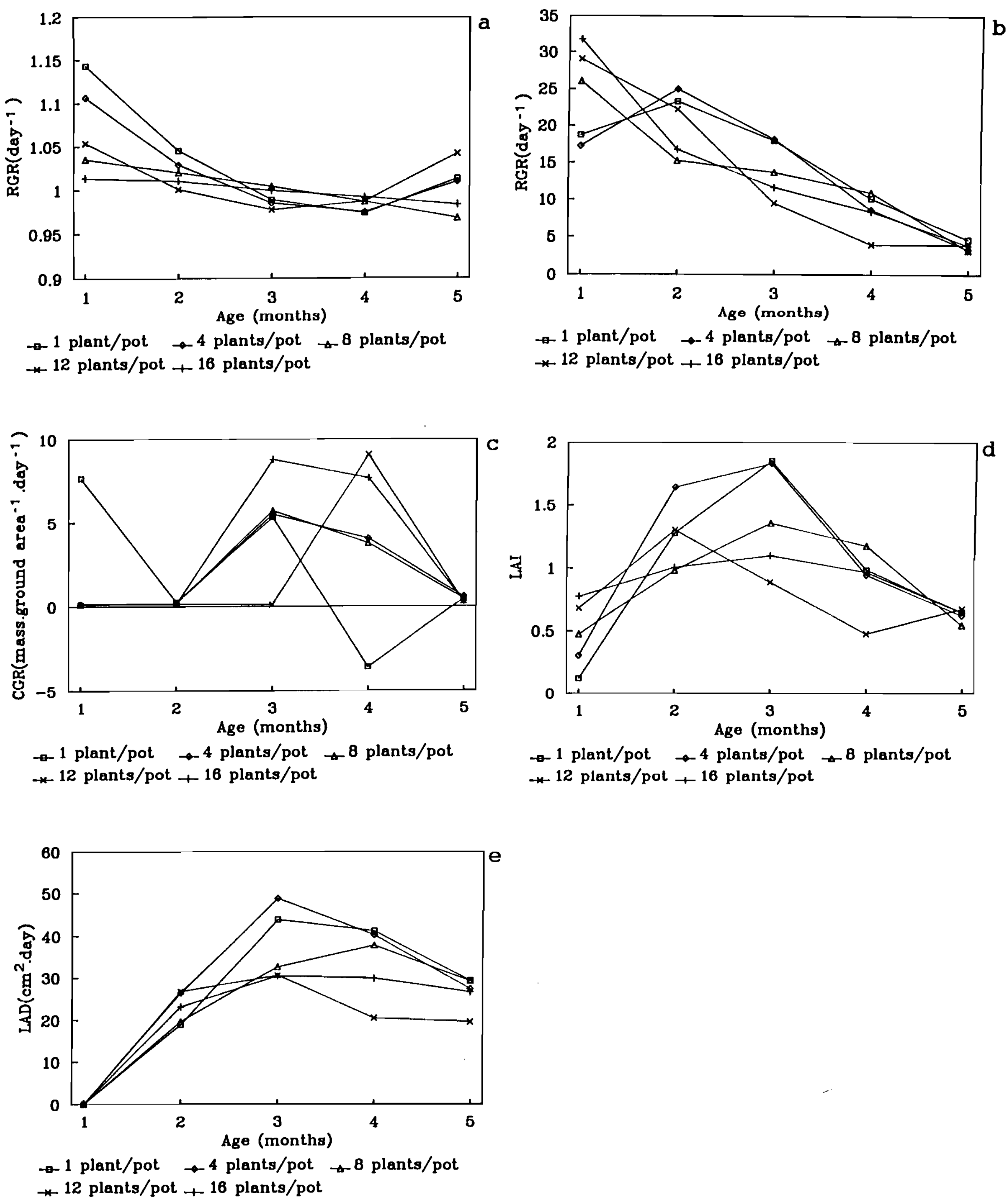

Figure 4 The relative growth rate (RGR) of the (a) leaf area (LA) and (b) leaf area ratio (LAR) of <u>Eragrostis</u> <u>curvula</u> at varying densities as well as the (c) crop growth rate (CGR) (d) leaf area index (LAI) and (e) leaf area duration (LAD) over the growing season.

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

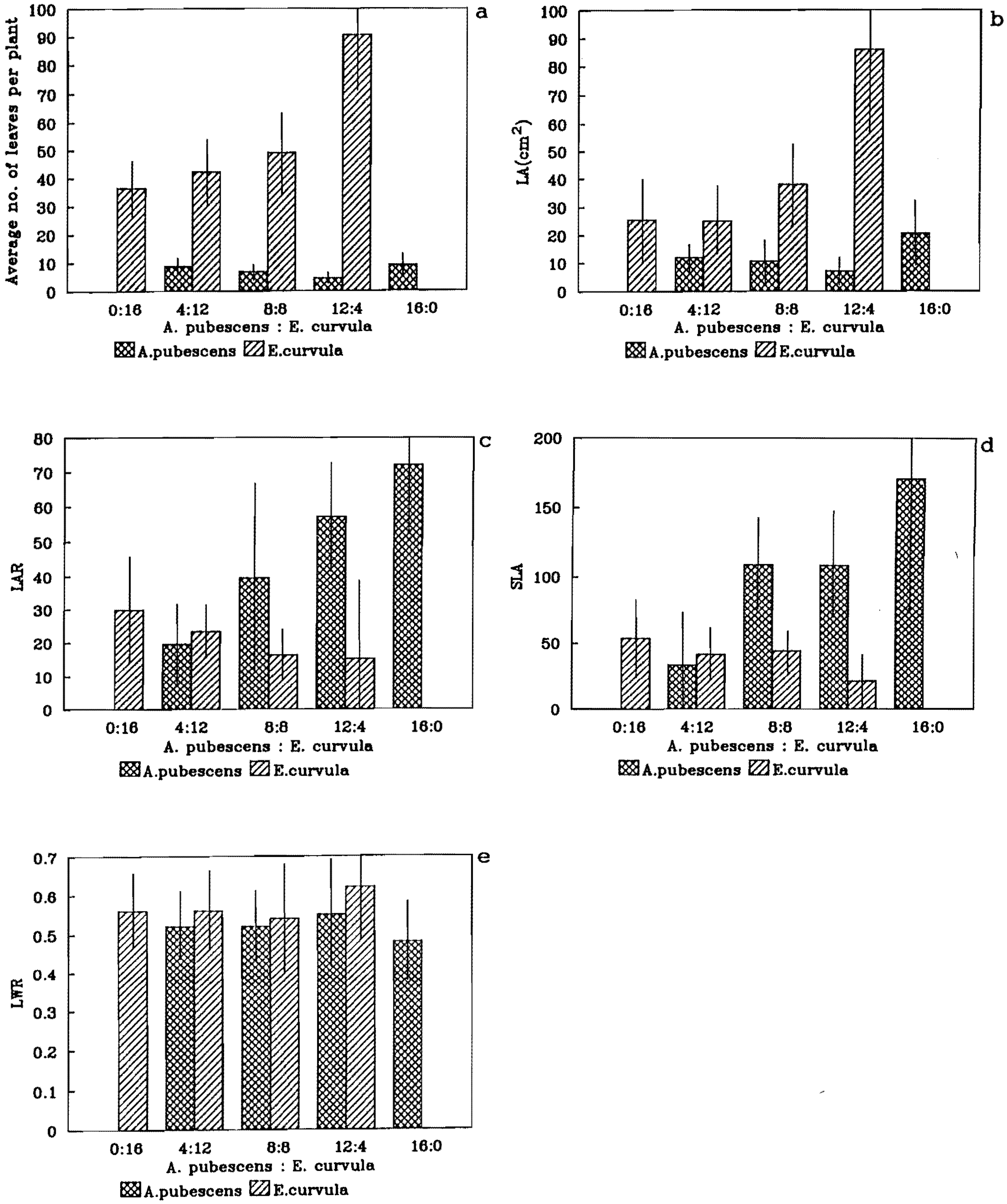

Figure 5 The effect of competition on the (a) average number of leaves per plant (b) leaf area per plant (LA) (c) leaf area ratio (LAR) (d) specific leaf area (SLA) and (e) leaf weight ratio (LWR) of <u>Anthephora pubescens</u> and <u>Eragrostis curvula</u> in a replacement series at the third monthly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