Adaptive Responses of Soybean and Cotton to Water Stress
I. Transpiration Changes in Relation to Stomatal Area and Stomatal Conductance

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Abstract: The adaptive responses of soybean and cotton to various irrigation levels were explored in terms of transpiration, stomatal role in transpiration, leaf temperature ($T_L$) and CO$_2$ assimilation rate ($A_N$). Compared with cotton, soybean showed a lower flow rate of stem sap (FRSS), transpiration rate ($E$), stomatal conductance ($g_s$), stomatal density and $A_N$ and had a smaller stomatal area but larger leaf area, heavier root dry matter and higher $T_L$ at all irrigation levels. Under water stress conditions, FRSS, $E$, $g_s$, and $A_N$ decreased and $T_L$ increased more in soybean than in cotton. Stomatal area decreased in response to water stress though nonsignificantly but stomatal density was not affected by water stress in soybean. Stomatal area decreased significantly in response to water stress in cotton. We concluded that soybean and cotton adapted to water stress differently. Soybean adapted to water stress by reducing transpiration while cotton adapted to water stress by maintaining higher transpiration as compared with soybean. Soybean reduced the transpiration rate by reducing $g_s$. Reduction of $g_s$ in soybean was due to reduced FRSS, which might have resulted from the lower root moisture absorption efficiency. The higher transpiration in cotton was due to a higher $g_s$, which was supported by a higher FRSS, larger stomatal area, and probably the diaheliotropism. The higher $g_s$ and transpiration rate suppressed the increase in $T_L$ thus preventing the decrease of $A_N$ in response to water stress.

Key words: Glycine max (L.) Merr., Gossypium hirsutum L., Leaf movement, Stomatal area, Transpiration, Water stress.

Heliotropic leaf movements have been reported in soybean [Glycine max (L.) Merr.] (Wofford and Allan, 1982) and cotton (Gossypium hirsutum L.) (Ehleringer and Forseth, 1989). Cotton moves its leaves diaheliotropically throughout the day. Soybean leaves face the sun (diaheliotropism) in the morning, leaves avoid direct sunlight by steep inclination angles (paraheliotropism) at midday, and again face towards the sun in the afternoon (Forseth, 1990).

Paraheliotropic leaf movement substantially contributes to avoid heat and drought by reducing the amount of solar radiation incident on the leaf (Shackel and Hall, 1979; Isoda and Wang, 2001). A peanut cultivar with active paraheliotropism controlled leaf temperature mainly by leaf movement; but the cultivar with active diaheliotropism controlled it mainly by transpiration (Isoda et al., 1996). Isoda and Wang (2002) reported that cotton could avoid heat stress by high transpiring ability, while soybean adapted to arid conditions by the combination of paraheliotropic leaf movement and reduced transpiration.

In this study, keeping in view the findings of Isoda and Wang (2002), we compared the drought adaptation mechanism of soybean with that of cotton extensively. The objectives were (i) to explore the role of stomata in regulating the transpiration rate, (ii) to study change in leaf temperature of the two crops due to changes in transpiration, and (iii) to investigate the photosynthetic activities at various irrigation levels in the two crops.

Materials and Methods

The experiment was conducted using 1/2000 a Wagner pots (height 30 cm, average diameter 24 cm) in a greenhouse at the Faculty of Horticulture, Chiba University, Matsudo, Chiba, Japan, in summer, 2003. Forty-eight pots were divided into four irrigation treatment groups of 12 pots each, six for soybean and six for cotton. Pots were arranged in a randomized complete block design having three replications in a split plot arrangement. Irrigation was used as the mainplot factor and crop as the subplot factor. Seeds of soybean cultivar 'Tachinagaha' and cotton cultivar 'Xinluzao 8' were sown on 5 June. Five seeds were sown per pot, and thinned to one plant per pot after emergence. The four irrigation treatment groups were 100% (control) (T1), 50% (T2), 25% (T3) and 10% (T4) of the control irrigation. The four irrigation treatment groups were 100% (control) (T1), 50% (T2), 25% (T3) and 10% (T4) of the control irrigation. In T1, irrigation was applied at a dose equal to the average evapotranspiration calculated by weighing control
pots with an electronic balance (Fig. 1). Irrigation treatment was started on 26 July, when soybean was at the initiation of pod setting stage, R3 (Fehr and Caviness, 1977) and cotton was at the square formation stage. Irrigation was applied daily in the evening between 1800 hr and 1900 hr. However, judging from the physical condition of the plants, irrigation was not applied on July 30 and Aug. 9, 14, 16, 17 and 19 because of the excessive rainfall and high air humidity. To ensure that the irrigation water should reach directly to the root zone of the plants, water was applied to the pots through a small L-shaped PVC pipe (diameter 10 mm) fitted in a small hole in the bottom portion in each pot very near the base. Data were collected for several days. The data for the day with the most stable sunny weather condition (25 Aug.) were used here. Leaf area and root dry matter weight were measured on 26 Aug. During data collection, soybean was in the seed development stage, R5 (Fehr and Caviness, 1977) and cotton in the boll formation stage.

Leaf temperature (T_L), stomatal density and area, transpiration rate (E), stomatal conductance (g_s), and CO2 assimilation rate (A_N) were measured on the terminal leaflet of the mainstem in the uppermost layer in soybean and on the first fully expanded leaf at the top of the plant in cotton. Stomatal density and area data were examined on the abaxial surface of leaves because stomatal density in both crops is larger on abaxial surface (Ciha and Brun, 1975, Wise et al. 2000). T_L measuring thermocouples were attached to the abaxial side of the leaflets. The data were collected at one-minute intervals from 0600 hr to 1800 hr with a datalogger (Eto Denki Inc., Thermodac E, Japan) connected to a personal computer. The flow rate of stem sap per unit leaf area (FRSS), which is the transpiring rate per unit leaf area, was measured with a stem sap flow gauge (Model SGA10, Dynamax Inc., USA), using the stem heat balance method (Sakuratani, 1981). Sap flow gauges were attached tightly around the stems of the plants at the base above the soil surface. Each gauge was covered with aluminum foil to reduce the effects of external radiation on the heat balance of the stem. Each gauge was connected with dataloggers which collected FRSS data simultaneously with T_L.

Roots were taken out from the pots and gently washed. Fine roots were collected by sieving the soil water mixture through a fine mesh screen. Roots were then dried in oven (Sanyo Convection Oven, Mov-212F, UK) for 48 h at 80°C and weighed. Soybean roots had nodules but the nodule weight was neglected due to small number and size. Leaf area was measured with an automatic leaf area meter (Type AAM-8, Hayashi Denko Co. Ltd., Tokyo, Japan).

Stomatal data were collected according to Hirose et al. (1992). A small drop of a fast-sticking adhesive was taken on a cover glass and attached to the abaxial surface of leaf. After removal from the leaf, the
cover glass was placed on a microscopic slide to see the stomatal image through a computer-controlled digital microscope (Axioplan 2 imaging, Carl Zeiss Co. Germany). Data were collected in the morning (0900 hr), noon (1200 hr) and afternoon (1500 hr) on three cover glasses in three plants per treatment. The stomata were counted in three randomly chosen microscope fields from each image on the cover glass and thus a total of 27 microscope fields were examined for determining stomatal density in each treatment. Each microscope field had an area of 0.6003 mm² at 100 X magnification. The stomatal area was measured on photoprints taken at 400 X according to Wise et al. (2000). Five stomata were randomly selected from each of the 27 prints for studying stomatal area and thus 135 stomata were used for calculating stomatal area in each treatment.

Stomatal conductance (gₛ), transpiration rate (E) and CO₂ assimilation rate (A₅) were measured using LI-6400 Photosynthetic Measurement Systems (LI-COR, Lincoln, NE, USA) in the morning (0900 hr), noon (1200 hr) and afternoon (1500 hr). During these measurements, the leaf was held in a leaf chamber of the instrument facing the sunlight. Air entering the system was drawn from the greenhouse, and passed through a 4-liter buffer volume before entering the system.

All data were analyzed using Genstat 5, Release 4.1 (Lawes Agricultural Trust, IACR, Rothamsted, 1998). The significance of differences between treatments was determined using Duncan’s Multiple Range test. Correlation coefficients were also determined on

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Fig. 2. Diurnal changes in leaf temperature (Tₕ), air temperature and flow rate of stem sap per unit leaf area (FRSS) of soybean and cotton under various irrigation treatments. Data were collected every minute from 0600 hr to 1800 hr. Fig. 2 shows the average of every 60-minute data collected from 0600 hr to 1800 hr on 25 Aug. 2003.
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Results

1. Amount of irrigation water and solar radiation

Fig. 1 shows the amount of irrigation water given to soybean and cotton in normal irrigation treatment (T1) and the daily solar radiation from the beginning of irrigation treatment (July 26) to the date of data collection (Aug. 25). From July 26 to Aug. 4, when soybean was in the pod initiation stage, R3 (Fehr and Caviness, 1977) and cotton in the square formation stage, the water requirements (transpiration) of both crops were lower than in a later stage, judging from solar radiation. During this period the water requirements of cotton were slightly higher than that of soybean. After Aug. 5, when soybean was in the pod filling stage and cotton was in the flowering stage, the water requirements of both crops increased judging from solar radiation. During this period the water requirements of cotton were slightly higher than that of soybean. After Aug. 5, when soybean was in the pod filling stage and cotton was in the flowering stage, the water requirements of both crops increased judging from the solar radiation. On bright sunny days like Aug. 10 and 11, and after Aug. 21, difference between the water requirements of the two crops was comparatively higher showing a higher increase in the transpiration rate in cotton than in soybean. Irrigation water given to soybean and cotton in T1 on Aug. 25 (the day of data collection) was 1381 and 1577 ml, respectively, showing a 12% lower transpiration rate in soybean than in cotton.

2. Diurnal change in leaf temperature (T_l)

Leaf temperature (T_l) of both crops was generally higher than air temperature (Fig. 2) except in cotton at noon when its T_l was almost equal to the air temperature in T1 and T2. In T1, T_l of both crops was lower than in other treatments. With increase in water stress, T_l increased, particularly, in soybean. In soybean the maximum T_l was 40.8°C around 1400 hr in T1, but was 44.1 and 44.3°C in T2 and T4 at noon, respectively. In cotton the maximum T_l was 37.8°C in T1 and 38.7°C in T4. These results showed that the maximum T_l in T4 was only 0.5% higher than that in T1 in cotton but it was 8% higher in soybean. The maximum T_l in soybean in T1 and T4 was 7.8% and 14.5% higher than that in cotton, respectively, suggesting that T_l rose in response to water stress more greatly in soybean than in cotton.

3. Diurnal change in flow rate of stem sap per unit leaf area (FRSS)

FRSS of both crops decreased in response to water stress and the decrease was greater in soybean than in cotton (Fig. 2). The maximum FRSS recorded in cotton was 4.2, 2.1, 2.1 and 2.0 g dm⁻² h⁻¹ in T1, T2, T3 and T4 respectively. In soybean, the maximum FRSS was 3.5, 1.9, 1.7, and 1.3 g dm⁻² h⁻¹ in T1, T2, T3 and T4 respectively. This showed that the maximum FRSS in T4 was 52% and 63% lower than that in T1 in cotton and soybean, respectively. Furthermore, in T1, FRSS in soybean was 17% lower than that in cotton but in T4, it was 35% lower, suggesting that FRSS decreased in response to water stress more greatly in soybean than in cotton.

Fig. 3. Diurnal changes in leaf temperature (T_l) and flow rate of stem sap per unit leaf area (FRSS) in soybean and cotton under various irrigation treatments. Data were collected every minute from 0600 hr to 1800 hr. Fig.3 shows the average of every 60-minute data collected from 0600 hr to 1800 hr on 25 Aug. 2003.

selected data using Genstat 5.
In Fig. 3, FRSS in soybean and cotton were plotted against their TL. TL increased as FRSS decreased in both crops and a larger decrease in FRSS resulted in a larger increase in TL. In soybean FRSS in T1 (control) (3.5 g dm⁻² h⁻¹) decreased to 1.3 g dm⁻² h⁻¹ in T4 (water stress) and the TL in T1 (40.8 ºC) increased to 44.3 ºC in T4. Similarly in cotton, FRSS in T1 (4.2 g dm⁻² h⁻¹) decreased to 2.0 g dm⁻² h⁻¹ in T4, and the maximum TL in T1 (37.8 ºC) increased to 38.7 ºC in T4. These results indicated that the 63% and 52% decrease in the FRSS caused by water stress resulted in an 8% and 0.5% increase in maximum TL in soybean and cotton, respectively. These results showed that a larger decrease in transpiration of soybean under water stress resulted in a larger increase in leaf temperature.

5. Average leaf area and root dry-matter weight

Soybean had a significantly larger leaf area per plant than cotton (Table 1) and the leaf area of soybean decreased more in response to water stress than that of cotton. In T1 (control), soybean had a 61.2 dm² leaf area which decreased to 34 dm² in T4 showing a 44% decrease. Cotton had a 37.7, and 21.7 dm² leaf area in T1 and T4, respectively, showing a 42% decrease in response to water stress. Soybean had a significantly
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heavier root dry matter than cotton (Table 1). Root dry-matter weight decreased with decrease in irrigation in the same pattern in both crops.

6. Stomatal characteristics

Significant difference was found between the leaf stomatal density of soybean and cotton (Table 2). Cotton had 392.7 stomata per mm² while soybean had 264 stomata per mm². Irrigation had no effect on the leaf stomatal density.

Stomatal area in cotton was significantly larger than that in soybean (Table 3). Water stress caused a significant decrease in stomatal area in cotton. In soybean, the stomatal area was the smallest in T4, though not significantly different from that in T1. The crop-irrigation-time interaction affected the stomatal area significantly. In cotton, the stomatal area in water stress treatments was significantly smaller than that in the control at all times of the day. In both soybean and cotton, the stomatal area after higher water stress treatment (T4) was smaller in the morning and greater at noon as compared with morning. The stomatal area was significantly larger at noon in both crops than in the morning or afternoon.

7. Transpiration rate (E), stomatal conductance (gₛ) and CO₂ assimilation rate (A₅₀):

Transpiration rate (E) (Fig.4A, B, C), stomatal conductance (gₛ) (Fig.4D, E, F) and CO₂ assimilation rate (A₅₀) (Fig.4G, H, I) of both crops were decreased

| Time       | Irrigation treatment | Soybean | Cotton |
|------------|----------------------|---------|--------|
| Morning (0900 hr) | Normal irrigation (T1) | 22.6a   | 54.2a  |
|            | 50% of the normal (T2) | 23.8a   | 44.3b  |
|            | 25% of the normal (T3) | 22.1ab  | 41.9b  |
|            | 10% of the normal (T4) | 15.4b   | 31.2c  |
| Noon (1200 hr) | Normal irrigation (T1) | 27.9a   | 79.5a  |
|            | 50% of the normal (T2) | 32.1a   | 59.0b  |
|            | 25% of the normal (T3) | 27.4a   | 38.9c  |
|            | 10% of the normal (T4) | 27.7a   | 41.3c  |
| Afternoon (1500 hr) | Normal irrigation (T1) | 22.3a   | 47.9a  |
|            | 50% of the normal (T2) | 24.0a   | 48.0a  |
|            | 25% of the normal (T3) | 21.2a   | 28.2b  |
|            | 10% of the normal (T4) | 18.1a   | 25.0b  |
| Average:  | Normal irrigation (T1) | 24.3ab  | 60.5a  |
|           | 50% of the normal (T2) | 26.6a   | 50.4b  |
|           | 25% of the normal (T3) | 23.6ab  | 36.3c  |
|           | 10% of the normal (T4) | 20.4b   | 32.5c  |

Significance:

|                  | Soybean | Cotton |
|------------------|---------|--------|
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** represents significant difference at 1% level.

Means in the same crop and time followed by a common letter are not significantly different at 1% level according to Duncan’s Multiple Range Test.
by water stress treatments. The decrease was greater in soybean than in cotton. The crop-irrigation-time interaction affected $g_s$ and $A_N$ significantly. In the morning, $g_s$ and $A_N$ in soybean were 89% and 62% lower in T4, while in cotton, the values of these parameters in T4 were 78% and 30% lower than that in T1, respectively. At noon, $g_s$ and $A_N$ of soybean and cotton decreased by 95% and 85%, and 58% and 52% respectively, by water stress in T4 when compared with T1, respectively. In the afternoon, $g_s$ and $A_N$ of soybean decreased by 93% and 74% in T4, respectively, while in cotton these parameters decreased by 91% and 60%, respectively. Thus the drought stress reduced $g_s$ and $A_N$ more strongly in soybean than in cotton. The decrease was larger especially at noon when light and heat stresses were also higher (light and heat stress data not shown).

The crop-irrigation-time interaction had no significant effect on $E$ in either crop (Fig.4A, B, C). However, the crop-irrigation interaction affected $E$ significantly (Table 4). Under a normal irrigation (T1), $E$ in cotton was 12.0 mmol m$^{-2}$ s$^{-1}$, and it decreased to 2.7 mmol m$^{-2}$ s$^{-1}$ in T4 showing 78% decrease. In soybean, $E$ decreased from 10.3 mmol m$^{-2}$ s$^{-1}$ in T1 to 1.3 mmol m$^{-2}$ s$^{-1}$ in T4 showing 87% decrease. The results also showed that in T1, $E$ in soybean was 14%
Table 4. Transpiration rate and stomatal conductance of soybean and cotton under various irrigation treatments. Data represent means of the values measured in the morning (900 hr), noon (1200 hr) and afternoon (1500 hr).

| Treatment                      | Transpiration rate (mmol m\(^{-2}\) s\(^{-1}\)) | Stomatal conductance (mol m\(^{-2}\) s\(^{-1}\)) |
|-------------------------------|-----------------------------------------------|-----------------------------------------------|
|                               | Soybean | Cotton | Soybean | Cotton |
| Normal irrigation (T1)        | 10.3a   | 12.0a   | 0.38a   | 0.43a   |
| 50% of the normal (T2)        | 2.6b    | 7.1b    | 0.08b   | 0.23b   |
| 25% of the normal (T3)        | 1.5c    | 4.1c    | 0.03bc  | 0.15c   |
| 10% of the normal (T4)        | 1.3c    | 2.7d    | 0.02c   | 0.12c   |
| Average:                      | 3.9c    | 6.5     | 0.13c   | 0.23    |

Significance

- Crop: **
- Irrigation: **
- Crop X Irrigation: **

** represents significant difference at 1% level. Means in the same crop followed by a common letter are not significantly different at 1% level according to Duncan’s Multiple Range Test.

Fig. 5. Correlation of stomatal area with flow rate of stem sap (FRSS) (A), transpiration rate (E) (B), CO\(_2\) assimilation rate (\(A_\text{N}\)) (C), and stomatal conductance (\(g_s\)) (D) of soybean and cotton under various irrigation treatments. Data are the means of the stomatal area, FRSS, E, \(A_\text{N}\) and \(g_s\) measured in the morning (0900 hr), noon (1200 hr) and afternoon (1500 hr).

Symbols are the same as in Fig.3. * and ** represent significant difference at 5% and 1% levels of probability, respectively.
lower than that in cotton but in T4, it was 52% lower. Thus the decrease in E in soybean under drought stress was larger.

At noon, E and gₛ in both crops were larger but Aₑ was lower than in the morning or afternoon (Fig.4). Cotton showed a greater increase in E and gₛ at noon, while decrease in Aₑ was smaller than that in soybean especially under water stress conditions.

8. Correlation between size of stomatal area and FRSS, E, gₛ, and Aₑ

In cotton, the size of stomatal area was positively and significantly correlated with E, gₛ, and Aₑ (Fig.5B, C, D). It was also highly correlated with FRSS (Fig.5A). In soybean, however, there were no significant correlations. Stomatal conductance (gₛ) was positively and significantly correlated with FRSS and E in both crops (Fig.6A, B). It was also correlated with Aₑ in both crops (Fig.6C), although the correlation in soybean was not statistically significant. These correlations showed that stomatal area did not affect FRSS, E, gₛ, and Aₑ in soybean under water stress conditions. In cotton, it might play a major role in regulating these parameters.

Discussion

In this experiment, cotton and soybean differently adapted to water stress i.e. the former continued to show high transpiration although the latter showed a reduced transpiration rate under water stress. Isoda and Wang (2002) reported that cotton could avoid heat stress and maintain turgor pressure of cells probably by the supply of a sufficient amount of water by a well-developed root system, which leads to higher drought resistance. On the other hand, soybean may adapt to arid conditions by the combination of paraheliotropic leaf movement and reduced transpiration. In addition, we found some interesting relations between the stomatal characteristics and transpiration in soybean and cotton.

In cotton, the stomatal area significantly decreased under water stress as expected. The high correlations of FRSS, E, and gₛ with stomatal area at various irrigation levels showed that these parameters are largely regulated by the stomatal area in cotton. In soybean, however, the stomatal area did not show any significant correlation with FRSS, E, and gₛ. Several reports showed significant decrease in stomatal aperture (physical distance between the two walls of the stomatal pore) and gₛ under water stress (Shimshi, 1963; Li, et. al. 2004). However, some authors including Rodiyati et. al. (2004) reported no decrease in stomatal aperture under drought stress. Shimshi (1963) reported a decrease in transpiration of maize
due to increase in the resistance of mesophyll cells, which could not be attributed to stomatal closure. The same phenomenon was reported by Jarvis and Slatyer (1970). Although the stomatal area did not correlate with FRSS and E in soybean, g, significantly correlated with FRSS and E in both cotton and soybean. Cochard et al. (2002) reported that the regulation of g, is the main mechanism by which plants control transpiration. Stomatal resistance (opposite of conductance) involves the resistance to the evaporation of water from the outer surfaces of the mesophyll cells, and the resistances to the diffusion of water through the intercellular spaces and the stomatal pore (Kramer, 1983). It was reported that reduced hydraulic conductance decreased g, and E in *Betula occidentalis* and that g, was responsive to changes in hydraulic conductance of the soil to leaf (Sperry et al. 1993, Hubbord et al. 2001). We observed very little moisture exudation from the basal cut end of the stem in soybean as compared with cotton (data not shown), showing the possibility of lower root moisture extraction efficiency and/or lower hydraulic conductivity within roots or stem in soybean. Slower FRSS in soybean under water stress indicated decreased stem hydraulic conductivity of the crop, which might be affected by the size of xylem vessels (Lovisolo and Schubert, 1998) and/or the supply of water from roots (Boyer, 1971; Jones et al. 1983). Lower root water extracting efficiency and lower FRSS might therefore be the major factors responsible for lower g, and thus lower E, in soybean. In this experiment, soybean wilted on days having a high evaporating demand especially in water stress treatments probably due to the high resistance to water transport as reported by Boyer (1971). The lack of any significant correlation between g, and stomatal area in soybean, therefore, suggested that g, and thus E, would depend on hydraulic conductance from soil to leaf regardless of stomatal area. Isoda et al. (1994) reported that soybean cultivars with a higher transpiring ability showed less active paraheliotropic leaf movement. Therefore, a soybean cultivar with active paraheliotropic leaf movement may have lower hydraulic conductivity, especially in roots. The increase in T, and decrease in A, were greater in soybean than in cotton under water stress. Water stress accompanying high T, might have decreased A, in soybean by causing photoinhibitory damages to the photosynthetic apparatus as reported by Ludlow and Björkman, (1984), and/or the decrease might be due to the larger amount of dissipation of excess excitation energy as heat accompanied by the down regulation of PSII efficiency (Souza et al., 2004). Stomatal conductance of both crops was highly correlated with A, at various irrigation treatments, but at noon, when g, increased, A, in both crops decreased. Decrease in A, at noon of both crops especially soybean, might be due to the dynamic photo inhibitory effects caused by a high T, which involves a down regulation of photosystem II efficiency and a larger amount of dissipation of excess excitation energy as heat (Ludlow and Björkman, 1984; Osmond, 1994; Souza et al., 2004). In the accompanying report, we describe the diurnal changes in A, of soybean and cotton in detail under various irrigation levels in terms of the efficiency of PSII (Inamullah and Isoda, 2005).

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