The effect of drought stress on the morphology of *Anthephora pubescens* Nees

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The effect of drought stress on the morphology of *Anthephora pubescens* Nees was examined at three phenological stages, i.e. during the vegetative stage (P1), at the onset of reproduction (P2) and during the late reproductive stage (P3). This was induced by withholding water from the plants for 15 days. The morphology of *A. pubescens* was adversely affected by drought stress during its actively growing stage (P1) in that both leaf area and leaf length were reduced. However, it caused an increase in vegetative tillering of both P1 and P2 plants. Reproduction of *A. pubescens* was negatively influenced by drought stress, as reproductive tillering was reduced at both P1 and P2 stages, and the reproductive tillers formed at stage P3 were shorter.

**Keywords:** *Anthephora pubescens*, drought, morphology, phenophases, tillering, water stress, Wool-grass.

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**Introduction**

*Anthephora pubescens* Nees is a valuable species for dryland pastures in the semi-arid to arid regions of southern Africa because of its drought-tolerance characteristics. Previous studies undertaken on *A. pubescens* concentrated on establishment, forage production, fertilization requirements and nutritional value (Donaldson et al. 1972; Burger et al. 1975; Fourie et al. 1984, 1987; Du Pisani et al. 1986; Dannhausser 1991). Very little is known of the growth and development of this species under conditions of drought stress, and to increase the potential of *A. pubescens* as a pasture species in arid regions, it is imperative to understand the response of this species to drought.

*Anthephora pubescens* is classified as a short grass species because the internodes of the vegetative tillers are not elongated (Baines 1989). Short grasses, with a large number of tillers, are well adapted to regions with low, irregular rainfall, because it is advantageous to divide growth between meristems to ensure rapid regrowth after a period of drought stress. Tall grass species occur more frequently in areas with a more predictable rainfall where it is advantageous to reduce the number of tillers and to invest more in each individual tiller.

The impact of drought stress on the morphology of a grass plant is greater than the effect on the physiology, and cell division appears to be less sensitive to drought stress than cell elongation (Turner & Begg 1978). The most important effects of drought stress are therefore reduced leaf area and decreased growth rate (Pande & Singh 1985; Rozijn & van der Werf 1986; Baruch 1994; Busso & Richards 1995). Drought stress is also known to result in a decrease in total non-structural carbohydrate and protein content (Pande & Singh 1985) as well as an increase in proline and abscisic acid concentration (Frank 1994). Sensitivity to drought stress also depends on the phenological or growth stage of the grass plant (Alcocer-Ruthling et al. 1989; Sieling et al. 1994). It has been reported that drought stress, imposed at an early growth stage, reduces the number of vegetative tillers (Alcocer-Ruthling et al. 1989). If grass plants are subjected to drought stress before the initiation of the reproductive phase, the production of reproductive tillers may be either delayed or accelerated and the number of reproductive tillers produced may also be less than for non-stressed plants (Rozijn & van der Werf 1986; Alcocer-Ruthling et al. 1989). Although the total growth of a grass plant may decrease during drought stress, the negative effect on root growth is usually less than that on tiller growth (Begg & Turner 1976; Turner & Begg 1978).

The aim of this study was to determine the effects of drought stress, applied at different phenological stages, on the morphology of *A. pubescens*, with special reference to the number of tillers (vegetative and reproductive), leaf length and leaf area. Understanding plant growth and morphological development of *A. pubescens* under drought stress may assist in the development of management practices aimed at the increased survival and forage production of this species when grown in dryland pastures.

**Methods**

The experiment was conducted under controlled environmental conditions at the Range and Forage Institute from December 1990 to June 1991. The mean minimum and maximum temperatures for that period were 18°C and 30°C respectively and relative humidity ranged from 41 to 58%.

*Caryopsis* of *Anthephora pubescens*, ecotype VH20, were obtained from the Biosivialekra Research Station near Vryburg in the Northern Cape (24°28’E; 25°57’S). Eight caryopses were sown per pot and germination took place after 4 days. After 4 weeks the seedlings were thinned to one per pot. The pots, with a volume of 5 500 cm³ (300 mm deep) were filled with a 15-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) to a mass of 7.95 kg. The amount of water held by the soil in the pot at field water capacity was determined gravimetrically (Graven 1968). This value was termed 'potwater capacity'. Every second day the pots were weighed and the amount of water needed to obtain a mass, corresponding to 85% of pot water capacity, was added. Corrections were made for the fresh mass of the plant material in the pot. Control plants received water every second day for the duration of the experiment. All plants received UAN 32 (urea ammonium nitrate; 10 ml UAN 32/1.5 000 ml H2O) once, early in their vegetative stage. The experimental layout was a randomized block design with four replicates of each of five treatments (blocks) and four harvest times per treatment. Pots were rotated fortnightly to avoid the effects of uneven temperatures and light conditions within the greenhouse.

The effect of drought stress on the morphology of *A. pubescens* was examined at three phenological stages i.e. vegetative stage (6 weeks after germination: P1), onset of reproduction (8 weeks after germination: P2) and late reproductive stage (11 weeks after germination: P3). Drought stress was imposed by withholding water from the
plants for 15 days. The length of this period was predetermined and taken as the time needed to reduce the soil water content to 3.3% (m/m), which represented a soil water potential of -1 500 kPa (permanent wilting point).

The following parameters were measured every second day after the onset of drought stress: (1) number of tillers (vegetative and reproductive) per plant, (2) number of live leaves per marked tiller, and (3) total leaf length of the living part of the leaves per marked tiller. After rewetting, leaf length was recorded for another week, whereas the number of tillers was monitored for another 8 weeks.

Eight days after rewetting of the stressed plants (recovery period), four plants per treatment were harvested and the following parameters measured: (1) length of the peduncle, (2) height of the flag leaf (from soil surface), (3) length of the inflorescence axis, and (4) leaf area of the laminae (measured with a LiCor 3100 leaf area meter, LiCor, Lincoln, Nebraska 68504, USA).

![Figure 1](image1.png)  
**Figure 1** The number of (a) vegetative, (b) reproductive, and (c) total number of tillers per plant, of control plants (P1C) and plants that were water stressed at the vegetative stage (P1). Shaded areas represent the time intervals where the polynomials did not differ significantly at $P < 0.01$.

![Figure 2](image2.png)  
**Figure 2** The number of (a) vegetative, (b) reproductive, and (c) total number of tillers per plant, of control plants (P2C) and plants that were water stressed at the initiation of reproduction (P2). Shaded areas represent the time intervals where the polynomials did not differ significantly at $P < 0.01$. 
Polyunomial functions were fitted for the data points collected over time, i.e. number of tillers per plant and the total leaf length per marked tiller. The method of Groenewald (1970) was used to determine the confidence limits ($P < 0.05; P < 0.01$) for the linear combinations of contrasts among polynomials. When only two treatments were compared, the Student's t-test (Sokal & Rohlf 1982) was used to determine statistically significant differences at a significance level of $\alpha = 0.05$ and $\alpha = 0.01$.

Analysis of variance (ANOVA) was done to compare more than two treatments. Bartlett's test was used to determine whether the variance was homogeneous, and Bonferroni's test was used to determine statistically significant differences at a level of $\alpha = 0.05$ (Sokal & Rohlf 1982).

**Results**

**Number of tillers**

At stage PI there were initially no significant differences ($P > 0.01$) in the number of vegetative tillers on stressed and unstressed (control) plants (Figure 1a). After 4 days, however, the number of vegetative tillers on stressed plants was significantly less ($P < 0.01$) than on control plants. During the post-stress recovery period there was an increase in vegetative tiller production in stressed plants so that after a 22-day recovery period the number of vegetative tillers on the stressed plants was significantly greater than that of control plants. After a 6-day post-stress recovery period the number of reproductive tillers on stressed plants was significantly less ($P < 0.01$) than that of control plants (Figure 1b). After 40 days recovery, stressed plants overcame this backlog. For plants stressed at stage P1, from 4 days after drought stress was induced until 13 days into the recovery period, the total number of tillers was significantly less than that of control plants (Figure 1c). After a 27-day recovery period the total number of tillers of stressed plants (P1) was significantly greater ($P < 0.01$) than that of control plants, and after 68 days this difference between treatments was no longer apparent.

The number of vegetative tillers of plants stressed at stage P2 did not differ significantly ($P > 0.01$) from that of control plants during the drought stress period (Figure 2a, c). However, after a 6-day post-stress recovery period the number of vegetative tillers on stressed plants (P2) was significantly greater ($P < 0.01$) than that of control plants. This difference disappeared after a 41-day recovery period. The total number of tillers followed a similar trend. Six days after drought stress was induced, the number of reproductive tillers on stressed plants was significantly less than that of control plants (Figure 2b). Stressed plants were only able to overcome this backlog after a recovery period of 22 days.

At stage P3 drought stress did not affect vegetative (Figure 3a) or total tiller production (Figure 3b). It was not possible to fit an appropriate polynomial for the number of reproductive tillers.

**Figure 3** The number of (a) vegetative, and (b) total number of tillers per plant, of control plants (P3C) and plants that were water stressed at the late reproductive stage (P3).

**Figure 4** The total leaf length per marked tiller of plants that were water stressed at (a) the vegetative stage (PI), and (b) the initiation of reproduction (P2), with that of their respective controls (PI C and P2C).
Total leaf length and leaf area

During the first six days after drought stress was induced, no significant difference in the total leaf length between plants stressed at stage P1 and control plants was noted (shaded areas, Figure 4a). However, after 6 days of drought stress the total leaf length of stressed plants was significantly less than that of control plants. This difference was maintained during the post-stress recovery period. In the case of plants stressed at stage P2, the total leaf length did not differ significantly from that of the control plants (shaded area, Figure 4b) during the first three days of the drought stress period. However, from the fourth to the eighth day of the drought stress period, the total leaf length of the stressed plants was significantly greater than that of the control plants. After 9 days of stress the total leaf length of the stressed plants decreased and for the rest of the monitoring period there were no significant differences in total leaf length between stressed and control plants.

After an 8-day post-stress recovery period, only plants stressed at stage P1 had a significantly lower ($P < 0.05$) leaf area than control plants (Figure 5) while the difference between leaf areas of stressed and non-stressed plants was not significant at stages P2 and P3 (Figure 5).

Height of the flag leaf, length of the peduncle and inflorescence axis

Only at stage P3 were there enough reproductive tillers to measure these parameters. There was no significant difference ($P > 0.01$) in the height of the flag leaf between stressed and control plants (Table 1). However, the length of the peduncle and the inflorescence axis of the stressed plants (P3) were significantly lower ($P < 0.01$) than those of the control plants.

Discussion

Drought stress imposed at the vegetative stage (P1) of A. pubescens initially caused a significant decrease in the number of vegetative as well as the total number of tillers. A reduction in tillering with a decrease in soil moisture availability was also reported by Turner & Begg (1978) and Alcocer-Ruthling et al. (1989) for other grass species. Upon rewatering P1-stressed Anthephora pubescens plants, stimulated tillering resulted in significantly more vegetative tillers on stressed plants. Similar results were obtained in Agropyron smithii (Turner & Begg 1978), with tillering being stimulated by a decrease in soil moisture availability. However, towards the end of the observation period there were no significant differences in vegetative and total tiller numbers on stressed and control plants of A. pubescens. The effect of drought stress at stage P2 (onset of reproduction) followed a similar pattern, except that there was no initial decrease in tiller production. Reproductive tiller production was inhibited by drought stress in both stages P1 and P2, but not in stage P3 (late reproductive stage). Similarly, Alcocer-Ruthling et al. (1989) found that drought stress imposed during the flowering stage did not affect the reproductive capacity of Bouteloua scorpiodes. In a study on the grain yield of cereals, Baruch (1994) found that the yield decreased when drought stress was applied at a later phenological stage.

Total leaf length per tiller in A. pubescens was less when the plants were stressed during the vegetative (P1) stage. According to Turner & Begg (1978), the reduction in leaf elongation caused by drought stress is mainly due to the inhibition of cell enlargement. The elongation of leaves of P2-stressed plants ceased 7 days after the onset of drought stress (leaf water potential $<-1.2$ mPa). Leaf elongation of Panicum maximum ceased at a leaf water potential of $-1.0$ mPa (Turner & Begg 1978). Reductions in green leaf number, rate of leaf initiation, height and total leaf area were reported for two tuft grasses in Utah, when leaf water potential fell below $-2.5$ mPa (Busso & Richards 1995). During pot trials carried out on Themeda triandra and Sporobolus fliribratus, Danckwerts (1988) found that the green leaf length per tiller increased steadily while water was abundant, reaching a maximum at 40% water depletion, thereafter degenerating rapidly.

Drought stress in the vegetative stage (P1) of A. pubescens, reduced leaf area by 58%. However, drought stress induced either at the onset of reproduction (P2) or later during the reproductive stage (P3) did not reduce leaf area significantly. In contrast, leaf area of Bouteloua scorpiodes plants (Alcocer-Ruthling et al. 1989) as well as maize (Denmead & Shaw 1960) was reduced by drought stress at all phenological stages.

According to Denmead & Shaw (1960), tiller elongation and the length of the inflorescence axis of maize was lowered by drought stress induced only at the vegetative stage, suggesting that drought stress could only influence plant growth during the actively growing vegetative period of a plant. However, in the case of A. pubescens, peduncle length as well as inflorescence axis length were lower on P3-stressed plants than on control plants.

*Anthephora pubescens* is a valuable cultivated pasture in the

Table 1 The height of the flag leaf, length of the peduncle and inflorescence axis of control and plants water stressed at the late reproductive stage (P3). Measurements were taken after an 8-day recovery period. The values in brackets represent the standard deviation of the treatments. ***Treatments which differ significantly at $P < 0.01$.

| Parameters            | Water stress | Control |
|-----------------------|--------------|---------|
| Height of flag leaf (mm) | 374.7 (108.6) | 430.6 (76.2) |
| Length of the peduncle (mm) | 576.4 (260.4)** | 861.4 (197.7) |
| Length of the inflorescence axis (mm) | 92.7 (7.9)** | 107.5 (15.6) |
semi-arid regions of South Africa. Although it is not a high-yielding pasture in terms of kilograms dry matter per hectare, it is very palatable and nutritious (Fair 1989; Dannhauser 1991). High animal performance on *A. pubescens* pasture, therefore, largely offsets the low dry-matter yield (Fair 1989; Dannhauser 1991). In contrast to many other pasture grasses, the palatability and nutritional value of *A. pubescens* do not decline in autumn and it can therefore provide good-quality grazing in autumn and winter (Fair 1989).

Results of this study indicate that *A. pubescens* is sensitive to drought stress in its actively growing stages, i.e. the vegetative stage (PV) and during the initiation of reproduction (P2), as reproductive tillering, total leaf length and leaf area are reduced. Reproductive tillers produced on stressed plants are shorter due to a reduction in the length of the peduncle and inflorescence axis. However, provided water stress is not continuous, *A. pubescens* plants have the ability to compensate for the effect of drought stress by increased tillering. On the basis of these results it seems advisable not to use *A. pubescens* that has been subjected to drought stress early in the season, it should rather be used as autumn and winter fodder.

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