Adaptive Responses of Soybean and Cotton to Water Stress
II. Changes in CO₂ Assimilation Rate, Chlorophyll Fluorescence and Photochemical Reflectance Index in Relation to Leaf Temperature

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Abstract: Adaptive changes were studied comparatively in soybean and cotton grown in pots under four irrigation conditions i.e. normal irrigation (equal to the evapotranspiration of the crop), and 50%, 25% and 10% of the normal irrigation. In soybean, the maximum quantum yield of PSII (Fv/Fm) was generally higher while the actual quantum yield of PSII (∆F/∆F’m) and CO₂ assimilation rate (A₀) were lower than in cotton. The intensity of the decrease in Fv/Fm, ∆F/∆F’m and A₀ by water-stress treatments was larger in soybean than in cotton. The decrease in ∆F/∆F’m in soybean under water stress was accompanied by a significant increase in non-photochemical quenching (NPQ) and significant decrease in photochemical reflectance index (PRI). Chlorophyll content decreased significantly under severe water stress only in soybean. The increase in leaf temperature (Tₗ) in response to water stress was significantly larger in soybean than in cotton. Tₗ was highly and negatively correlated with Fv/Fm, A₀, PRI and ∆F/∆F’m while it was highly and positively correlated with NPQ of both crops. Especially in soybean, the correlations of Tₗ with A₀, Fv/Fm and PRI were significant. It was concluded that soybean adapted to water stress by dissipating the excess excitation energy thermally with the down-regulation of PSII activity to protect its photosynthetic apparatus from the photodamaging effect of water stress and high Tₗ. This photoprotective mechanism might be supported by the paraheliotropic leaf movement of the crop. Cotton adapted to water stress by keeping Tₗ lower to protect the photosynthetic apparatus from photodamage. Probably higher transpiration kept Tₗ of the crop lower under drought stress.

Key words: Chlorophyll fluorescence, Glycine max (L.) Merr., Gossypium hirsutum L., Leaf movement, Photoinhibition, Photosystem II.

Previously, we reported that the decrease in CO₂ assimilation rate and increase in leaf temperature in water-stress condition were larger in soybean than in cotton (Inamullah and Isoda, 2005). The decrease in CO₂ assimilation rate was attributed to photohitory damage caused by water stress and higher leaf temperature as reported by Ludlow and Björkman (1984) and/or to the down-regulation of photosystem (PS) II and dissipation of excess excitation energy as heat (Krause, 1988; Bilger et al., 1995; Lu et al., 2001; Alves et al., 2002). In soybean (Glycine max (L.) Merr.), paraheliotropic leaf movement may help the crop to avoid photohitory (Hirata et al., 1983), while in cotton (Gossypium hirsutum L.) diaheliotropic leaf movement (Ehleringer and Forseth, 1989; Wise et al., 2000), may increase transpiration to keep its leaf temperature low (Isoda and Wang, 2002; Inamullah and Isoda, 2005). Photohitory is typically characterized by a reduction in quantum yield of PSII (Fv/Fm) (Demmig and Björkman, 1987). The term photoinhibition includes not only photodamage to the photosynthetic apparatus causing irreversible inactivation of PSII but also some photoprotective mechanism causing slow and reversible reduction of the photosynthetic efficiency or down-regulation of PSII and the dissipation of excess excitation energy as heat (Krause, 1988; Chow, 1994; Bilger et al., 1995; Lu et al., 2001; Alves et al., 2002). The fluorescence parameter NPQ (non-photochemical quenching) has been widely used for measurement of the thermal dissipation of excess energy at the leaf level (Bilger and Björkman, 1990). A reflectance-based remote sensing photosynthetic index called chemical reflectance index (PRI) has also been reported as a good indicator of the thermal dissipation of excess excitation energy (Gammon et al., 1993; Peñuelas et al., 1995) that involves the xanthophyll cycle and a low thylakoid pH. In the xanthophyll cycle, photoprotective zeaxanthin and antheraxanthin pigments are formed from antenna pigment violaxanthin under the condition of excess excitation energy. Many investigators including Peñuelas et al. (1995) reported a linear relationship
between actual quantum yield of PSII (ΔF/Fm’) and PRI.

The primary objective of this experiment was to study various adaptive changes in the photosynthetic efficiency in soybean and cotton comparatively in relation to changes in leaf temperature (TL) under water stress. For this purpose, (i) we examined changes in TL, chlorophyll content, CO2 assimilation rate (A50), quantum efficiency of PSII, and the thermal dissipation of excess excitation energy of the two crops under various irrigation treatments; and (ii) analyzed the correlation of changes in TL with Fv/Fm, AN, NPQ, and PRI. A secondary objective was to test whether PRI can be used to detect down-regulation in the actual quantum yield of PSII (ΔF/Fm’) and thermal dissipation of excess excitation energy at the leaf level in cotton and soybean under water stress.

**Materials and Methods**

Experiments were conducted in 1/2000 a Wagner pots (height 30 cm and average diameter 24 cm) in a greenhouse at the Faculty of Horticulture, Chiba University, Matsudo, Chiba, Japan, in the summer of 2002 and 2003. A total of 48 pots were divided into four groups for irrigation. Each group was comprised of twelve pots, six for soybean and six for cotton. Pots were arranged in a randomized complete block design having three replications with a split plot arrangement. Irrigation was the main-plot factor and crop the subplot factor. Seeds of soybean cultivar ‘Tachinagaha’ and cotton cultivar ‘Xinluzao 8’ were sown on 7 June (2002) and 5 June (2003). Five seeds were sown per pot, and thinned to one plant per pot after emergence. Four irrigation treatments comprising the normal irrigation (T1), and 50% (T2), 25% (T3) and 10% (T4) of the normal irrigation were used. Irrigation treatments were assigned randomly to the four groups of pots. In the normal irrigation treatment (control), irrigation was applied daily at a rate equal to the average evapotranspiration of the crop calculated by weighing the pots daily with an electronic balance. Averages of the irrigation requirements of all the plants of soybean and cotton in normal irrigation (T1) were calculated every day, and those in T2, T3 and T4 treatments, were regarded as 50%, 25% and 10% of the average irrigation requirement in T1, respectively. Irrigation treatment was started on 4 Aug. in 2002 and 26 July in 2003, when soybean was at the initiation of pod setting stage, R3 (Fehr and Caviness, 1977) and cotton at the square formation stage. Irrigation was applied in the evening between 1800 hr and 1900 hr. 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. Changes in the data collected in various irrigation treatments took place almost in the same pattern in both years. Therefore the data collected in 2003 on the day with the most suitable sunny weather conditions (25 Aug.) were used. During data collection, soybean was in the seed development stage, R5 (Fehr and Caviness, 1977) and cotton in the boll formation stage.

Data were collected on the terminal leaflet of the mainstem in soybean and on the first fully expanded leaf (top of the plant) in cotton. Leaf temperature (TL) was measured simultaneously when measuring the actual quantum yield of PSII (ΔF/Fm’) with a PAM-2000 chlorophyll fluorometer using the Leaf-Clip Holder 2030-B (Walz, Effeltrich, Germany). Leaf chlorophyll content was measured with a SPAD-502 chlorophyll meter (Minolta, Co., Ltd., Japan). The maximum quantum efficiency of PSII (Fv/Fm, where Fv = Fm-Fo) of dark-adapted and ΔF/Fm’ (where ΔF = Fm’-Ft) of illuminated leaves were measured with a PAM-2000 chlorophyll fluorometer. Fo and Fm are the minimal and maximal fluorescence yields of dark-adapted leaves, respectively. Fm’ is the maximal fluorescence yield of an illuminated leaf induced by a saturation pulse and Ft represents the steady state fluorescence yield, measured at any given time. Fv/Fm was determined in the early morning before direct sunlight hit the leaves. Non-photochemical quenching (NPQ) was calculated as (Fm/Fm’)-1 (Bilger and Bjorkman, 1990).

Reflectance was measured with a Photonic Multichannel Spectral Analyzer PMA-11 (Hamamatsu, Photonics K.K., Japan). After data collection, the photochemical reflectance index (PRI) was calculated as (R531-R570)/(R531+R570) (Peñuelas et al., 1995), where R denotes reflectance, and 531 and 570 denote wavelengths (nm).

CO2 assimilation rate (A50) was measured using LI-6400 Photosynthetic Measurement Systems (LI-COR, Lincoln, NE, USA). Air entering the system was drawn from the greenhouse, passed through a 4 liter buffer volume before entering the system. Airflow through the chamber was maintained at 500 µmol s-1. T1, Δ F/Fm’, A50, and reflectance data were collected in the morning (0900 hr), noon (1200 hr) and afternoon (1500 hr). Data were analyzed using Genstat 5, Release 4.1 (Lawes Agricultural Trust, IACR, Rothamsted). The significance of differences between treatments was determined using Duncan’s Multiple Range Test. Correlation coefficients were also determined using Genstat 5.

**Results**

1. **Leaf temperature (TL)**

Leaf temperature (TL) in both crops increased with the increase in water stress; the increase was larger in soybean (Fig.1A). In soybean, TL increased from 38.2°C in T1 to 41.3°C in T4 while in cotton, the TL...
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increased from 38.1°C in T1 to 39.7°C in T4. Soybean showed significantly larger increase in T1 as compared with cotton in T4 at noon (Fig.2B) and afternoon (Fig.2C). The T1 of soybean was almost equal to that of cotton in T1 in the morning (Fig.2A), noon (Fig.2B) and afternoon (Fig.2C) but in the highest water-stress treatment (T4), the increase in T1 of soybean was higher at noon and in the afternoon.

2. CO₂ assimilation rate (Aₙ)

The average CO₂ assimilation rates (Aₙ) in both crops decreased significantly in water-stress treatments, and soybean showed a larger decrease than cotton (Fig.1B). In cotton and soybean, Aₙ decreased by 46% and 73%, respectively, in T4 as compared with T1.

The CO₂ assimilation rate (Aₙ) was lower at noon (Fig.2E) than in the morning (Fig.2D) or afternoon (Fig.2F) in both crops, and was lower in soybean than in cotton especially in water-stress treatments. In the morning, noon and afternoon, Aₙ in T4 was 50%, 52% and 60%, respectively, lower than that in T1 in cotton, and was 62%, 85% and 74%, respectively, lower in soybean. Thus, the decrease in Aₙ under water stress was larger in soybean than in cotton, and at noon when light and/or heat stress was higher than in the morning or afternoon (light and heat data not shown).

3. Chlorophyll fluorescence

Irrigation affected the maximum quantum yield of PSII (Fv/Fm, (C)), actual quantum yield of PSII (∆F/Fm', (D)), non-photochemical quenching (NPQ, (E)), photochemical reflectance index (PRI, (F)), and chlorophyll contents (SPAD value, (G)) in soybean and cotton under various irrigation treatments. Columns except in (C) and (G) represent means of the measurements taken in the morning (0900 hr), noon (1200 hr) and afternoon (1500 hr).

Columns representing the same crop having different letters are significantly different according to Duncan’s Multiple Range Test. * and ** represent significance of the differences in the crop x irrigation interaction at 5% and 1% levels of probability, respectively.

Fig. 1. Leaf temperature (Tₙ, (A)), CO₂ assimilation rate (∆ₙ, (B)), maximum quantum yield of PSII (Fv/Fm, (C)), actual quantum yield of PSII (∆F/Fm', (D)), non-photochemical quenching (NPQ, (E)), photochemical reflectance index (PRI, (F)), and chlorophyll contents (SPAD value, (G)) in soybean and cotton under various irrigation treatments. Columns except in (C) and (G) represent means of the measurements taken in the morning (0900 hr), noon (1200 hr) and afternoon (1500 hr).
decrease was observed in Fv/Fm in soybean in higher water-stress treatments. Soybean showed a maximum Fv/Fm of 0.80 in T1, which decreased to 0.76 in T3 and T4, showing a 5% decrease, while cotton recorded Fv/Fm of 0.77 in T1 and 0.75 in T3 and T4, showing a 3% decrease. A smaller decrease in Fv/Fm in cotton under higher water-stress treatments (T3 and T4) suggested that water stress caused comparatively smaller photodamage to its photosynthetic apparatus.

The actual quantum yield of PSII ($\Delta F/Fm'$) was decreased by water-stress treatments in both crops (Fig.1D), particularly in soybean. The $\Delta F/Fm'$ in cotton was higher than that in soybean under all irrigation treatments. The $\Delta F/Fm'$ in soybean was 0.17 in T1, and only 0.07 in T4, which was a 59% decrease. The $\Delta F/Fm'$ in cotton was 0.21 in T1; in T3 it was 0.14 and in T4 it was 0.17, showing a 33% and 19% decrease, respectively, as compared with T1. The $\Delta F/Fm'$ followed the same pattern of changes in both crops (data not shown), showing lower values in the water-stress treatments and at noon as compared with morning and afternoon.

Non-photochemical quenching (NPQ), which measures the thermal dissipation of excess excitation energy, was increased by water-stress treatment in both crops, but significantly only in soybean (Fig.1E). NPQ in soybean increased by 197% in T4 as compared with T1, while that in cotton increased by only 25%. These results suggested that under water stress, the thermal dissipation of excess excitation energy increased in both crops; however, only soybean showed significantly larger thermal dissipation of excess excitation energy, which may have caused significantly larger down-regulation of PSII activity (Fig.1D).

4. Photochemical Reflectance Index (PRI)

The PRI, which like NPQ indicates the thermal dissipation of excess excitation energy due to the activation of xanthophyll cycle, significantly decreased in water-stress treatments in soybean (Fig.1F), suggesting that the concentration of xanthophyll cycle photoprotective pigments of antheraxanthin and zeaxanthin increased to dissipate excess energy as heat. Cotton did not show any significant decrease in PRI in water-stress treatments.

5. Chlorophyll content (SPAD Value)

Soybean contained more chlorophyll than cotton in all irrigation treatments except in T4. The chlorophyll content of soybean decreased significantly in water-stress treatments, and that of cotton also decreased in water-stress treatments though the decrease was not statistically significant (Fig.1G). Soybean had maximum SPAD value of 45.2 in T1 which decreased...
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6. Correlation of Tₜ with Fv/Fm, ΔF/Fm', NPQ, PRI and Aₑ

Leaf temperatures (Tₜ) in soybean were significantly and negatively correlated with Aₑ (Fig.3B), and highly significantly and negatively correlated with Fv/Fm (Fig.3C) under various irrigation levels. Tₜ in soybean was highly and negatively correlated with ΔF/Fm' (Fig.3A) and highly and positively correlated with NPQ (Fig.3D). In cotton, Tₜ was also highly and negatively correlated with ΔF/Fm’ (Fig.3A), Aₑ (Fig.3B), and Fv/Fm (Fig.3C) and highly and positively correlated with NPQ (Fig.3D) under various irrigation levels. Similarly, Tₜ was highly and negatively correlated with PRI in both crops, and this correlation was highly significant in soybean (Fig.3E) under various irrigation levels. This suggested that the increase in Tₜ activates the xanthophyll pigment cycle to safely dissipate the excess excitation energy as heat and the large increase in Tₜ causes a greater thermal dissipation of excess excitation energy as was observed in soybean. Thermal dissipation of excess excitation energy may cause the down-regulation of PSII activity which may lead to a decrease in the Aₑ of the crops. Further increase in Tₜ may cause irreversible photoinhibition giving severe damage to the photosynthetic apparatus of the crop (detected by decrease in Fv/Fm).

These correlations suggested that with the increase in Tₜ above the optimum level, reversible photoprotective photoinhibition or down-regulation of PSII may take place, accompanied by the thermal dissipation of excess excitation energy which lead to a decrease in Aₑ. After a critical Tₜ is reached, however, it might totally damage the photosynthetic apparatus of the crops.

7. Relationships among ΔF/Fm’, NPQ and PRI

Highly significant and significant negative correlations were observed between ΔF/Fm’ and NPQ in soybean and cotton, respectively, under various irrigation treatments (Fig.4A). The significant correlation between ΔF/Fm’ and NPQ in both crops especially in soybean suggested the down-regulation of PSII activity due to thermal dissipation of excess excitation energy. A high and positive correlation was observed between ΔF/Fm’ and PRI in soybean, but
a very weak and positive correlation was observed in cotton (Fig. 4B). Similarly, the correlation between NPQ and PRI was high and negative in soybean while weak and negative in cotton.

These correlations suggested that NPQ could efficiently represent the thermal dissipation of excess excitation energy with down-regulation of PSII activity in both crops under water stress, although the thermal dissipation of excess excitation energy was not significant (Fig.1E) and the accompanied down-regulation of PSII activity was comparatively smaller in cotton (Fig.1D). PRI, on the other hand, showed a high correlation with $\Delta F/F_m'$ only in soybean in which the thermal dissipation of excess excitation energy was higher (Fig.1E and 1F) and was accompanied by a larger down-regulation of the actual quantum yield of PSII ($\Delta F/F_m'$) under water stress (Fig.1D). This suggested that PRI could measure the thermal dissipation of excess excitation energy and the down-regulation of the PSII activity under water stress only when increase and decrease in these measurements was great, respectively.

**Discussion**

$CO_2$ assimilation rates ($A_N$) in both crops decreased under drought stress and the decrease in $A_N$ was larger in soybean. The lower $A_N$ in soybean in higher water-stress treatments and at noon could be related to the direct photodamaging effect of water scarcity and/or to the photodamaging effect of the higher leaf temperature ($T_L$), caused by water-stress as reported by Ludlow and Björkman (1984). In cotton, the decrease in $A_N$ was smaller probably because of its higher soil-moisture absorption capability as we reported earlier (Inamullah and Isoda, 2005) and the smaller increase in $T_L$. The decrease in $A_N$ in cotton under water stress was mostly due to the reduced stomatal opening (Inamullah and Isoda, 2005).

Under water-stress, the decrease in actual quantum yield of PSII ($\Delta F/F_m'$) or down-regulation of PSII (decrease in $\Delta F/F_m'$) (Lu et al., 2001) occurred in both crops. In soybean, a larger down-regulation of PSII was observed accompanied by a significantly larger increase in the thermal dissipation of excess excitation energy as compared with cotton. Thermal dissipation of excess excitation energy was measured as an increase in NPQ (Bilger and Björkman, 1990) and as a decrease in PRI (Gamon et al., 1993; Peñuelas et al., 1995). Berry and Björkman (1980) reported that the photosynthetic apparatus is the main site of damage caused by high temperatures and that PSII within the photosynthetic apparatus is the most heat-sensitive part. In soybean, therefore, the larger down-regulation of PSII and larger increase in thermal dissipation of excess excitation energy in water-stress treatments were probably due to the larger increase in $T_L$. The higher $T_L$ might have down-regulated the PSII activity and increased its xanthophyll cycle activity to dissipate the excess excitation energy as heat in soybean. The down-regulation of PSII activity and increase in thermal dissipation of excess excitation energy have been considered to be associated with the xanthophyll pigment cycle, which is proposed to provide photoprotection of the photosystem by the dissipation of excess absorbed light energy (Demmig-Adams, 1990; Demmig-Adams and Adams, 1992). At the same time, a decrease in $Fv/Fm$ under water-stress was observed in both crops. In soybean, the decrease was comparatively larger. The sustained decrease in $Fv/Fm$ indicates the occurrence of photoinhibitory damage in response to one or more than one environmental stresses (Maxwell and Johnson, 2000). Although the decrease in $Fv/Fm$ in soybean was comparatively large, the significant down-regulation of PSII with a significant increase in thermal dissipation of excess excitation energy in the higher water-stress
treatments suggested that larger portion of the PSII reaction centers was still functionally intact in soybean. It seems that in soybean the photosynthetic apparatus was protected from total photodamage under water stress due to its higher ability to down-regulate PSII activity and its active xanthophyll cycle pigment conversion ability to dissipate excess excitation energy as heat. This photoprotection process may be supported by the paraheliotropic leaf movement of the crop (Hirata et al., 1983).

In cotton, the $\Delta F/Fm'$ decreased significantly under water-stress, but it was generally higher than in soybean especially under drought-stress. In cotton, drought stress increased neither NPQ nor PRI significantly, but significantly increased $T_L$, though only slightly. This suggested that the cotton crop might have not allowed a large increase in $T_L$ even under severe water-stress due to its high transpiration rate (Inamullah and Isoda, 2005) and higher PSII activity was carried out at a comparatively low temperature. Flagella et al. (1996) reported no and some decrease in $\Delta F/Fm'$ in drought-tolerant and drought-susceptible wheat cultivars, respectively, and no change in the efficiency of excitation capture by the open PSII reaction center in the two cultivars at the vegetative stage under severe drought stress when the leaf water potential declined significantly. Genty et al. (1987), on the other hand, reported no change in PSII photochemistry and non-photochemical quenching in pot-grown cotton under very low leaf water potential. Although we could not measure the leaf water potential in this experiment, the high $\Delta F/Fm'$ in cotton suggested that a large portion of the PSII reaction centers ($q_P$) might be open and/or the energy capture efficiency of the open PSII reaction centers ($Fv/Fm'$) might be high even under drought stress or low leaf water potential, which ultimately leads to a high $A_\infty$ (Lu et al., 2001; Colom and Vazzana, 2003).

The significant correlation of $T_L$ with $\Delta F/Fm'$, NPQ and $Fv/Fm'$ suggested that when $T_L$ rises above an optimum level, it causes down-regulation of the actual quantum yield of PSII and the thermal dissipation of excess excitation energy, which leads to a reversible decline in the photosynthetic efficiency of the crop as we observed in the two crops in this experiment. Finally when $T_L$ increases above a critical point, it may cause an irreversible photoinhibitory damage (a sustained decrease in $Fv/Fm'$) as was observed in soybean in higher water-stress treatments.

In this study, both NPQ and PRI showed higher correlations with $\Delta F/Fm'$ in soybean, but in cotton, only the NPQ showed a higher correlation with $\Delta F/Fm'$ under various irrigation treatments. Furthermore, NPQ and PRI were highly and negatively correlated in soybean only. In soybean, the decrease in $\Delta F/Fm'$ and thermal dissipation of excess excitation energy were larger than those in cotton under water stress, which suggested that PRI could be used to detect the thermal dissipation of excess excitation energy and the down-regulation of PSII activity only when there was a larger dissipation of excess excitation energy as heat and a larger down-regulation of PSII activity.

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