The effect of drought stress on the dry matter production, growth rate and biomass allocation of *Anthephora pubescens* Nees

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The effect of drought stress on the dry matter production, growth rate and biomass allocation of *Anthephora pubescens* Nees was examined at three phenological stages, i.e. vegetative stage (P1), initiation of reproduction (P2) and late reproductive stage (P3). Relative to control plants, total dry mass of P1, P2 and P3 plants, harvested after an 8-day post-stress recovery period, was reduced by 78%, 60% and 35% respectively. However, at the end of the growing season, there were no differences (P > 0.05) in total dry matter accumulation between stressed and non-stressed plants. This recovery of *A. pubescens* can possibly be explained by the phenotypic plasticity in leaf allocation in stages P1 and P2, and by the increase in the leaf area ratio of P1 and P2 plants, following drought stress.

**Keywords:** *Anthephora pubescens*, biomass allocation, leaf allocation, phenology, primary production, reproductive allocation, water stress.

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Introduction

*Anthephora pubescens* Nees is a drought-tolerant species which is widely advocated for use in pasture production systems in the semi-arid to arid regions of southern Africa (Donaldson et al. 1972; Fourie et al. 1984; Du Pisani et al. 1986; Fourie et al. 1987; Dannhauser 1991).

In general, water deficits reduce plant production (Begg & Turner 1976; Turner & Begg 1978). The degree of reduction depends largely on the season when drought stress occurs and the duration and frequency of the stress periods (Alcocer-Ruthling et al. 1989). It also depends on the phenological stage of the plant at the time of drought stress (Alcocer-Ruthling et al. 1989; Sieling et al. 1994).

Growth analysis is the first step in the analysis of primary production and is a useful tool to examine the effect of different environmental conditions on primary production (Kvet et al. 1971; Causton & Venus 1981; Hunt 1982, 1990). Biomass allocation refers to the proportion of total biomass stored in each organ (Harper & Ogden 1970). The biomass allocation pattern adopted by a species is determined by its genotype (Fenner 1985) and is refined through the process of natural selection to improve its chances of survival (Barbour et al. 1980; Gross et al. 1983; Bazzaz & Reekie 1985; Reekie & Bazzaz 1987).

The aim of this study was to examine the effect of drought stress, imposed at different phenological stages, on the dry matter production, growth rate and biomass allocation pattern of *A. pubescens*.

**Methods**

The experiment was conducted in a greenhouse at the Range and Forage Institute from December 1990 to June 1991. The mean minimum and maximum temperatures in the greenhouse for that period were 18°C and 30°C respectively and relative humidity ranged from 41% to 58%. A detailed description of the seed source, soil type and general experimental layout is provided in Moolman et al. (1996).

Plants of *Anthephora pubescens*, ecotype VII20, were grown from seed in pots with a volume of 5 500 cm³, filled with a 15-mm layer of gravel and topped with a sandy loam soil. Plants were grown at a density of one per pot and four replicates were used per treatment. The amount of water held by the soil in the pot at field capacity (termed ‘pot water capacity’) was determined gravimetrically (Graven 1968). Pots were weighed every second day and the amount of water needed to obtain a mass corresponding to 85% of pot water capacity was added.

Drought stress was imposed at three phenological stages, i.e. P1: vegetative stage (6 weeks after germination); P2: initiation of reproduction (8 weeks after germination); and P3: late reproductive stage (11 weeks after germination). Two additional drought-stress treatments were applied 2 weeks after germination onwards, i.e. 2 weeks drought stress, alternated with 1.5 weeks of watering (A1) and two weeks drought stress, alternated with 2.5 weeks of watering (A2).

Control plants received water every second day for the duration of the experiment. Drought stress was induced by withholding water from plants for 15 days. The length of this period was predetermined as the time needed to reduce the soil water potential to −1 500 kPa (permanent wilting point), at which stage the soil water content was 3.3% (m/m).

Four plants of treatments P1, P2 and P3, and their respective controls were harvested just prior to the water-stress period being implemented, after an 8-day post-stress recovery period, as well as at 18 weeks and 21 weeks after germination. Plants of the A1 and A2 treatments were harvested only at 18 and 21 weeks after germination. At each harvest, the plant material was divided into laminae, tillers (including the leaf sheath), inflorescences (including the peduncle), and roots. Leaf area was measured with a LiCor 3100 leaf area meter (LiCor, Lincoln, Nebraska 68504, USA).

The dry mass of each plant component was used to determine dry matter production of the whole plant and the biomass allocation patterns of tillers, laminae, reproductive structures and roots. The biomass allocation of a specific plant component was obtained by expressing its dry mass as a percentage of the plant’s total dry mass. Relative growth rates (R) and leaf area ratios (LAR) were also determined. Relative growth rates of the individual plant components were also calculated, i.e. that of the tillers (Rt), leaf laminae (Rl) and the roots (Rr). The formulae used for the calculations were based on those of Kvet et al. (1971), Causton & Venus (1981), Coombs et al. (1985) and Hunt (1990).

An analysis of variance (ANOVA) was done by means of the
program Genstat 5 Edition 3.1 (1987, Lawes Agricultural Trust, Rothamstead Experimental Station). The LSD$_{t-27}$(Sokal & Rohlf 1982) was computed to compare the values at a level of $P<0.05$ (***) and $P<0.01$ (**). Where appropriate the LSD values are indicated in the Figures.

Results

Dry matter production

The total dry mass of P1, P2 and P3 plants was less ($P<0.05$) than that of their respective controls (Figure 1). At stage P1, the dry mass of the tillers and laminae of stressed plants was less ($P<0.01$) than that of control plants, whereas there was no significant difference ($P>0.05$) in root dry mass. At stages P2 and P3, these relationships were reversed (Figure 1, caption). The dry mass of the reproductive components of the plants stressed at all three phenological stages (Figure 1) was lower ($P<0.05$) than that of control plants.

When drought stress was applied during the vegetative stage (P1) of A. pubescens, the stressed plant’s total dry mass was decreased by as much as 78%, whereas those stressed at the onset of reproduction (P2) showed a reduction of 60%, and those stressed in their late reproductive stage (P3) showed a reduction of only 35%.

At 18 weeks after germination, the total dry mass of only the P3 and A1 stressed plants was still significantly lower than that of control plants (Figure 2). However, the dry mass of the reproductive structures of P1, P3, A1 and A2 drought-stressed plants was lower than that of control plants (Figure 2). In none of the treatments could a difference in the dry mass of the roots be found.

At 21 weeks after germination there were no significant differences in the total dry mass production between any of the drought-stress treatments and that of the control (Figure 3). However, the reproductive dry mass of the plants which were repeatedly drought stressed (A1 and A2) was lower ($P<0.05$) than that of control plants (Figure 3).

Relative growth rate

The relative growth rate ($R$) of plants stressed at stage P1 ($-0.0022$ g g$^{-1}$ day$^{-1}$) and P2 ($0.0445$ g g$^{-1}$ day$^{-1}$) was significantly lower ($P<0.05$) than that of their respective controls (P1C = $0.0643$ g g$^{-1}$ day$^{-1}$; P2C = $0.0815$ g g$^{-1}$ day$^{-1}$), whereas there was no significant difference in $R$ between stressed and unstressed plants at stage P3 (Table 1). The reduction in $R$ of stressed plants at stage P1 was due to reductions in the relative growth rates of the tillers, laminae and roots. At stage P2, only the relative growth rate of the roots (Table 1) was reduced ($P<0.05$) compared with the control.

Leaf area ratio (LAR)

The leaf area ratio of a plant characterises the relative size of its assimilatory organs, and therefore it expresses the efficiency of the plant as a producer of leaf area (Coombs et al. 1985). It can be used to indicate differences between plants on the basis of genetic factors, the environment, or different treatments (Kvet et al. 1971). The leaf area ratio of P1 (56.3 cm$^2$ g$^{-1}$) and P2 plants (47.6 cm$^2$ g$^{-1}$) was higher than that of their corresponding controls (P1C = 29.6 cm$^2$ g$^{-1}$; P2C = 30.8 cm$^2$ g$^{-1}$), whereas the LAR of P3 plants was not affected by drought stress (Figure 4). There-

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**Figure 1** Average dry mass of plants water stressed at three phenological stages (P1: vegetative stage; P2: initiation of reproduction, and P3: late reproductive stage), with their respective controls (P1C, P2C and P3C). The plants were harvested after an 8-day recovery period.

| Plant component          | Treatment |
|--------------------------|-----------|
|                          | P1        | P2    | P3    |
| Reproductive structures  | ***       | **    | **    |
| Laminae                  | ***       | -     | -     |
| Tillers & leaf sheaths   | ***       | -     | -     |
| Roots                    | -         | ***   | **    |
| Above-ground parts       | ***       | -     | -     |
| Total plant              | **        | **    | **    |

**Figure 2** Average dry mass, 18 weeks after germination, of plants subjected to different water-stress treatments (C: control; P1: stressed at the vegetative stage; P2: stressed at the onset of reproduction; P3: stressed at the late reproductive stage; A1: 2 weeks water stress alternated with 1.5 weeks of watering; and A2: 2 weeks water stress alternated with 2.5 weeks of watering.

| Plant component          | LSD$_{t-27}$ (P < 0.05) |
|--------------------------|--------------------------|
| Reproductive structures  | 5.96                     |
| Above-ground parts       | 11.53                    |
| Total plant              | 16.61                    |
and P3:

Figure 4  The leaf area ratio of plants water stressed at three phenomenological stages (P1: vegetative stage, P2: initiation of reproduction, and P3: late reproductive stage), with their respective controls (P1C, P2C and P3C).

Figure 3  Average dry mass, 21 weeks after germination, of plants subjected to different water-stress treatments (C: control, P1: stressed at the vegetative stage, P2: stressed at the onset of reproduction, P3: stressed at the late reproductive stage; A1: 2 weeks water stress alternated with 1.5 weeks of watering; and A2: 2 weeks water stress alternated with 2.5 weeks of watering.

Table 1  The relative growth rates of (a) the entire plant (R), (b) laminae (Rl), (c) tillers including the leaf sheaths (Rt), (d) above-ground parts (Ra), and (e) roots (Rr), of plants water stressed at three phenomenological stages (P1: vegetative stage, P2: initiation of reproduction, and P3: late reproductive stage), with their respective controls

| Stage   | Control | Water stress |
|---------|---------|--------------|
| P1      |         |              |
| R       | 0.0643 ± 0.014 | -0.0022 ± 0.021* |
| Rl      | 0.0623 ± 0.019 | 0.0091 ± 0.025* |
| Rt      | 0.0717 ± 0.023 | 0.0076 ± 0.021* |
| Ra      | 0.0773 ± 0.022 | 0.0133 ± 0.021* |
| Rr      | 0.0518 ± 0.012 | -0.0167 ± 0.022* |
| P2      |         |              |
| R       | 0.0815 ± 0.013 | 0.0445 ± 0.022* |
| Rl      | 0.0771 ± 0.016 | 0.0567 ± 0.029 |
| Rt      | 0.0885 ± 0.020 | 0.0589 ± 0.030 |
| Ra      | 0.0920 ± 0.019 | 0.0585 ± 0.030 |
| Rr      | 0.0718 ± 0.010 | 0.0299 ± 0.015* |
| P3      |         |              |
| R       | 0.0184 ± 0.017 | -0.0029 ± 0.015 |
| Rl      | 0.0009 ± 0.014 | -0.0107 ± 0.010 |
| Rt      | 0.0251 ± 0.014 | 0.0195 ± 0.017 |
| Ra      | 0.0259 ± 0.018 | 0.0071 ± 0.013 |
| Rr      | 0.0060 ± 0.016 | -0.0201 ± 0.018

* Denotes a statistically significant difference at α = 0.05

fore, when A. pubescens is stressed at the vegetative stage (P1) or at the onset of reproduction (P2), the efficiency of the plants to produce leaf area is increased. However, 18 weeks after germination the differences in LAR between the various treatment were no longer significant.

Biomass allocation

Biomass allocation of plants from which water was withheld at the three phenomenological stages is given in Figure 5. Drought stress, induced at stages P1 and P2, resulted in a significant increase in leaf allocation. Although leaf allocation of these drought-stressed plants was higher than that of control plants, the amount of available material was less on the stressed individuals. For example, at stage P1, leaf allocation of stressed plants was 29.9% as opposed to 22.1% of control plants. However, the leaf dry mass of stressed plants was only 0.7 g as against 2.4 g of control plants. Reproductive allocation was significantly reduced only if drought stress was applied early in the reproductive stage (P2). The biomass allocation pattern of A. pubescens was not affected by drought stress applied at the late reproductive stage (P3). None of these plants (P1, P2 and P3), harvested directly after an 8-day recovery period showed any effect of stress on root allocation.

However, at 18 weeks after germination, root allocation of P1, A1 and A2 drought-stressed plants was significantly higher than that of control plants (Figure 6). This increase in root allocation in stressed plants was accompanied by a decrease in reproductive allocation (Figure 6).

However, 21 weeks after germination, there were no significant differences in biomass allocation between any of the stressed and control plants (Figure 7).

Discussion

Drought stress generally reduces plant growth (Pande & Singh 1985; Rozijn & van der Werf 1986; Alcocer-Ruthling et al. 1989; Baruch 1994). The effect of drought stress on the production and biomass allocation patterns of Anthephora pubescens depends on
the phenological stage when stress occurs. After an 8-day poststress recovery period, the total dry mass of P1, P2 and P3 plants was reduced by 78%, 60% and 35% respectively, relative to their controls. However, at the end of the growing season, total dry matter production of stressed plants was not significantly lower than that of control plants. Busso & Richards (1995) also found that herbage accumulation, by two tussock grasses in Utah, at the end of the season was not reduced after a single season's drought stress.

Drought stress during the vegetative stage or early reproductive stage of *A. pubescens* is the most detrimental in terms of the plant's short-term production and growth rate. Drought stress did not affect the growth rate of plants if applied during the late reproductive stage.

The recovery of *A. pubescens* late in the growing season following earlier drought stress is possibly because *A. pubescens* displays phenotypic plasticity in its biomass allocation. Leaf allocation was stimulated by drought stress, induced at the vegetative stage or during the onset of reproduction. Increased investment in leaves led to an increased LAR, allowing the plant to compensate for losses caused by drought stress. For example, the increase in dry matter of control plants between 18 (Figure 2) and 21 weeks (Figure 3) after germination was low (3 g), when compared to the increase in dry matter of stressed plants, especially that of P3 plants (21 g).

An increase in root allocation with an increase in moisture stress has been reported by various authors (Gales 1979). In *A. pubescens*, root allocation showed no immediate reaction to drought stress. Only at the harvest at 18 weeks was a significant increase in root allocation noticeable in some of the treatments.

According to Turner & Begg (1978), the cell numbers of plants exposed to water deficits are of the same general order of magnitude as control plants, although the cells are of a smaller size. Furthermore, plants that are frequently water stressed exhibit more rapid growth when recovering from drought stress. The sensitivity of cell enlargement to water deficits also results in a reduction in the leaf area of a plant. In *A. pubescens*, the elongation of leaves is retarded during drought stress (Moolman 1993;
Moolman et al. 1996), but when the plants recover they produce thinner leaves, which is demonstrated by the increase in the leaf area ratio and specific leaf area (Moolman et al. 1996) of especially P1 plants.

The reproduction of A. pubescens is negatively affected by drought stress. The dry mass of the reproductive structures decreased by 93%, 90% and 63% following stress induced at stages P1, P2 and P3 respectively. This reduction could be the result of the delay in the reproduction phase, as well as the abortion of newly formed reproductive tillers. However, only the dry mass of the reproductive structures of plants that were subjected to alternating drought stress throughout the growing season (A1 and A2), was still significantly less than that of control plants at the end of the growing season. The reaction of A. pubescens to drought stress differs from that of Bouteloua scoparia as Alcocer-Ruthling et al. (1989) concluded that the reproductive dry matter production of B. scoparia was not influenced by drought stress in any of the phenological stages.

Conclusions

Although drought stress caused a significant reduction in dry matter production in the short term, stressed plants apparently have the ability to compensate for this loss over the entire growth season. In general, it can be concluded that A. pubescens is more vulnerable to drought-stress conditions in its vegetative stage, and to a lesser degree at the onset of reproduction. Although drought stress negatively affects the production of A. pubescens in the short term, only the reproductive dry matter production of plants that were stressed throughout the growing season was permanently harmed. This suggests that A. pubescens should not be used as summer-grazing pastures in areas which are subjected to drought stress in the growing season. However, A. pubescens can be utilised as forage in winter, as the effect of drought stress on production is negligible.

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