

Effects of N Fertility on Plant Water Relations and Stomatal Responses to Water Stress in Irrigated Cotton¹

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ABSTRACT

Cotton (*Gossypium hirsutum* L.) was grown in Phoenix, AZ, in 1981 and 1982. In both years it was irrigated with either 10 or 15 cm of water per application; N was supplied at three rates within each water treatment. Stomatal conductances of the most recently expanded leaves were followed during irrigation cycles to determine effects of N fertility on stomatal responses to water stress. Differences in N status between treatments were small in 1981 but were much greater in 1982. In July 1982 (early in the fruiting period), stomata of low-N plants closed as leaf turgor neared zero, but stomata of high-N plants remained open well past this point. As the season progressed, the differential response to water stress was lost as stomata of high-N plants became more responsive to declining water potentials. Nitrogen had little effect upon predawn osmotic potential (determined by pressure-volume procedures as the water potential for zero turgor), but low N eliminated the diurnal osmotic cycling seen in high-N plants. Diurnal oscillations of osmotic potential in high-N plants had an amplitude of 0.4 MPa early in the fruiting period, then declined to zero only to reappear as fruits matured and vegetative growth resumed. Nitrogen concentrations of the most recently expanded leaves also increased during regrowth. Seasonal changes in stomatal responses to water stress seemed unrelated to either osmotic potentials or overall leaf N status. The loss of the differential response to stress did coincide roughly with a decline in petiole nitrate-N concentrations to very low levels in all treatments. Seedcotton yields were significantly affected by water in 1981 and by water and N in 1982. In the 2nd year, full irrigation increased yields only on high N; on low N, full irrigation did not affect yield but greatly decreased water-use efficiency. The effects of N fertility on stomata explain in part the complex effects of N on water use.

Additional index words: *Gossypium hirsutum* L., Stomatal conductance, Osmotic adjustment, Water-use efficiency, Leaf area index.

THE growth and yield of cotton (*Gossypium hirsutum* L.), like most crops, depend strongly upon the availability of N and water during the season. Management of these two inputs has received much attention. Several investigators have reported a significant interaction of N and water on yield (2, 5, 16). The primary effect of N may be to prolong the productive season by delaying maturity (5). However, Scarsbrook et al. (16) also found an interaction of N and water on water-use efficiency (WUE), suggesting that the two factors may affect the relationship between transpiration and biomass production (or harvest index). The fundamental plant water relations which may underlie such changes have not been reported.

Recent work showed that in controlled environments, N nutrition exerts complex effects on cotton plant water relations. Suboptimal N increases stomatal closure in response to water stress (12, 14, 15). This increased closure during drought results from both greater accumulation of abscisic acid (ABA) in

stressed leaves and greater stomatal response to increments of leaf ABA (12, 15). Similar effects of N on stomatal behavior have been seen in bean (*Phaseolus vulgaris* L.) (17), tea (*Camellia sinensis* L.) (10), and *Panicum maximum* grown in controlled environments (8), but not in wheat (*Triticum aestivum* L.) (9), coffee (*Coffea arabica* L.) (18), or *P. maximum* grown outdoors (8). This paper describes experiments to explore the effects of N fertility on water relations and stomatal behavior of irrigated cotton in the field, and to compare those effects to effects on yield and WUE.

MATERIALS AND METHODS

Experiments were conducted at the Univ. of Arizona Cotton Research Center, Phoenix. The soil is an Avondale clay loam (a member of the fine-loamy, mixed, hyperthermic family of Typic Torrifluvents). Preplant irrigations were applied to wet the soil throughout the rooting zone. 'Deltapine 70' cotton was planted in rows 1 m apart on 2 Apr. 1981 and 7 Apr. 1982 and thinned after emergence to populations of about 100 000 plants ha⁻¹. After thinning, berms were constructed around basins 10 rows wide × 30 m long arranged in a 6 × 6 Latin square. During subsequent irrigations, water was pumped into each basin through gated pipe. In 1981, all plots were irrigated on 21 May, 12 and 26 June, 9 and 24 July, and 7 and 24 August. In 1982, all plots were irrigated on 26 May, 18 June, 1, 15, and 29 July, and 13 August. The intermediate- and high-N plots also received water on 25 Aug. 1982. Plots received either 10 or 15 cm at each irrigation. The latter amount allowed evapotranspiration to proceed at essentially the potential rate through most of the 2-week cycle (3). Total water applied during the season (including rainfall) was 137 and 102 cm for the fully irrigated and stressed plots in 1981, and 140 and 104 cm for the same plots in 1982 (except that the low-N plots received 125 and 94 cm in 1982).

In both years, three N rates were studied. In 1981, plots received either a preplant application of N (low N), a preplant plus one postplant application (intermediate N), or a preplant plus two postplant applications (high N). The first and second postplant applications were on 3 June and 22 July. The total N applied (as urea) was 77, 161, and 218 kg ha⁻¹ in the three treatments. In 1982, the low-N treatment received no applied N. In the fully irrigated plots, the intermediate and high-N treatments received 161 and 240 kg ha⁻¹ as preplant plus postplant applications. In the stressed plots, the N rates were 84 and 163 kg ha⁻¹ applied postplant in the intermediate- and high-N treatments, respectively. These rates include 22 kg ha⁻¹ urea-N applied to high-N plots as foliar sprays during August. The surface soil contained 24 mg kg⁻¹ NO₃-N before 1982 planting (mean across all treatments). No soil tests were run in 1981.

Crop N status was followed in both years by analysis of petiole NO₃-N. Petiole samples were collected weekly, dried, ground to pass a 40-mesh screen, extracted with hot water, and analyzed by a modification of the technique of Cataldo et al. (1). In 1982, reduced N was also determined in expanded leaves at the top of the canopy. Sampling was

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limited to low-N and high-N plots during the last half of the season. Three leaves from each plot were harvested, frozen, and lyophilized, then digested and analyzed as described (11). Because NO_3^- -N levels were low, the reduced N was assumed to be equivalent to total N.

Stomatal conductances were determined with a LiCor³ LI-1600 steady state porometer. Measurements were restricted to the early afternoon (between 1230 and 1430) on sunny days and were taken only on recently expanded leaves in full sunlight near the top of the canopy. Leaf temperatures, measured with the same instrument, varied between 34 and 40°C. Reported leaf conductances are the sums of parallel conductances of the abaxial and adaxial surfaces and are means of at least two determinations on separate leaves per plot. Simultaneously with the stomatal measurements, leaves were sampled for determination of xylem pressure potentials (hereafter equated with leaf water potentials, Ψ_w) with a pressure chamber. Leaves were immediately sealed in plastic bags upon excision and were stored in a moist insulated container until analysis.

Leaf areas and other indicators of plant growth were determined through the season on weekly harvests of all plants within a 1-m section of a row (1 m² ground area). Each time, two of the six replicate plots of each treatment were sampled. Leaf areas were measured with a LiCor LI-3000 leaf area meter. Data are tabulated for the period between the cessation and the resumption of vegetative growth (cutout). Numbers of flowers and bolls were also monitored.

Osmotic potentials (Ψ_π) of leaves were assessed both before dawn and in the early afternoon by a pressure-volume technique. Leaves harvested predawn were brought to the laboratory and immediately treated as described earlier (15). Leaves harvested in the afternoon were rehydrated overnight with their petioles in water, then subjected to the pressure-volume procedure the next morning. Tests showed that leaf Ψ_π increased by approximately 0.15 MPa during rehydration (comparisons made at the same water content). Therefore, the Ψ_π readings of the afternoon samples were corrected for this change. In all cases, the water potential for zero turgor (wilting point) was estimated from the pressure-volume curves and was taken as a measure of leaf Ψ_π . Determinations were made approximately 1 week after irrigations. Each reported value is the mean of six leaves, one from each replicate plot.

Seedcotton yields were measured on two interior rows of each plot and were used to calculate water-use efficiency. Soil water content was followed through the season with neutron probes. A single access tube was placed in a yield row of each plot, about 8 m from the end. Once each week, soil water content was measured in 30-cm strata to a depth of 180 cm. Reported WUE values are based upon measured soil moisture depletion within the six strata comprising the root zone.

For greenhouse experiments, plants were grown in large redwood bins filled with 0.6 m³ of a synthetic rooting mix. Each bin contained 16 plants. The bins were watered three times per week with 16 L of half-strength Hoagland solution containing 5 mM NO_3^- (high N) or 1 mM NO_3^- + 4 mM Cl^- (low N). Water was applied as needed between fertilizations. During fruiting, the N levels of both nutrient solutions were doubled. On the date of first flower appearance, one bin was switched from high N to low N, while

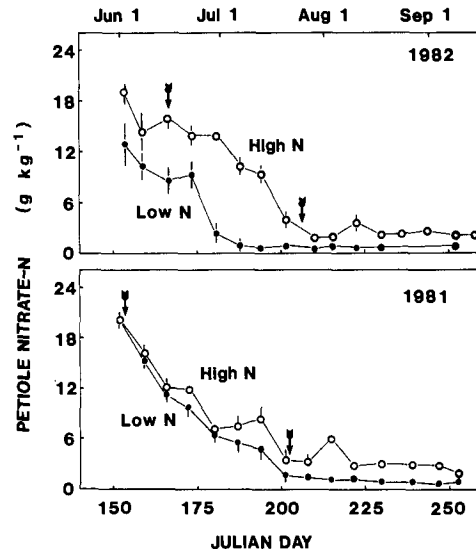


Fig. 1. Petiole NO_3^- -N levels of cotton plants in 1981 and 1982. Arrows indicate times of postplant applications of N to high-N plots. Values are shown \pm 1 SE, except for those points with an SE less than 400 mg kg^{-1} .

other bins were maintained on each of the two nutrient solutions. Plants were then grown to the cessation of flowering (cutout), at which point watering was stopped. Stomatal conductances and leaf water potentials were followed during drying. The petioles of leaves used in the pressure chamber were detached, dried, and combined for NO_3^- -N analysis. When stomatal conductances had declined to low values, the bins were rewatered and three representative leaves from each bin were detached the following day for osmotic determinations by the pressure-volume procedure.

Standard statistical procedures were followed for analysis of variance (ANOVA) (6). Treatment means were separated by Duncan's Multiple Range Test (6). Regressions and correlations were calculated by standard programs on a Wang 2200S minicomputer (19).

RESULTS AND DISCUSSION

The normal irrigation scheme in Phoenix is to apply 15 cm every 2 weeks from before flowering to maturity (4). Even though irrigating on that schedule but with less water (10 cm) increased water stress toward the end of the irrigation cycle, there was no significant effect on leaf Ψ_π or on the relationship between stomatal conductance and leaf Ψ_w . Therefore, data on stomatal behavior are combined across irrigation levels. Growth and yield were affected by irrigation regime, though, and these data are reported separately.

In 1981, both low-N and high-N plots received a preplant application of N. Petiole analyses showed little difference in N status between the high-N and low-N plots during the early part of the season (Fig. 1; data shown only for the fully irrigated plots). Beginning in late July, petiole NO_3^- -N levels stabilized at about 2500 and 500 mg kg^{-1} for high-N and low-N plants, respectively. In 1982, the low-N plots received no preplant N, and treatment differences in petiole NO_3^- -N levels were much greater than in 1981 until late July (Fig. 1). However, after the second postplant application of N to high-N plots, petiole

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NO_3^- -N stabilized at the same levels as in 1981. In the intermediate-N treatment, petiole NO_3^- -N levels were intermediate to the values shown. In the water-stressed plots, petiole NO_3^- -N levels tended to be lower than in fully irrigated plots, but the effects of N and of time were the same as shown.

In 1981, growth rates and leaf areas indicated no serious N deficiency in the low-N plots. This failure could have been from high residual soil N, as the plots were in only the 2nd year after alfalfa. With both high N and low N, the leaf area index (LAI) reached unusually high values exceeding 6.0 (not shown). In 1982, the low-N treatment was more severe, and the N deficiency was readily apparent. Both low N and insufficient water advanced the onset of cutout (Table 1). During cutout, plants grown on either low N or insufficient water were shorter, with fewer mainstem nodes and less leaf area (Table 1). In none of these cases were the effects additive. Both low-N and high-N plants underwent substantial regrowth near the end of the season.

Stomatal conductances and leaf water potentials were followed during irrigation cycles throughout the

Table 1. Dates for the cessation of boll set in 1982, and crop characteristics during cutout. Means within a column followed by the same letter are not different at the 95% probability level.

Treatment	Cessation of boll set	Plant height cm	Mainstem nodes no. plant ⁻¹	Leaf area index
10-cm irrigations				
Low N	21 July	71 a	23 a	2.2 a
High N	21 July	79 a	25 a	3.3 b
15-cm irrigations				
Low N	28 July	77 a	23 a	2.4 a
High N	11 August	91 b	28 b	4.8 c

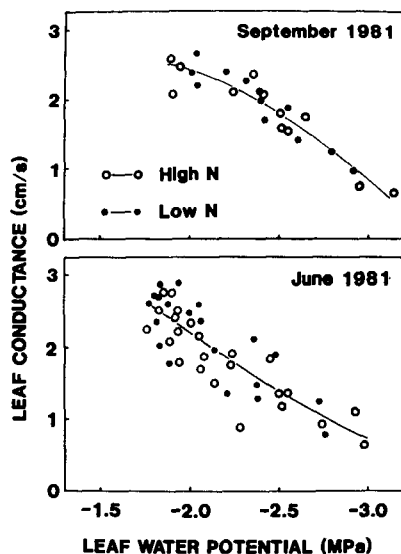


Fig. 2. Relationship between leaf water potential and leaf conductance to water vapor during two irrigation cycles in 1981. Data from 10-cm and 15-cm irrigation treatments are combined. Quadratic regressions were fitted to pooled data from low-N and high-N plots as follows: for June, $Y = 7.297 - 3.30x + 0.37x^2$ ($r = 0.844$); for September, $Y = 1.192 + 2.02x - 0.71x^2$ ($r = 0.937$).

season. In 1981, at no time did N application alter the relationship between Ψ_w and stomatal conductance. In June, incipient stomatal closure occurred at about -1.8 MPa in both high-N and low-N plants (Fig. 2). Conductance had decreased by 50% at about -2.5 MPa. In September, stomata began to close at about -2.0 MPa and half-maximum conductance occurred at -2.8 MPa for both N levels (Fig. 2).

In 1982, effects of N on stomatal behavior were evident early in the fruiting cycle (Fig. 3). In mid-July, stomata of high-N plants closed slowly over the entire range of Ψ_w but stomata of low-N plants closed more rapidly beginning at about -1.7 MPa. The points of 50% closure were separated by an estimated 0.5 MPa. In early August, the separation between N treatments was decreased to about 0.2 MPa and, in early September, stomatal responses to water stress were not detectably different. Thus, over a 2-month period the stomatal responses to stress in high-N and low-N plants became identical.

Leaf osmotic potentials were followed throughout the season in 1982 by determining the Ψ_w for zero turgor (wilting point). In high-N plants there was significant diurnal osmotic cycling (the Ψ_s decreased 0.2 to 0.4 MPa from before dawn to early afternoon) which depended upon the stage of plant growth. The amplitude of the diurnal osmotic cycling reached a peak in mid-July, then rapidly declined to zero as the fruit load became larger in late July and August (Fig. 4). In early September, when the fruits had mostly matured and growth had resumed, diurnal osmotic cycling reappeared. Predawn Ψ_s remained relatively stable throughout the season at about -1.8 MPa. In low-N plants there was no diurnal osmotic cycling at any time during the season (Fig. 4). Both predawn and afternoon Ψ_s remained at -1.8 to -1.9 MPa

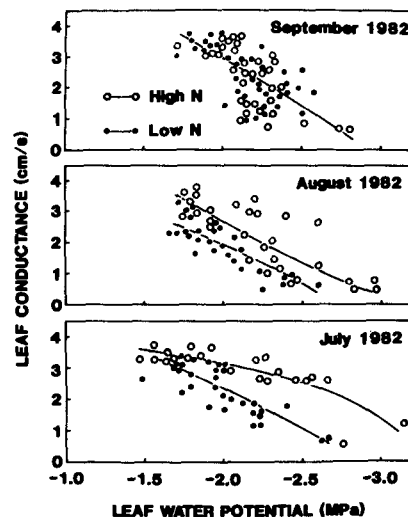


Fig. 3. Relationship between leaf water potential and leaf conductance to water vapor during three irrigation cycles in 1982. Data from 10-cm and 15-cm irrigation treatments are combined. Quadratic regressions were fitted to data from low-N and high-N plots (except for September data which were pooled for analysis) as follows: July, low N, $Y = 4.950 - 0.30x - 0.52x^2$ ($r = 0.826$); July, high N, $Y = 1.177 + 2.90x - 0.95x^2$ ($r = 0.846$); August, low N, $Y = 3.347 + 0.87x - 0.78x^2$ ($r = 0.815$); August, high N, $Y = 7.798 - 2.54x + 0.011x^2$ ($r = 0.844$); September, $Y = 8.390 - 2.37x - 0.17x^2$ ($r = 0.680$).

until September, when they both began to decrease rapidly (indicative of long-term osmotic adjustment). This late-season change is attributable to severe water stress after the cessation of irrigation. The data shown are for fully irrigated plots only. In stressed plots, effects of N were similar but diurnal osmotic cycling in high-N plants occurred for a slightly shorter period (data not presented).

In both July and August, the divergence in stomatal response to stress (Fig. 3) greatly exceeded the differences in Ψ_s (Fig. 4), whether the predawn or afternoon Ψ_s 's are compared. Thus, little of the N effect on stomatal behavior can be explained as an effect on Ψ_s and turgor maintenance. In early September, N had no effect upon either afternoon Ψ_s or stomatal response to water stress.

The seasonal loss of the N effect on stomatal behavior resulted mostly from increasing sensitivity to stress in high-N plants, rather than decreasing sensitivity in low-N plants (Fig. 3). In high-N plants early in the fruiting cycle, stomata remained open considerably past the leaf wilting point (Fig. 3 and 4). The loss of this tendency could have been associated with late-season N withdrawal from leaves of the high-N plants (Fig. 1). However, the N levels of both high-N and low-N leaves increased during the late season as plants emerged from cutout (Table 2). Further, an effect of N fertility on leaf N level persisted even as stomatal responses to stress converged. Thus the seasonal patterns of stomatal behavior seemed unrelated to total N levels of the leaves. Nonetheless, the shift in stomatal responses of high-N plants did coincide with a decline in petiole NO_3^- -N levels (Fig. 1). This relationship was explored further in experiments in the greenhouse. Plants were grown on nutrient solutions containing low N or high N or they were switched from high N to low N at first flower. The last treatment was designed to simulate declining N availability in the field. In the high-N plants, stomatal

closure began at a Ψ_w of -2.1 MPa and was 50% complete at about -2.5 MPa (Fig. 5). In both low-N plants and plants switched from high N to low N, stomatal closure commenced at -1.8 MPa and was 50% complete at about -2.1 MPa. Thus, the convergent responses to stress of field-grown plants could be mimicked in the greenhouse by partial withdrawal of the N supply from high-N plants during the fruiting period. Midday Ψ_s 's of the high-N, high→low-N, and low-N plants were -2.5 , -2.4 , and -2.2 MPa, respectively. Petiole NO_3^- -N levels were 2492, 1120, and 868 mg kg^{-1} for the same treatments, respectively.

Table 2. Nitrogen concentration of recently expanded leaves in 1982. Any means followed by the same letter are not significantly different at the 95% level.

Treatment	Nitrogen concentration	
	28 July	3 September
	g kg^{-1}	
10-cm irrigations		
Low N	25.9 a	30.8 b
High N	30.6 b	37.7 d
15-cm irrigations		
Low N	26.7 a	31.6 b
High N	33.2 bc	35.2 cd

Table 3. Seedcotton yields and water-use efficiencies of cotton plants in 1981 and 1982. Means within a column followed by the same letter are not different at the 95% probability level.

Treatment	Seedcotton yield		Water-use efficiency	
	1981	1982	1981	1982
	kg ha^{-1}		$\text{Mg ha}^{-1} \text{ m}^{-1}$	
10-cm irrigations				
Low N	4391 a	2917 a	4.55 a	3.24 b
Intermediate N	4335 a	3650 bc	4.49 a	3.66 c
High N	4391 a	3390 b	4.55 a	3.43 bc
15-cm irrigations				
Low N	5936 b	2865 a	4.49 a	2.65 a
Intermediate N	5811 b	4203 d	4.39 a	3.55 bc
High N	5883 b	3956 cd	4.45 a	3.21 b

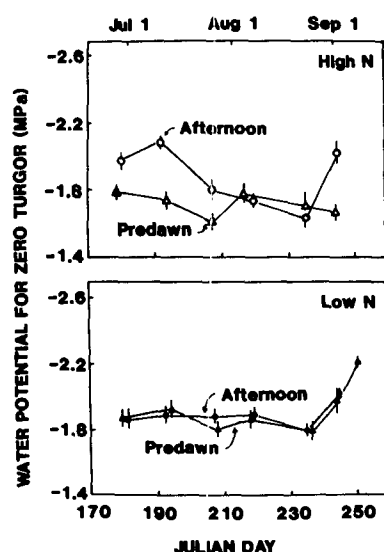


Fig. 4. Osmotic potentials (water potentials at zero turgor) of leaves harvested before dawn or in the early afternoon during the 1982 season. Osmotic potentials were determined with a pressure-volume technique. Each value is the mean of six determinations and is shown \pm one SE.

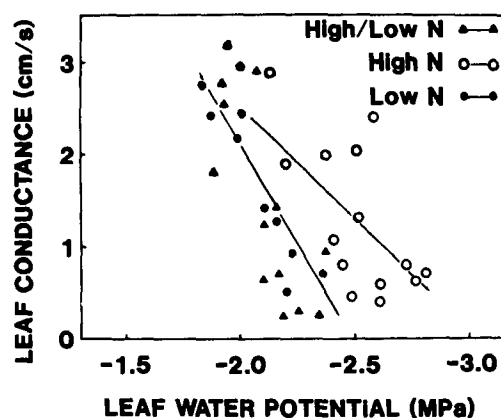


Fig. 5. Leaf conductances to water vapor in greenhouse-grown plants during imposed drought. Plants were grown on high-N or low-N nutrient solutions, or they were switched from the former to the latter at first flower. Measurements were taken after the onset of cutout. Linear regressions were fitted to high-N data and to pooled data from low-N and high-N→low-N plants as follows: for high N, $Y = 7.378 - 2.44x$ ($r = 0.654$); for low N and high N→low N, $Y = 11.037 - 4.47x$ ($r = 0.784$).

In vegetative cotton plants grown in controlled environments, high N delays stomatal closure during an imposed drought (12, 14, 15). Data presented here extend these observations to the field. Stomatal behavior seemed to be affected by plant N status, in that differences between N treatments were most easily apparent when petiole NO_3^- -N levels were grossly different (i.e., the early part of the season). The results from the greenhouse experiments are consistent with this interpretation. One should note, though, that the convergence of stomatal behavior in low-N and high-N plants lagged behind the convergence of petiole NO_3^- -N levels by about 1 month. Despite the apparent correspondence with petiole NO_3^- -N levels, stomatal behavior seemed unrelated to total leaf N. This indicates that stomatal closure was conditioned by events elsewhere in the plant (perhaps the root) or that it was affected by some nitrogenous leaf constituent comprising only a very small fraction of the total N.

The interaction of N and plant age on diurnal osmotic cycling deserves comment. It seems likely that the phenomenon results from photosynthesis exceeding translocation during the early portion of the day. Thus, the failure to exhibit this cycling indicates a "source-limited" condition, i.e., sink demands which exceed the ability of the sources to supply them and therefore drain the sources of available solutes. This condition is seen in high-N plants only during the period of most rapid fruit growth (Fig. 4). In low-N plants, though, decreased leaf area and photosynthetic rate apparently convert them into "source-limited" plants throughout the fruiting period. The enhancement of source limitation by low N is opposite to its effect in vegetative cotton plants, in which leaf expansion is the major sink activity and low N specifically inhibits leaf expansion (11, 13).

The physiological effects of N suggested that N might interact with irrigation regime to affect yield and WUE. Crowther (2), Scarsbrook et al. (16), and Hearn (5) reported interactions of N and water on yield, but Jackson and Tilt (7) found no significant interaction. Scarsbrook et al. (16) further found that N increased WUE. Although our experimental design in 1982 was not a true factorial, the level of each factor did affect response to the other. In 1982, N increased seedcotton yield much more in fully irrigated plots than in water-stressed plots. Yields on low N were almost unaffected by irrigation regime, but on high or intermediate N they were significantly increased by full irrigation (Table 3). Applied N also increased WUE much more at the higher irrigation level than at the lower one. The WUE was unaffected by irrigation regime at high or intermediate N, but was improved by the lower irrigation regime at low N (Table 3). In 1981, when N availability was high across all treatments, full irrigation increased yield but high N rates did not. The WUE was unaffected by any combination of applied N and water (Table 3). If all 1981 treatments are considered to have high N availability, then the effects on WUE in the 2 years are consistent. Although low N did not improve WUE, it did allow the amount of applied water to be cut severely in 1982 without further loss of yield.

CONCLUSIONS

High levels of N caused stomata to remain open to very low Ψ_w in irrigated cotton during the early part of the fruiting cycle, but this effect was lost as the season progressed. In July, stomata of high-N plants closed at a Ψ_w considerably below the wilting point; in September, closure occurred much closer to the wilting point. In low-N plants, stomatal closure was more closely associated with the wilting point throughout the season. The changing stomatal behavior of high-N plants was apparently related to petiole NO_3^- -N levels but not to total leaf N. The effects of low N on plant water relations and water use were such that 10-cm irrigations produced as much yield as, and a higher WUE than, 15-cm irrigations.

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