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DIFFERENCES IN STOMATAL RESPONSE WITHIN A COTTON CANOPY

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HITRON O. and ZUR B. *Differences in stomatal response within a cotton canopy.* BIOTRONICS 19, 39–48, 1990. Potted cotton plants were grown in the open to investigate the causes for differences in the dynamic behavior of stomata of top and bottom leaves of cotton plants. Half of the plants were subjected to a six day long drying cycle. The leaf water potential, abaxial (lower leaf surface) and adaxial (upper leaf surface) stomatal resistance, leaf temperature, initial osmotic potential and bulk modulus of elasticity of top and bottom leaves were studied in detail. Our results show that abaxial stomata of bottom leaves have a threshold leaf water potential of -1.3 MPa compared to -2.0 MPa for abaxial stomata of top leaves. The threshold leaf water potential value for adaxial stomata was in the range of -1.0 MPa for both top and bottom leaves. Leaf-air temperature difference was influenced to a large extent by leaf position in the canopy. Initial osmotic potential was similar for top and bottom leaves. Bulk modulus of elasticity was lower in top leaves and decreased with an increase in the level of leaf water deficit. It is postulated that the lower bulk modulus of elasticity of top leaves is responsible for their lower threshold leaf water potential actuating the stomatal feedback system. The observed differences resulted in a delay of two days in the closure of abaxial stomata of top leaves.

Key words: Cotton (*Gossypium hirsutum* L.); top and bottom leaves; stomatal feedback system; bulk modulus of elasticity.

INTRODUCTION

Leaves make up the major surface area through which plants exchange solar energy, carbon dioxide and water vapor with the atmosphere. The distribution of leaves in the canopy space results in mutual shading and in an exponential dissipation of the solar energy flux as it penetrates the canopy space. As a result the radiation load on individual leaves in the canopy is not uniform. Leaves positioned at the outer shell of the upper part of the canopy intercept most of the incoming solar energy flux. As a result, leaves located within the outer shell of the upper part of the canopy assimilate the bulk of the carbon and transpire most of the water. Shaded leaves contribute less than their share in total leaf area to the photosynthetic and transpirational activity of the canopy. Thus, the most productive leaves in the canopy are also the leaves which are most susceptible to the development of damaging water deficits.

Stomatal feedback system can be characterized by the relationship between stomatal resistance, R_s , or stomatal conductance, G_s , and leaf water potential (9, 5). Such a relationship can be divided into two major parts, a non-sensitive part terminated by threshold leaf water potential and a sensitive part where stomatal resistance increases, G_s decreases, with a further decrease in leaf water potential. Therefore, the threshold leaf water potential for the initiation of stomatal closure and the leaf water potential representing complete stomatal closure characterize the stomatal feedback system. The specific characteristics of the stomatal feedback control system is different for different plants (1, 9).

Turner and Incoll (12) and Turner and Begg (11) were among the first to report higher stomatal resistance values in leaves at the bottom of the canopy, compared to leaves at the top of the canopy, for water stressed maize, sorghum and tobacco plants. Their results suggest that the top leaves of these plants were less sensitive to the development of water deficits. Turner and Begg (11) attributed their observations to the fact that lower leaves are exposed to lower radiation levels and are at various stages of senescence. Jordan *et al.* (5) reported similar behavior in greenhouse grown water stressed cotton plants. They explained the observed differences in stomatal response between bottom and top leaves as a result of differences in their age rather than a result of differences in light intensity. Their observed differences in stomatal response could not be explained by the loss of potassium from older leaves or by the accumulation of abscisic acid. Kirkham and Smith (6) reported lower leaf water and osmotic potentials and higher turgor potentials in top leaves than in bottom leaves of some wheat cultivars. Stomatal resistance of both upper and lower leaf surfaces was lower in top leaves than in bottom leaves of these wheat cultivars, suggesting a different stomatal response in top and bottom leaves.

The objectives of the present study were to characterize the stomatal feedback systems of upper and lower surfaces of top and bottom leaves of cotton plants, to investigate its origin and to assess its importance during the development of water deficits.

MATERIALS AND METHODS

Five Cotton seeds (*Gossypium hirsutum* L. S.J.2) were planted into 5.2 kg dry clay soil, packed into a black plastic bag 20 cm in diameter up to a height of 30 cm. Eighty bags were placed in rows 20 cm apart and the distance between rows was 50 cm. Irrigation was applied following the planting date, August 22 1984, placing individual emitters into each bag. Water was applied daily to bring the soil to field capacity (47% by weight). Ten days after planting the seedlings were thinned to two plants per bag.

A six day drying cycle treatment, in which water was withheld from the plants, was initiated 60 days after planting on half of the bags. During this period the other half of the bags continued to be irrigated daily and is referred to as the wet treatment. During the drying cycle the following measurements were taken from leaves on the main stem: leaf water potential, stomatal resistance, temperature,

initial osmotic leaf water potential and leaf bulk modulus of elasticity.

Top leaves were defined as the leaves occupying the third position from top leaf. Bottom leaves were defined as the leaves occupying the sixth position from top leaf. Plants were selected randomly from each treatment for the various tests. Pairs of measurements of top and bottom leaves were always taken from the same plant. Statistical tests were performed with SAS-82 (8).

Stomatal resistance to water vapor diffusion was measured using a transient porometer (Li-Cor-700). Four to five readings were taken from each side of the sampled leaves. Abaxial and Adaxial resistances were computed from the average of the last three readings. Leaf resistance was calculated assuming parallel resistance of abaxial and adaxial leaf surfaces. Leaf water potential was measured using a commercial pressure bomb (Soil Moisture Equipment Inc. 3005), using a procedure recommended by Turner (10). These measurements followed immediately the measurements of stomatal resistance. Measurements of leaf water potential and stomatal resistance were taken five to seven times per day from each treatment during daylight hours. At each sampling three to four top leaves and three to four bottom leaves were used for these measurements. Leaf temperatures were measured using copper-constantan thermocouples. The thermocouple junction was attached to the lower surface of the cotton leaves with the aid of a fast hardening glue. Each data point is an average of two measurements of two different leaves. Leaf and air temperatures were recorded every two minutes during noon hours. Temperature readings were averaged and represent daily noon-time values. Initial leaf osmotic potential and leaf bulk modulus of elasticity were obtained from measurements of pressure-volume curves (13), determined on leaves from the main stem. For these measurements leaves were sampled during early morning hours and cut under water to prevent entrance of air bubbles. Prior to the pressure-volume test leaves were placed in a humidified dark chamber for a period of 90 to 120 min in order to assure their water saturation (10). The cumulative volume of sap collected from the cut petiole was plotted as a function of the inverse of the applied pressure. Initial leaf osmotic potential was obtained from the intercept of the linear part of the curve with the y-axis which represents the osmotic potential at saturated cell volume.

Bulk modulus of elasticity of the cotton leaves were estimated from the local slope of the curves relating turgor potential to leaf water content multiplied by the maximal volume of water stored in these leaves.

RESULTS AND DISCUSSION

The effectiveness of the experimental treatments on the noon values of the water potential of cotton leaves is demonstrated in Fig. 1. Under the wet treatment noon leaf water potential values were essentially constant at -0.5 MPa for both top and bottom leaves. In the plants subjected to a drying cycle noon leaf water potential values decreased, slowly at first and then faster, as the drying cycle progressed. On the sixth day of the drying cycle noon leaf water potential values of the top leaves decreased to -2.6 MPa compared to -2.3 MPa for the bottom

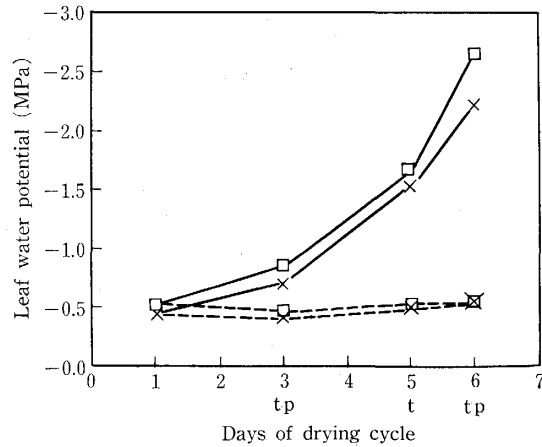


Fig. 1. Noon values of leaf water potential during the drying cycle. —, dry treatment; ----, wet treatment; □, top leaves; ×, bottom leaves; p, leaf position differed significantly; t, treatments differed significantly.

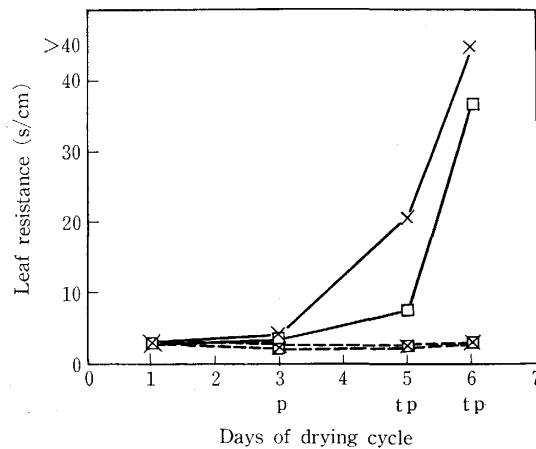


Fig. 2. Noon values of leaf resistance during the drying cycle. —, dry treatment; ----, wet treatment; □, top leaves; ×, bottom leaves; p, leaf position differed significantly; t, treatments differed significantly.

leaves.

Noon values of leaf resistance are presented in Fig. 2. Cotton leaves under the wet treatment had an essentially constant value of stomatal resistance of 4 s/cm during noon hours throughout the test period. For the first three days of the drying cycle leaf resistance values of top and bottom leaves were maintained at about 4 s/cm. On days 5 and 6 noon leaf resistance values increased considerably in both top and bottom leaves and were significantly higher for the bottom leaves. Stomatal closure was reached on day 6 for both top and bottom leaves. Jordan *et al.* (5), Kirkham and Smith (6) and others also reported higher resistance values and lower leaf water potentials in top leaves than in bottom leaves.

Average noon values of leaf-air temperature differences are presented in Fig. 3. Three important phenomena become apparent from the examination of these results. Under the wet treatment top leaves maintained higher noon leaf-air temperature

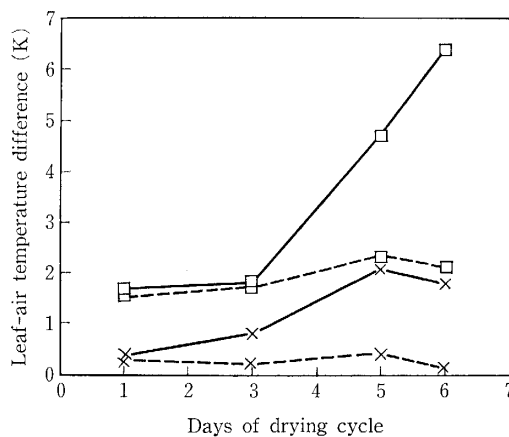


Fig. 3. Noon values of leaf-air temperature difference during the drying cycle. —, dry treatment; ----, wet treatment; □, top leaves; ×, bottom leaves.

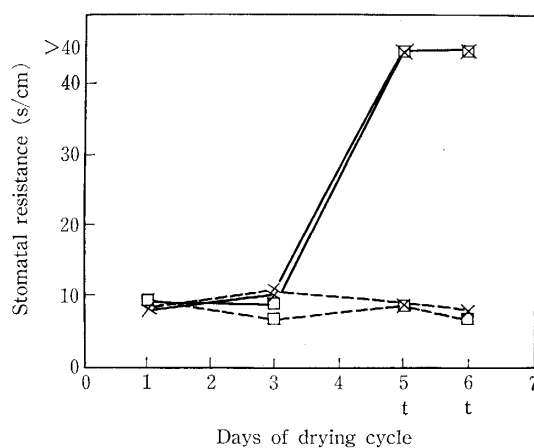


Fig. 4. Noon values of adaxial stomatal resistance during the drying cycle. —, dry treatment; ----, wet treatment; □, top leaves; ×, bottom leaves; t, treatments differed significantly.

differences than bottom leaves. This was also the case under the drying treatment in spite of the fact that during the last two days of this treatment stomatal resistance of bottom leaves was higher than that of top leaves. Top unstressed leaves under the wet treatment had a higher leaf-air temperature difference than that of bottom water stressed leaves under the drying treatment. Clearly, leaf-air temperature differences measured in the present study suggest that leaf position can influence this value almost as much as the degree of water deficit in the leaves.

It is of interest to examine separately the adaxial and abaxial (upper and lower leaf surfaces) stomatal resistance values of the cotton leaves. Noon values of adaxial stomatal resistance, Fig. 4, under the wet treatment were maintained at 8 s/cm throughout the test period for both top and bottom leaves. Noon values of adaxial stomatal resistance of both top and bottom leaves dramatically increased to over 40 s/cm on day 5 and remained at the same level on day 6. Noon values of

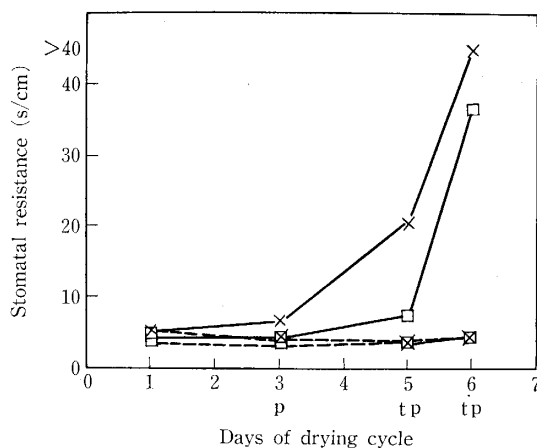


Fig. 5. Noon values of abaxial stomatal resistance during the drying cycle. —, dry treatment; ----, wet treatment; □, top leaves; ×, bottom leaves; p, leaf position differed significantly; t, treatments differed significantly.

abaxial stomatal resistance, Fig. 5, under the wet treatment were in the range of 3 s/cm for both top and bottom leaves throughout the test period. Noon values of abaxial stomatal resistance under the drying treatment increased substantially after the third day of drying. At all times the resistances of the abaxial stomata of top leaves were significantly lower than for those of the bottom leaves. Abaxial stomata of both top and bottom leaves were essentially closed on day 6.

Our results show that noon values of leaf water potential were significantly lower for top leaves, that noon values of leaf stomatal resistance and abaxial stomatal resistance were significantly higher for the bottom leaves. Noon leaf water potential values of top leaves were lower throughout the drying cycle and yet their noon leaf stomatal resistance values were consistently lower than those of bottom leaves. Thus it is apparent that the sensitivity of stomatal resistance to leaf water potential of bottom leaves of our cotton plants was different than that of top leaves. Similar observations were reported by Jordan *et al.* (5), Turner (9) and Kirkham and Smith (6). The relationships between noon values of leaf water potential and abaxial and adaxial stomatal resistances are presented in Fig. 6 for top leaves and in Fig. 7 for bottom leaves. The dispersion of our experimental results suggests that small differences in light intensity and probably other factors in addition to leaf water potential could influence stomatal resistance. Results presented in Fig. 6 suggest that the threshold leaf water potential for abaxial stomatal resistance of top leaves is about -2.0 MPa. Under lower leaf water potential values abaxial stomatal resistance rises quickly and stomata are essentially closed at a leaf water potential of about -2.5 MPa. The threshold leaf water potential for adaxial stomatal resistance of top leaves is estimated to be -1.0 MPa. Adaxial stomata of top leaves were essentially closed at a leaf water potential of -1.4 MPa.

The relationships between stomatal resistance and leaf water potential for bottom leaves are presented in Fig. 7. Threshold leaf water potential for abaxial stomatal resistance was estimated to be -1.3 MPa. Abaxial stomata were essentially closed when leaf water potential reached a value of about -2.3 MPa. The

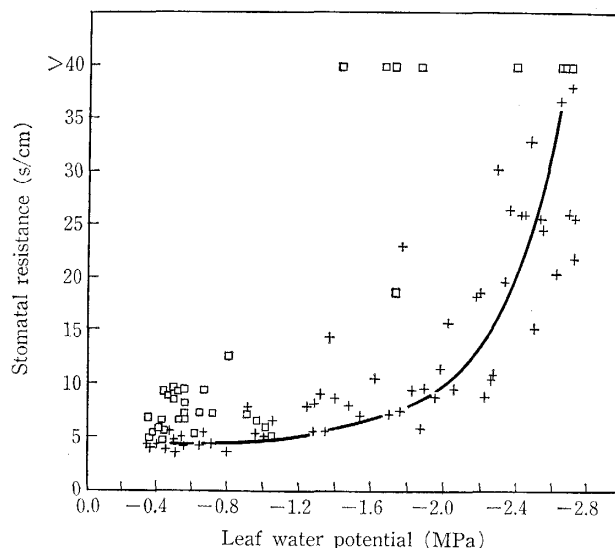


Fig. 6. Relation of stomatal resistance to leaf water potential for top leaves. □, adaxial leaf surface; +, abaxial leaf surface.

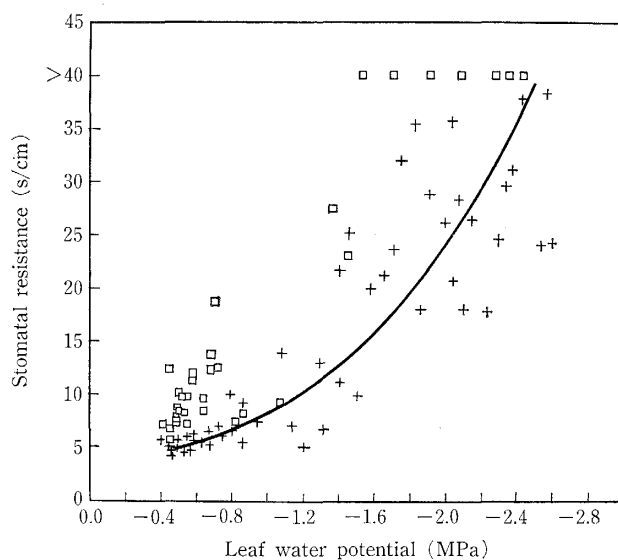


Fig. 7. Relation of stomatal resistance to leaf water potential for bottom leaves. □, adaxial leaf surface; +, abaxial leaf surface.

range of leaf water potentials in which adaxial stomata of bottom leaves were at various stages of closure was rather narrow. It is estimated that the threshold leaf water potential was about -1.0 MPa, and that adaxial stomata were essentially closed at leaf water potential of about -1.5 MPa.

The critical leaf water potential values estimated from our measurements on the cotton leaves were in the range of -1.3 to -2.0 MPa. Jordan and Ritchie (4) reported a critical leaf water potential value of -1.7 MPa for greenhouse grown

cotton plants. Under field conditions, where cotton plants experienced gradual increases in water deficits, stomatal resistance did not change even when leaf water potential reached values of -2.7 MPa. Similar observations were reported by Brown *et al.* (2), McMichael and Hesketh (7) and by Cutler and Rains (3). Thus, our experimental plants did not show any signs of adapting to soil water or environmental stresses because of the fast rate of water deficit development. The observed differences between the critical leaf water potential values of abaxial stomata of top and bottom leaves could then be the outcome of within canopy acclimation to leaf position with the resulting differences in the radiation load and in the transpiration flux. The influence of leaf position is confounded with that of leaf age and therefore difficult to separate.

Changes in the threshold leaf water potential could be the result of either changes in the initial osmotic potential or in the bulk modulus of elasticity of the cotton leaves. Estimated values of the initial osmotic potential of cotton leaves according to their position down the main stem are presented in Table 1. These values are averages of two samplings taken at the beginning and in the middle of the drying cycle. The leaves could be grouped into two major groups, leaves number 3 and 4 representing the top leaves and leaves number 5, 6 and 7 representing bottom leaves. Clearly, the differences in the estimated values of the initial osmotic potential between top and bottom leaves are too small and not significant.

Table 2 presents estimated values of the bulk modulus of elasticity of cotton leaves according to their position on the main stem and for three values of leaf

Table 1. Initial osmotic potentials of leaves along the main stem

Initial osmotic potential (MPa)		Leaf position
-1.65	A	3
-1.59	AB	4
-1.48	B	5
-1.54	B	6
-1.72	A	7

Numbers increase from top to bottom.

Different letters indicate statistical significance.

Table 2. Bulk modulus of elasticity of leaves of the main stem for three water potentials

Bulk modulus of elasticity (MPa)			Leaf position
lwp=-1.0	lwp=-0.75	lwp=-0.5	
13.2	18.5	24.6	3
12.4	19.7	23.5	4
15.8	19.2	26.2	5
18.5	22.8	28.7	6
18.2	23.0	29.4	7

Numbers of leaf position increase from top to bottom.

lwp=leaf water potential.

water potential representing three levels of water deficit development. Values of the bulk modulus of elasticity were higher for the bottom leaves than for the top leaves. This was true under the three average leaf water potentials. Also, values of the bulk modulus of elasticity decreased as the average leaf water potentials became more negative for all leaves. A lower value for the bulk modulus of elasticity represents a situation where the cell walls are more elastic and therefore the turgor potential is less sensitive to changes in leaf volume as a result of water loss. Also, the results in Table 2 suggest that for both leaf groups a decrease in leaf water potential, representing a loss of water from the leaves, results in a decrease in the bulk modulus of elasticity and therefore a decreased sensitivity of the turgor potential to additional water loss. Thus the top leaves, which are exposed to the full intensity of the radiation load, are better equipped to resist the potentially dangerous water loss and the resulting stomatal closure by preventing a damaging decrease in their turgor potential. It is not possible to establish whether the changes in bulk modulus of elasticity are a result of leaf aging or leaf position. However, the observed changes make sense in terms of inter canopy adaptation to the radiation load.

Results presented in Figs. 2 and 5 show that stomata of top leaves and specifically abaxial stomata exhibited a significant increase in resistance on day 5 and were completely closed on day 6 of the drying cycle. Stomata of bottom leaves started their significant increase in resistance probably on day 4 and were completely closed somewhere between days 5 and 6. It is probable that these differences in the dynamics of stomatal response to water deficits were due to differences in the bulk modulus of elasticity between top and bottom leaves.

CONCLUSIONS

Our results clearly demonstrate that there are definite differences in behavior between adaxial and abaxial stomata and between stomata of top and bottom leaves. Generally, adaxial stomata from both top and bottom leaves stay open only under very mild plant water deficits. Once leaf water potential decreases to values in the range of -0.6 to -1.0 MPa adaxial stomata close down. Below those critical potential values adaxial stomata are normally closed and gas exchange takes place through abaxial stomata only.

The biggest difference in the stomatal feedback systems between top and bottom leaves was found in abaxial stomata. Abaxial stomata of top leaves had a lower threshold leaf water potential (-2.0 MPa compared to -1.3 MPa for bottom leaves) and stayed partially open for two days longer than abaxial stomata of bottom leaves during the 6 day drying cycle. It is reasonable to assume that under field conditions the extra time of open abaxial stomata of top leaves would be longer.

The observed differences in the behavior of abaxial stomata between top and bottom leaves was not a result of an overall plant adjustment to water deficits. The development of water deficits during the six day drying cycle was too fast to facilitate adjustment. Rather, these differences are a result of intra canopy responses

to differences in the aerial environment to which different leaves in the canopy are exposed. Top leaves managed to maintain their turgor potential through changes in their bulk modulus of elasticity and as a result delayed the actuation of the stomatal feedback system. The observed increase in bulk modulus of elasticity as we move down the main stem could be the result of leaf age as well as leaf position.

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