



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 Antheophora 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 Anthehora 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 reprodktiewe 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 its 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 its 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 today's 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, Anthehora pubescens Nees and Eragrostis curvula (Schrad.) Nees. Anthehora 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. Anthehora 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° 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 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

Anthehora 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

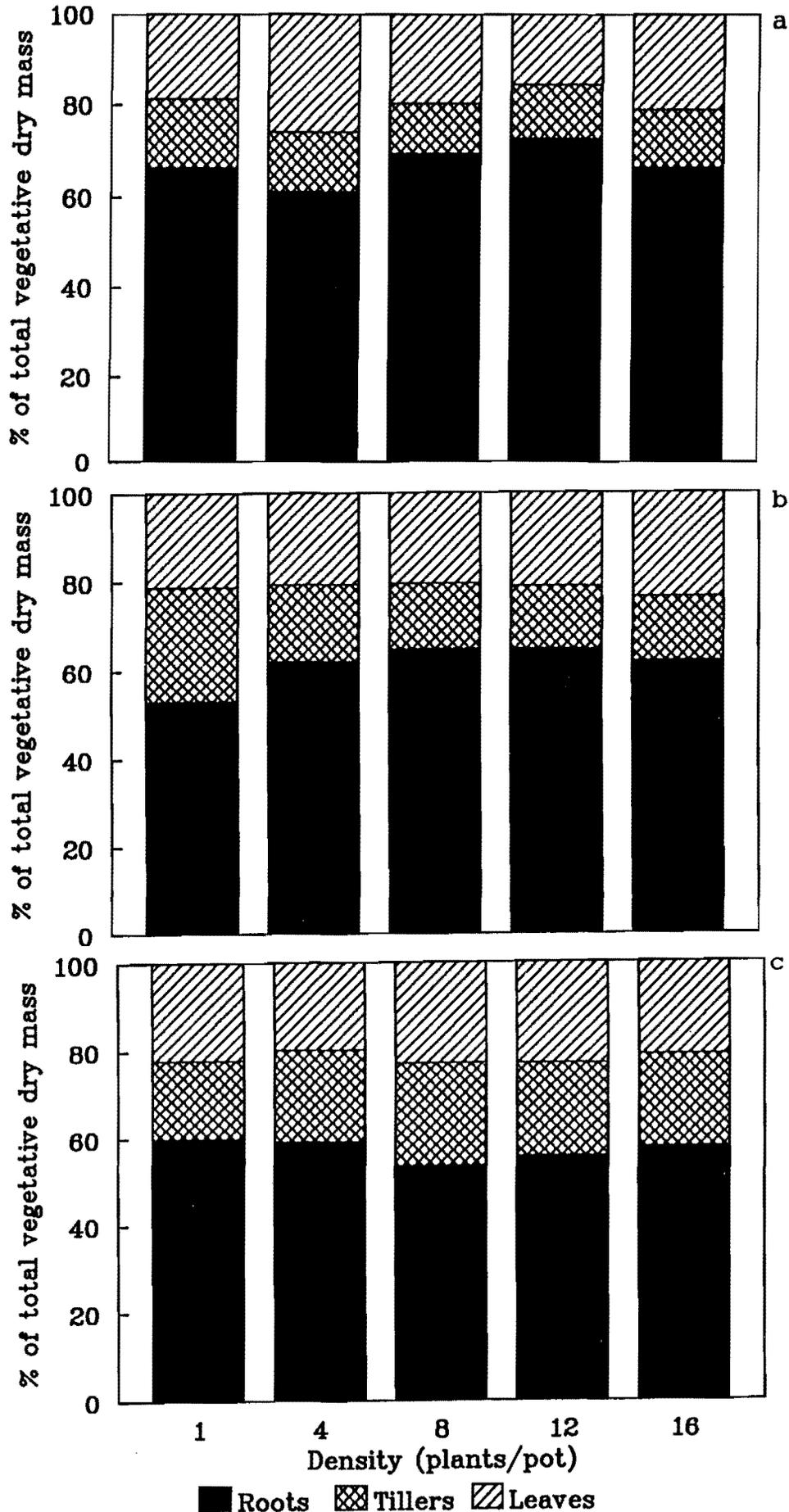


Figure 1 The effect of intraspecific competition on the percentage biomass allocation to vegetative structures of *Anthephora pubescens* at the (a) first (b) second and (c) third monthly harvest.

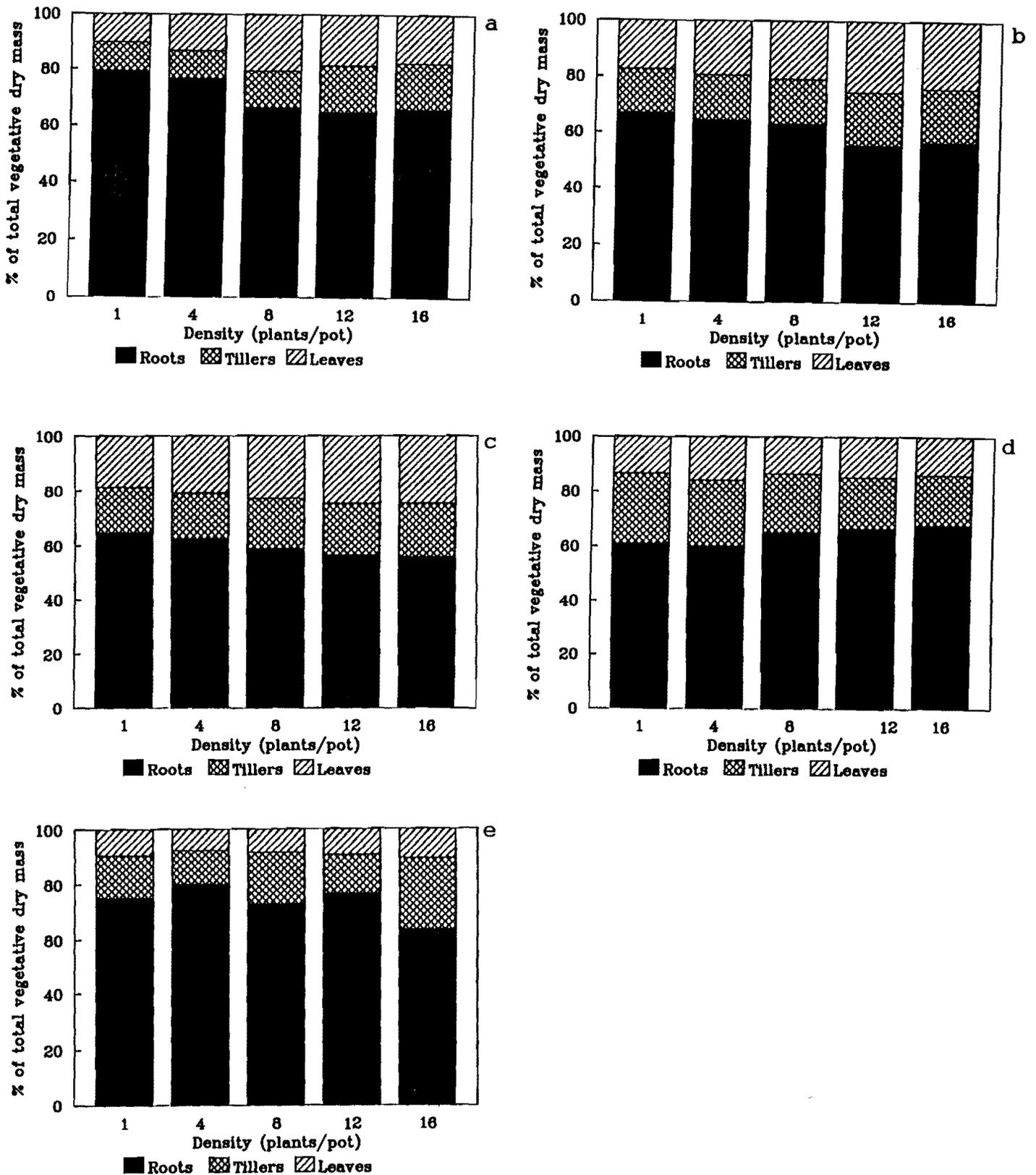


Figure 2 The effect of intraspecific competition on the percentage biomass allocation to vegetative structures of *Eragrostis curvula* at the (a) first (b) second (c) third (d) fourth and (e) fifth monthly harvest.

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 effect 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 Anthehora pubescens and Eragrostis curvula for each monthly harvest

Harvest	Roots		Tillers		Leaves	
	a*	r ²	a*	r ²	a*	r ²
<u>Anthehora pubescens</u>						
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
<u>Eragrostis curvula</u>						
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**Anthehora 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

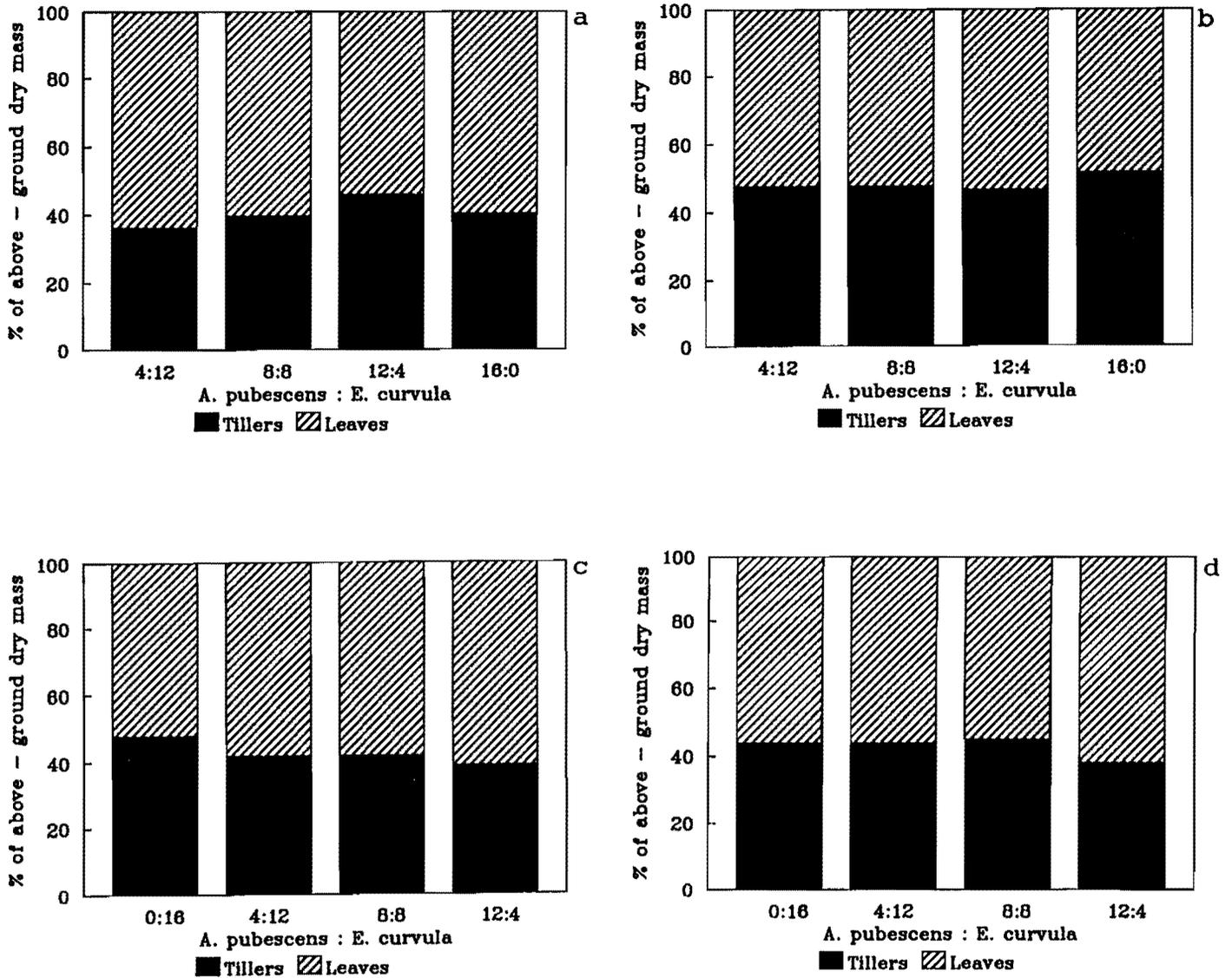


Figure 3 The effect of interspecific competition on the percentage biomass allocation to vegetative structures of (a) *Anthephora pubescens* at the first and (b) third monthly harvest (c) *Eragrostis curvula* at the first and (d) third monthly harvest in a replacement series.

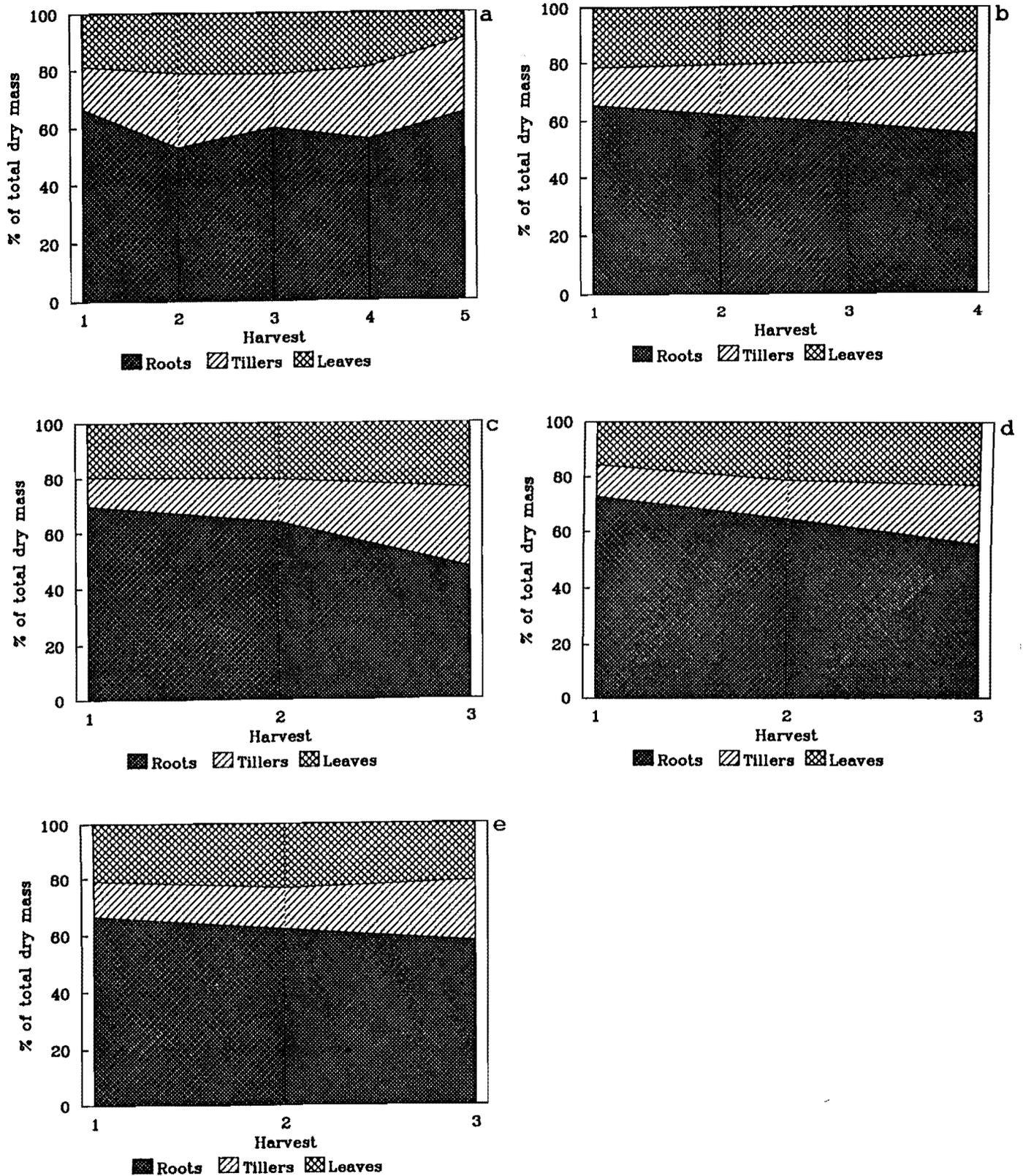


Figure 4 The biomass allocation of *Anthephora pubescens* to vegetative structures over the growing season at a (a) one - (b) four - (c) eight - (d) twelve - and (e) sixteen - plants per pot density.

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.

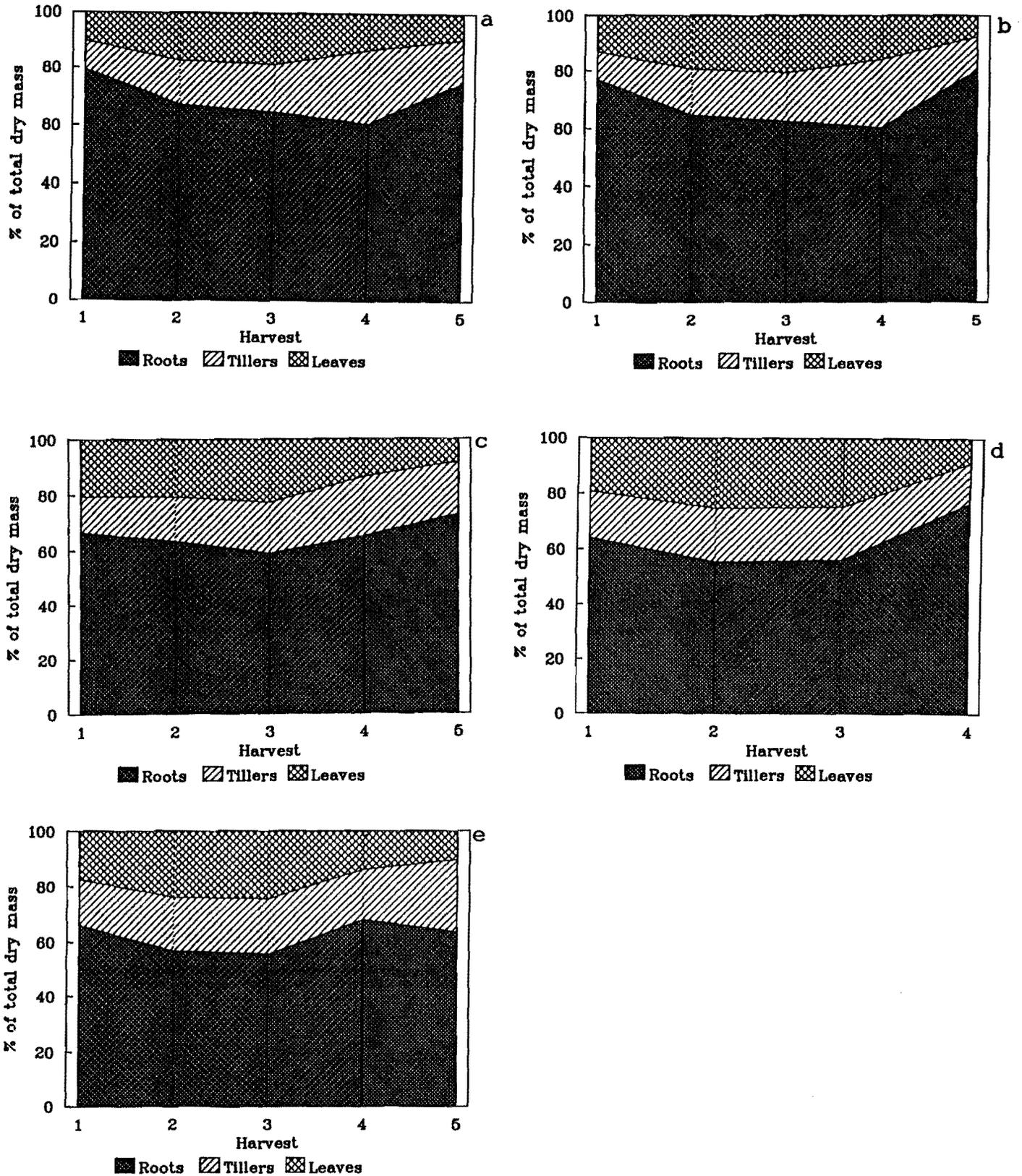


Figure 5 The biomass allocation of *Eragrostis curvula* to vegetative structures over the growing season at a (a) one - (b) four - (c) eight - (d) twelve - and (e) sixteen - plants per pot density.

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 than 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 effect 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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