

CHAPTER 7

THE EFFECT OF INTRASPECIFIC COMPETITION ON THE NET CO₂ UPTAKE OF
ANTHEPHORA PUBESCENS NEES AND ERAGROSTIS CURVULA (SCHRAD.) NEES

INTRODUCTION

Plants of the same species or of different species differ in their ability to draw their requirements from the environment or their requirements differ, resulting in differences in their ability to survive periods of stress. Two plants compete with each other when demand exceeds supply, i.e. when such factors as water supply, nutrient supply, oxygen, CO₂, light and heat become limiting. Harper (1964) did, however, point out that competition itself is only one facet of interference between plants, although at times it may be a dominating one. In the case where light is the limiting factor, certain plants may be photosynthetically or morphologically better adapted than other plants to intercept sufficient light. Plants which are not as well adapted may be denied their light energy requirements by more competitive neighbours and therefore grow slower than what they would have in the absence of competition. It is generally accepted that the more similar the needs of the two organisms, the more intense the contest.

Most of the radiation intercepted by a field crop is absorbed by leaf laminae. The architecture of the leaf canopy is therefore fundamental to light interception by plants. Competition for light is unique as there is no common pool from which plants continue to draw their supplies until it is depleted. Incoming light energy is instantaneously available, it must be used or be lost. According to Donald (1963) competition for light may occur whenever one plant casts a shadow on another or when one leaf shades another. Physical and dependent physiological variables must be measured in order to understand the interaction between the environment and a crop. The separation of the complex physiological system of grasses into components which respond to discrete elements of the physical environment is, however, not simple. There are several techniques which can be used to assess the influence of the environment on CO₂ uptake. One of these involves the use of infra - red gas analysis to determine the influence of an environmental factor on the net uptake of carbon dioxide by the crop (Biscoe et al. 1975). Another is the use of ¹⁴CO₂ to examine the influence of the environment on the distribution of labelled assimilates between the different growth centres of the crop (Ryle 1970; Singh & Coleman 1973).

The aim of this study was to examine the influence of intraspecific competition, on the net uptake of carbon dioxide by two key grass species, Antheophora pubescens Nees and Eragrostis curvula (Schrad.) Nees. It has been demonstrated in a previous investigation that competition had a significant affect on the

yield of the respective species (Mynhardt et al. 1992), and it would therefore be interesting to determine whether intraspecific competition also affected the rate of photosynthesis.

MATERIALS AND METHODS

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

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

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

RESULTS AND DISCUSSION

The effect of changing density on net rate of CO₂ uptake per unit leaf area of *A. pubescens* is represented in Figure 1a. The net CO₂ uptake rate per unit leaf area increased and then decreased; peaking at 4 plants per pot. The net CO₂ uptake rate per unit leaf area of 4 plants per pot was significantly higher than that of the other densities ($p < 0.05$). The effect of increasing density on stomatal conductance and stomatal resistance is represented in Figure 1b. It was evident that when stomatal conductance was highest and stomatal resistance was lowest, optimum CO₂ uptake occurred. The optimum net CO₂ uptake rate per unit leaf area at a density of 4 plants per pot did not correspond with an optimum in leaf production per plant, leaf area (LA) per plant or per leaf, leaf area index (LAI) or yield per pot at that density (Table 1). The calculated net CO₂ uptake

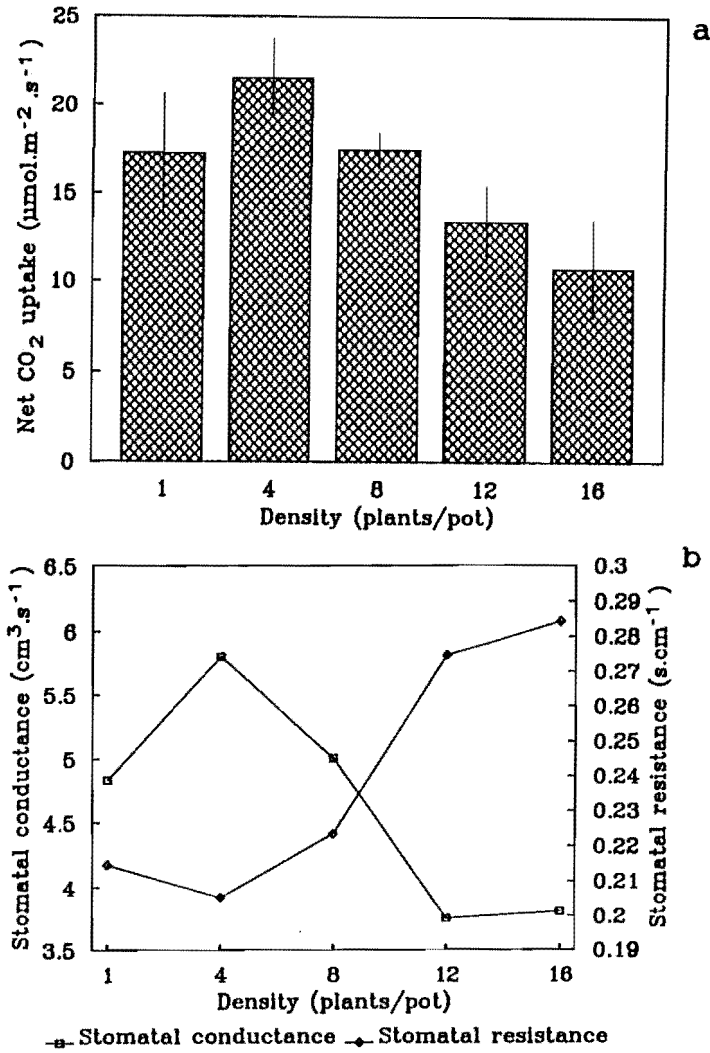


Figure 1 The effect of intraspecific competition on (a) the net CO₂ uptake rate per unit leaf area (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 1 8 4) and (b) the stomatal conductance and stomatal resistance of *Anthephora pubescens* at the third monthly harvest (stomatal conductance: 12 16 1 8 4; stomatal resistance: 4 1 8 12 16).

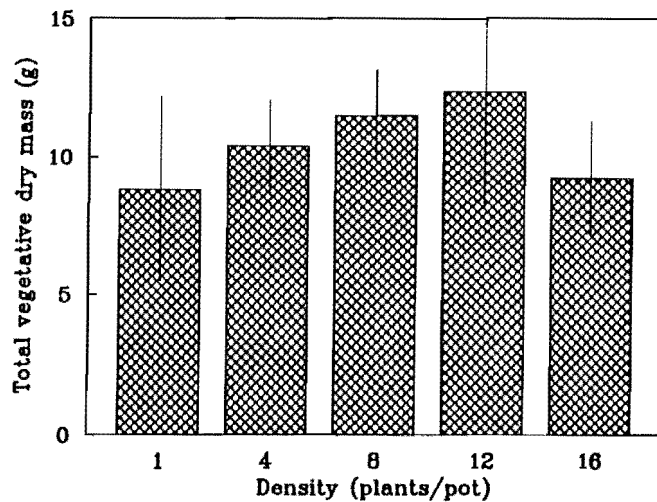


Figure 2 The effect of intraspecific competition on the average vegetative dry mass per pot of *Anthephora pubescens* at the third monthly harvest (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 8 4 1).

per pot (net CO₂ uptake per unit leaf area x leaf area per pot) reached a maximum at 8 plants per pot, whereas the yield per pot reached a maximum at 12 plants per pot (Figure 2).

The effect of changing density on net rate of CO₂ uptake per unit leaf area in E. curvula is represented in Figure 3a. An increase in density resulted in a progressive non - significant decrease in net CO₂ uptake rate per unit leaf area ($p < 0.05$). The effect of changing density on stomatal conductance and stomatal resistance is illustrated in Figure 3b. Maximal CO₂ uptake rate per unit leaf area was attained when stomatal conductance was highest and stomatal resistance was lowest. The calculated net CO₂ uptake per pot reached a maximum at 4 plants per pot, whereas the yield per pot reached a maximum at 12 plants per pot (Figure 4).

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



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

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

* Insufficient replicates to determine growth characteristics

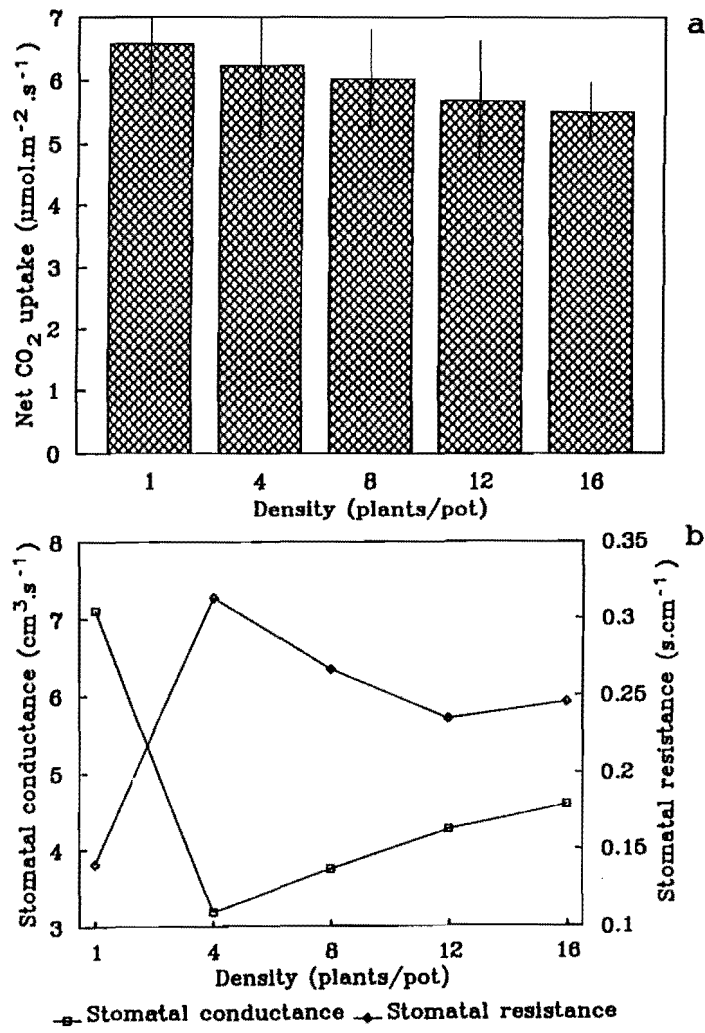


Figure 3 The effect of intraspecific competition on (a) the net CO₂ uptake rate per unit leaf area (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 8 4 1) and (b) the stomatal conductance and stomatal resistance of *Eragrostis curvula* at the third monthly harvest (stomatal conductance: 4 8 12 16 1; stomatal resistance: 1 12 16 8 4).

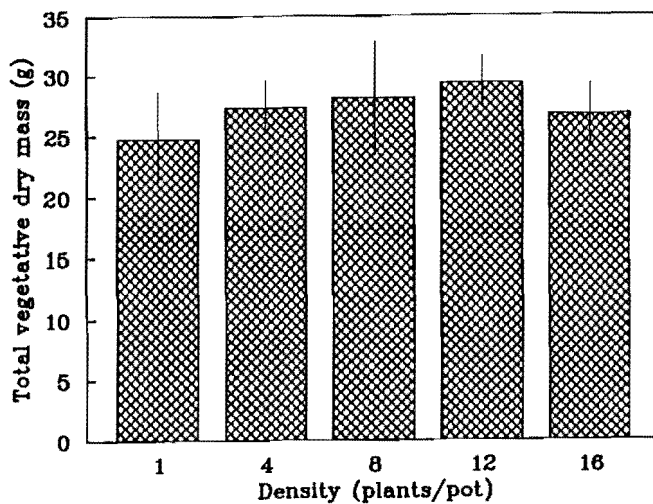


Figure 4 The effect of intraspecific competition on the average vegetative dry mass per pot of *Eragrostis curvula* at the third monthly harvest (statistical significance arranged from the smallest to the largest value is represented by a break in the solid line: 16 12 8 4 1).

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

The last decade researchers have referred to the "paradox" that no relationship exists between the rate of net CO₂ uptake per unit of leaf area and crop yield (Evans 1975; Moss 1976; Elmore 1980). Evans (1975) stated that there is no instance where selection for certain photosynthetic rates increased yield. Moss (1976) wrote that it is difficult to document that economic yield and photosynthesis are related in any direct way, and Elmore (1980) called attention to the "paradox" that no correlation exists between rates of CO₂ exchange per unit of leaf area and crop yield; in spite of the fact that it seems obvious that higher rates of photosynthesis should lead to higher yields. Good & Bell (1980) believe that this often - claimed "paradox" is a semantic problem.

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

CONCLUSIONS

It can be concluded that an increase in density results in shading and concomitant competition for light. Increasing density affects the rate of leaf production as well as the size of the leaves produced per plant. Maximal CO₂ uptake per unit leaf area was favoured under low competitive stress in both species. The effect of intraspecific competition on the net CO₂ uptake rate of A. pubescens and E. curvula differed significantly in that A. pubescens exhibited a peak in net CO₂ uptake rate per unit leaf area at 4 plants per pot, while E. curvula exhibited a decrease in net CO₂ uptake rate per unit leaf area with increasing density. It is evident that in A. pubescens and E. curvula, growth and increase in dry mass are not necessarily closely correlated with the rate of photosynthesis measured over short periods of time; instantaneous measurements of photosynthesis may therefore be misleading.

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