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PHYSIOLOGY

Drought-induced Changes in Shoot and Root Growth of Young Cotton Plants

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INTERPRETIVE SUMMARY

Cotton cultivars that can endure and recover from drought are needed to minimize yield loss in dryland areas and to reduce the water needs of irrigated production. An understanding of the response of cultivars to water deficits is also important in attempts to model cotton growth and estimate irrigation needs.

Planting early-maturing cultivars can decrease the amount of water used by cotton, but other traits may further decrease the amount of water used. Studies have shown that both canopy and root development are inhibited by drought. The same studies further indicate that drought inhibits shoot growth more than it does root growth. This study examined various measures of shoot and root growth of a long- and a short-season cotton cultivar after a drought of limited duration and a subsequent recovery period.

A long-season cotton, ‘Stoneville 506’ and short-season ‘Tamcot HQ95,’ were planted in pots with fritted clay and grown under fluorescent light banks. Plants were divided at 36 d after planting into drought-treatment and watered-control groups. The drought-treated plants were not watered for 13 d. At the end of the drought treatment (49 d after planting), control and drought-treated plants were sampled. Also at 49 d after planting the remaining drought-treated plants were watered for a 10-d recovery period, and both treatments were sampled again at 59 d after planting.

Both cultivars were similar in their response to drought and recovery. The results indicated that drought affected shoot growth more than it did root growth in these two cultivars. At the end of the drought and recovery periods all measures of shoot growth, including height, leaf area, number of nodes, and dry weights of the leaves and stems were less in the drought-treated plants than in the controls. No measure of root growth was decreased in the drought-treated plants, compared with the controls, until the end of the recovery period. The shoot:root ratio was less in the drought-treated plants than in the controls at the first sampling. Most importantly, the length of the taproot was greater in the drought-treated plants than in the control plants at the end of the drought and recovery periods.

Our observations with two different cotton genotypes further suggest that a common response to drought in cotton may well be an increase in length and a concomitant thinning of the taproot. This response may permit cotton plants to survive drought by accessing water from deeper in the soil profile than would be tapped during periods of adequate water supply.

ABSTRACT

An understanding of the response of plants to water deficits is important in efforts to model cotton (*Gossypium hirsutum* L.) growth, estimate irrigation needs, and breed drought-resistant cultivars. This study examined shoot and root growth of a long- and a short-season cotton cultivar after a brief drought and subsequent recovery period. Seeds were planted in fritted clay-filled pots in a growth room under fluorescent lights at about 27 °C. Plants were divided at 36 d after planting into drought-treatment and watered-control groups. Plants were sampled after a 13-d drought and again after a 10-d recovery period. There were no treatment-by-genotype interactions. At the end of the drought and recovery, height, leaf

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area, number of nodes, and the dry weights of the leaves and stems were less in the drought-treated plants than in the controls. Root growth was not decreased in the drought-treated plants, compared with the controls, until the end of the recovery period, when the shoot:root ratio was less in the drought-treated plants than the controls. Most importantly, at the end of the drought and recovery the length of the taproot, but not its dry weight, was greater in the drought-treated plants than in the controls. This observation in both tested cotton genotypes suggests that increases in taproot length at the expense of root thickening after drought may be a common response in cotton. This response may permit cotton plants to survive drought by accessing water from deeper in the soil profile than the levels tapped during periods of adequate water supply.

Cotton is grown dryland and irrigated. Cultivars are needed that can endure and recover from drought so as to minimize yield loss in dryland areas and to reduce the water needed in irrigated production. An understanding of the response of cultivars to water deficits is also important in modeling cotton growth and estimating irrigation needs.

Leaf expansion in several species has been shown to be sensitive to water stress (Hsiao, 1973; Masle and Passioura, 1987). Several studies have shown that drought inhibits cotton canopy development. Krieg and Sung (1986) determined that drought decreases the number of leaves on sympodial branches of cotton. Leaf area of glasshouse-grown cotton also was inhibited when the percentage of soil-available water was less than 51 ± 15% (Rosenthal et al., 1987).

Cutler and Rains (1977) concluded that predawn leaf water potentials below -0.5 MPa were accompanied by decreased leaf elongation rate. Leaf expansion of 55-d-old cotton plants slowed after 2 d of withholding water, which meant that leaf growth was more sensitive than root elongation to drought (Ball et al., 1994). Similarly, McMichael and Quisenberry (1991) found that terminal drought decreased the shoot:root ratio.

Drought also reduced the growth, development, and distribution of cotton roots (Malik et al., 1979; Taylor, 1983). Root growth of 55-d-old cotton was reduced after 6 d of withholding water (Ball et al., 1994). The number of roots elongating decreased by 35% during the drought.

Planting early-maturing cultivars can decrease the amount of water used by cotton, and other traits in future cotton cultivars may further decrease the amount of water used. Quisenberry et al. (1981) found considerable variability for heat tolerance, root growth, dry matter accumulation, and water use efficiency among exotic cotton strains under dryland conditions. Gerik and co-authors (1996) compared two short-season cotton cultivars and found that one, Tamcot HQ95, yielded more than other, GP74, regardless of the level of water stress. They concluded that the photosynthetic capacity of Tamcot HQ95 might be greater than that of GP74.

Root elongation during drought may help plants get deeper water, thus avoiding water deficits near the soil surface. Elongation also could reduce the water lost by drainage when precipitation allows recovery after the drought (Ludlow and Muchow, 1990). If, however, water is unavailable deeper in the soil profile, longer roots may reduce shoot dry weight and harvest index by allowing the preferential partitioning of photosynthate to roots at the expense of shoots.

This study examined various measures of shoot and root growth of one long- and one short-season cotton cultivar after a drought of limited duration and a subsequent recovery period.

MATERIALS AND METHODS

A long-season cotton, ‘Stoneville 506,’, and a short-season cotton, ‘Tamcot HQ95,’ were planted in pots (9-L volume, 20 cm deep) filled with fritted clay (Absorb-N-Dry, Balcones Co., Flatonia, TX). Filter paper at the bottom of the pots retained the fritted clay while allowing for drainage. Two plants were seeded per pot and were supplied with distilled water every other day for 10 d. The pots were then watered with a nutrient solution of 0.90 g L^{-1} of 20-20-20 NPK fertilizer (Peters Professional All Purpose Plant Food, Spectrum Group, Division of United Industries Corp., St. Louis, MO) until 36 d after planting.

This fertilizer was selected because soil tests showed that the fritted clay had very low levels of N, P, and K and that nutrients would be quickly leached from this well-drained soil. Water or nutrient solution, when applied, was added until an excess drained from the bottom of the pot. The experiment was conducted in a growth room under fluorescent lights providing a photosynthetic photon flux density of 700 μmol m^{-2} s^{-1} for 16 h d^{-1}. Temperature was maintained at ≈27 °C.

At 36 d after planting, plants were randomly divided into drought-treatment and watered-control groups. The drought-treated plants were not watered for 13 d. At the end of this drought treatment (49 d after planting), control and drought-treated plants were sampled and height, number of nodes, leaf area, and taproot length were measured. Secondary root length of fresh roots was measured by a Comair Root Length Scanner (Commonwealth Aircraft Corp. Ltd, Melbourne, Australia). Leaves, stems, and tap and secondary roots were dried for 48 h at 90 °C before dry weights were determined. The shoot:root weight ratio was calculated from the dry weights.

At 49 d after planting, the remaining drought-treated plants were watered during a 10-d recovery period. At 59 d after planting, both treatments were sampled as described above.

The experiment was a randomized complete block design with two blocks. Each block had four pots of each cultivar. Each pot had two plants. The experiment was repeated twice. There was no interaction between treatment and experimental run, so data from the two runs were pooled for statistical analysis. The cultivar primary effect was insignificant, so data also were pooled across cultivar. This analysis used the SAS System (SAS Institute, Cary, NC).

Table 1. Heights and dry weights of stem, leaf area and dry weight, and node number in drought-treated and control plants of Stoneville 506 and Tamcot HQ95 at the end of the drought, 49 d after planting.† Means are followed by standard errors of the mean in parentheses.

	Treatment	
Plant part	**Drought**	**Control**
Stem height (cm)	**20.0 (±1.1) ***	**27.9 (±1.4)**
Stem dry weight (g)	**1.13 (±0.05) ***	**1.39 (±0.06)**
Leaf area (cm^2)	**56 (±4) ***	**153 (±27)**
Leaf dry weight (g)	**1.41 (±0.10) ***	**2.16 (±0.33)**
Node number	**7.8 (±0.3) ***	**9.4 (±0.5)**

*** Means in a row are significantly different at the 0.05 probability level.**

† The drought treatment was imposed by withholding water for 13 d.

Table 2. Shoot:root ratios in drought-treated and control plants of Stoneville 506 and Tamcot HQ95 at the end of the drought 49 d after planting and after a recovery period (59 d after planting).† Means are followed by standard errors of the means in parentheses.

	Shoot:root ratio	
Treatment	**49 d after planting**	**59 d after planting**
Drought	**5.4 (±0.4) *****	**5.9 (±0.5)**
Control	**8.5 (±0.6)**	**6.3 (±0.5)**

***** Means in column are significantly different at the 0.001 probability level.**

† The drought treatment was imposed by withholding water for 13 d. Recovery involved supplying sufficient water and nutrients for 10 d.

Table 3. Taproot lengths and dry weights and secondary root lengths and dry weights in drought- treated and control plants of Stoneville 506 and Tamcot HQ95 at the end of the drought 49 d after planting.† Means are followed in parenthesis by standard errors of the mean.

	Treatment	
Plant part	**Drought**	**Control**
Taproot length (cm)	**24.5 (±1.4)***	**18.9 (±1.2)**
Taproot dry weight	**0.260 (±0.0227)**	**0.260 (±0.031)**
Secondary root length (cm)	**52.2 (±6.7)**	**42.5 (±4.9)**
Secondary root dry weight (g)	**0.221 (±0.030)**	**0.188 (±0.027)**

*** Means in a row are significantly different at the 0.05 probability level.**

† Recovery involved supplying sufficient water and nutrients for 10 d after withholding water for 13 d.

RESULTS AND DISCUSSION

At the end of the drought treatment, drought-treated plants had significantly ($P < 0.05$) lower height, less leaf area, fewer nodes, and lower dry weights of stems and leaves than did the controls (Table 1). Additionally, the drought-treated plants had a lower shoot:root ratio (Table 2) than did the controls at this sampling, 49 d after planting. There were no differences between the two treatments in the lengths of the secondary roots or in the dry weight of the secondary or taproots at the end of the drought period (Table 3). However, the drought-treated plants had a significantly ($P < 0.01$) greater tap root length than did the controls at this time (49 d after planting). The taproot dry weight in the drought-treated plants was identical to that of controls, so the drought-related elongation occurred at the expense of taproot thickening. While the drought-treated plants had a taproot dry weight per length of only 0.011 g cm^{-1}, the corresponding measurement for the well-watered controls were

Table 4. Heights and dry weights of stem, leaf areas and dry weights, and node numbers in drought-treated and control plants of Stoneville 506 and Tamcot HQ95 after a recovery period 59 d after planting.† Means are followed by standard errors of the mean in parentheses.

	Treatment	
Plant part	**Drought**	**Control**
Stem height (cm)	**24.3 (±1.2) ****	**33.1 (±1.6)**
Stem dry weight (g)	**1.64 (±0.06) ****	**2.41 (±0.11)**
Leaf area (cm^2)	**601 (±118) ****	**895 (±168)**
Leaf dry weight (g)	**2.34 (±0.31) ****	**3.46 (±0.64)**
Node number	**8.8 (±0.3) ****	**10.9 (±0.4)**

**** Means in a row are significantly different at the 0.01 probability level.**

† Recovery involved supplying sufficient water and nutrients for 10 d after withholding water for 13 d.

Table 5. Taproot lengths and dry weights and secondary root lengths and dry weights in drought-treated and control plants of Stoneville 506 and Tamcot HQ95 after a recovery † period at 59 d after planting. Means are followed by standard errors of the means in parentheses.

	Treatment	
Plant part	**Drought**	**Control**
Taproot length (cm)	**27.1 (±1.2)***	**22.5 (±1.1)**
Taproot dry weight	**0.381 (±0.037)***	**0.493 (±0.041)**
Secondary root length (cm)	**67.5 (±6.7)***	**96.4 (±8.9)**
Secondary root dry weight (g)	**0.301 (±0.035)***	**0.474 (±0.049)**

*** Means in a row are significantly different at the 0.05 probability level.**

† Recovery involved supplying sufficient water and nutrients for 10 d after withholding water for 13 d.

0.014 g cm^{-1}. Thus, dry matter was preferentially partitioned to tap root elongation in both genotypes during the drought period.

At the end of the recovery period (59 d after planting), drought-treated plants still had significantly ($P < 0.01$) lower height, less leaf area, fewer nodes, and smaller dry weights of stems and leaves than did the controls (Table 4). But, the leaf area of the drought-treated plants after the 10-d recovery period was much closer to that of controls than at 49 d after planting, the end of the drought period. At 59 d after planting, drought-treated plants had significantly ($P < 0.05$) smaller secondary root lengths and dry weights for the secondary and tap roots than did the controls at this sampling (Table 5). Photosynthate partitioning in the drought-treated plants was apparently preferentially directed to leaf-area expansion during the recovery period. The two treatments did not differ in shoot:root ratio at this time (Table 2). However, the drought-treated plants still retained a significantly ($P < 0.05$) greater tap root length than did the controls after the recovery period. The lower taproot dry weight of the drought-treated plants, compared with the controls, indicated that the longer roots of the drought-treated plants were thinner than the corresponding roots of the control plants. Thinner roots compared with controls also were reported for salt-stressed cotton (Kurth et al., 1986) and drought-treated maize, *Zea mays* L., (Sharp et al., 1988). While the drought-treated plants had a dry weight per unit length of only 0.014 g cm^{-1}, control dry weights per unit length were 0.022 g cm^{-1}. Elongation of the taproots in the drought-treated plants occurred at the expense of thickening.

The results indicate that drought affected the shoot growth of these two cotton cultivars more than it did their root growth. At the end of the drought and recovery periods, all measures of shoot growth, including height, leaf area, nodes, and the dry weights of the leaves and stems, were less in the drought-treated plants than in the controls (Tables 1 and 4). Root growth was not decreased in the drought-treated plants, compared with the controls, until the end of the recovery period (Tables 3 and 5). Fernández et al. (1996) also found that drought affected shoot growth before the root growth in young cotton plants grown in pots. Detrimental effects of drought on root growth were only observed after recovery. Preferential partitioning of photosynthate to leaf area expansion at the expense of root growth may have been responsible for the lower taproot dry weights of the drought-treated plants, compared with the controls, at the end of the recovery period. Finally, the shoot:root ratio was less in the drought-treated plants than in the controls at the first sampling (Table 2). This result from our time-limited drought was similar to the observation of McMichael and Quisenberry (1991) that terminal drought decreased the shoot:root ratio.

Most importantly, the length of the taproot was greater in the drought-treated plants than the control plants at the end of the drought and recovery periods (Tables 3 and 5). Our observation in two different cotton genotypes further suggests that increased taproot length, at the expense of thickening, in response to drought may be a common response in cotton. This response may permit cotton plants to survive drought by accessing water from deeper in the soil profile than the soil horizons tapped during periods of adequate water supply.

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