Osmoregulation in Cotton in Response to Water Stress[1]

III. EFFECTS OF PHOSPHORUS FERTILITY

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ABSTRACT

Cotton (*Gossypium hirsutum*) (L.) was grown in a sand and nutrient solution system at two levels of phosphorus (0.5 and 5.0 millimolar). Within each phosphorus treatment, plants were either watered daily or acclimated to water stress by subjection to several water stress cycles.

Stress acclimation increased leaf starch at the low phosphorus level, but not at the high phosphorus level. High phosphorus increased leaf sucrose and glucose concentration in both acclimated and nonacclimated plants, but had little effect on osmotic adjustment or the relationship between turgor and water potential.

In nonacclimated plants, high phosphorus increased both leaf conductance and photosynthesis at high water potentials. In acclimated plants, high phosphorus increased photosynthesis but decreased conductance, thus increasing water use efficiency at the single leaf level.

Recent evidence suggests that the partitioning of photosynthetically fixed carbon between sucrose and starch may be regulated by cellular Pi levels (6, 8, 9, 11). Cotton leaves accumulate starch as a consequence of water stress acclimation (2, 3). Moreover, water stress significantly depresses phosphorus uptake (5, 7, 16) and low cellular Pi levels lead to starch accumulation in isolated chloroplasts and leaves (6, 8, 9, 11). Consequently, phosphorus fertility may play a role in altering the response of plants to water stress by changing the ratio of starch to soluble sugars in leaf cells.

The influence of phosphorus fertility on internal water relations, leaf conductance, photosynthesis, and cellular carbohydrates in cotton is reported in this study.

MATERIALS AND METHODS

Plant Culture. Cotton (*Gossypium hirsutum* L. Tamcot SP37) was grown in 21-cm diameter plastic pots containing sand. Plants were thinned to two per pot after emergence. Conditions in the controlled environment chamber used for plant growth were as previously described (2, 3). Plants were watered twice daily; once with Hoagland complete nutrient solution and once with deionized H_2O.

After expansion of the second leaf, two phosphorus fertility regimes were started. One set of plants received a modified Hoagland solution containing 0.5 mM phosphorus as NaH_2PO_4.

A second set received the same nutrient solution containing 5.0 mM phosphate. Other nutrients were adjusted to maintain the standard Hoagland solution concentrations. Plants were watered with nutrient solution in the morning and deionized H_2O at night.

Beginning 1 month after emergence (5th leaf expanded), a series of water stress-recovery cycles was imposed on one-half of the plants in each phosphorus treatment. These plants were allowed to dehydrate until midday leaf water potentials approached −16 to −18 bars. Dehydration required 24 to 48 h, depending on plant age. Plants were then fully watered with nutrient solution and deionized H_2O for 4 d prior to a subsequent stress period. Five cycles of stress and recovery were imposed (acclimated plants). Control plants were fully watered twice daily.

Five days after the last stress cycle, all plants were subjected to dehydration. During this dehydration period, data were obtained from leaves at nodes 6 and 7.

Water Potential, Leaf Conductance, Photosynthesis, and Leaf Carbohydrates. Water potentials and osmotic potentials were determined with isopiestic thermocouple psychrometers (4) as previously described (1–3). Procedures for diffusion porometry and for measurement of photosynthesis, and determination of glucose, sucrose, and starch levels in the leaves were described earlier (1–3).

The data reported represent the combined results of three experiments. Based on plant height measurements, the two phosphorus fertility regimes did not differentially affect growth. Acclimated plants were shorter than the appropriate controls following cessation of the stress cycles as previously noted (3).

RESULTS

Phosphorus (P) fertility level did not significantly alter the relationship between leaf turgor and leaf water potential (Fig. 1). At any given water potential, plants grown on 5.0 mM P maintained leaf pressure potentials 0.5 to 1.0 bars higher than plants grown on 0.5 mM P. Although these differences were not statistically significant, the trends were consistent and quite reproducible.

Leaf conductances and photosynthetic rates of control plants grown on 5.0 mM P were higher than those of plants grown on 0.5 mM P (Fig. 2). The differences were maintained until leaf turgor approached zero. In acclimated plants, leaf conductances tended to be lower at the higher P level (Fig. 3). In spite of this, photosynthetic rates of plants grown on 5.0 mM P were consistently higher than those of plants grown on 0.5 mM P (Fig. 3). These data suggest that P level influences water use efficiency at the single leaf level, at least in stress-acclimated plants.

Phosphorus level had a significant impact on the concentration of sucrose, glucose and starch in both control and acclimated plants (Figs. 4 and 5). Leaf sucrose and glucose concentrations were higher in control plants grown on the higher P level (Fig.
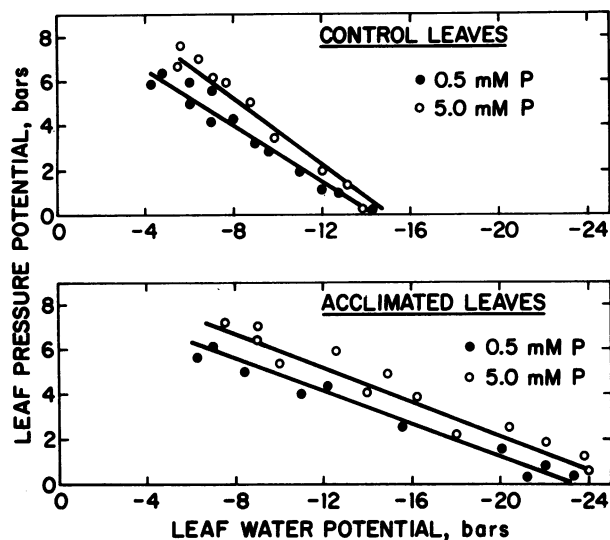
FIG. 1. Relationship between leaf water potential and leaf pressure potential in control and stress-acclimated cotton leaves. Each point is the mean of six to seven measurements obtained from three separate experiments. SE ranged from 0.5 to 1.1 bars.

FIG. 3. Photosynthesis and leaf conductance of stress-acclimated leaves of cotton in relation to leaf water potential. Each point is the mean of nine measurements obtained from three separate experiments. SE ranged from 0.06 to 0.19 cm s^{-1} for conductance measurements and 0.05 to 0.16 nmol cm^{-2} s^{-1} for photosynthesis measurements.
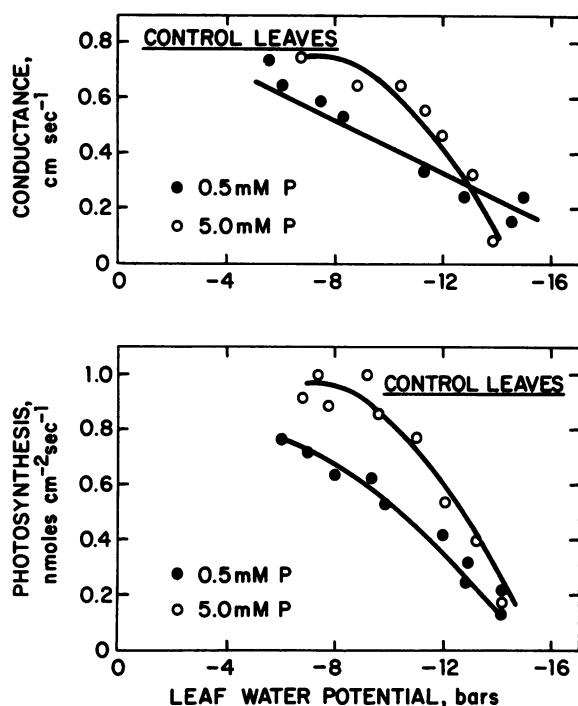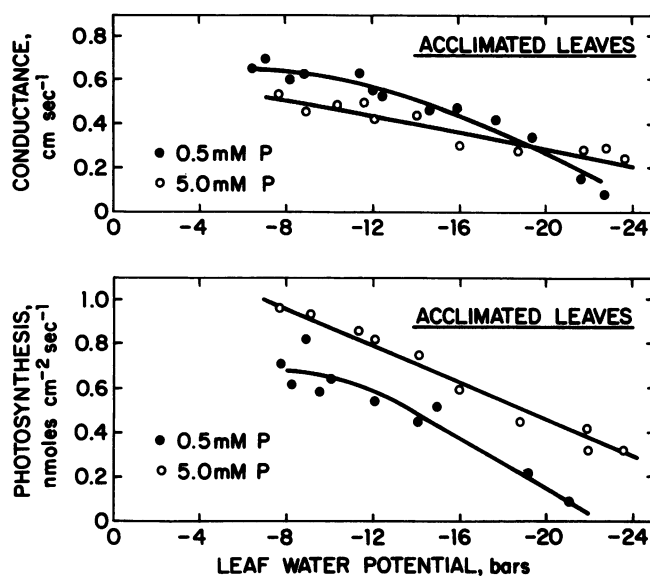

FIG. 2. Photosynthesis and leaf conductance of control cotton leaves in relation to leaf water potential. Each point is the mean of nine measurements obtained from three separate experiments. SE ranged from 0.08 to 0.22 cm s^{-1} for conductance measurements and 0.06 to 0.14 nmol cm^{-2} s^{-1} for photosynthesis measurements.
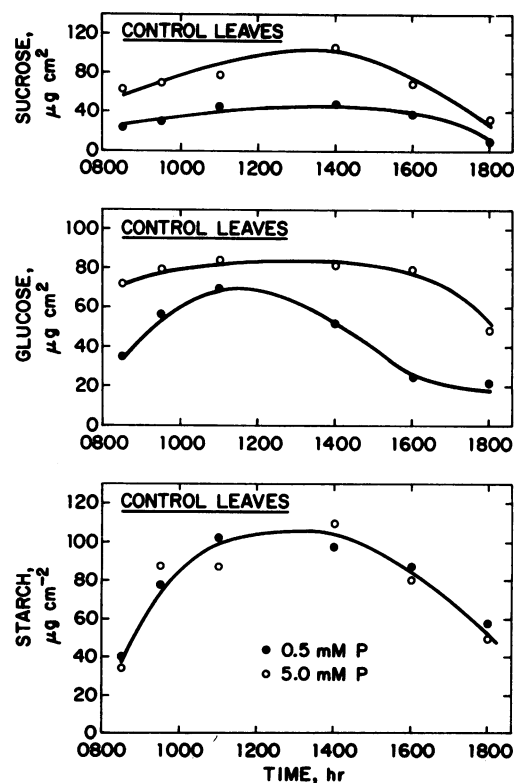

FIG. 4. Sucrose, glucose, and starch levels in control cotton leaves during dehydration. Data were pooled from three experiments with duplicate measurements at each time point in each experiment. SE were 12% or less of the mean values reported. The photoperiod started at 0730 and was terminated at 2200 h. Leaf water potentials were 4.6 ± 1.2 bars at the start of the photoperiod and 14.1 ± 0.8 bars by 1800 h.

4). Thus, during dehydration, when photosynthetic rates of the high P plants exceeded those of low P plants (Fig. 2), soluble sugars accumulated to a greater extent in the high P plants (Fig. 4). No detectable differences in leaf starch concentration existed in control plants as a consequence of P fertility level (Fig. 4). Glucose and sucrose concentrations in leaves of acclimated plants were higher when plants were grown on 5.0 mM P (Fig. 5). Starch levels were generally 2-fold lower in high P plants as compared with plants grown on 0.5 mM P. Thus, high P levels
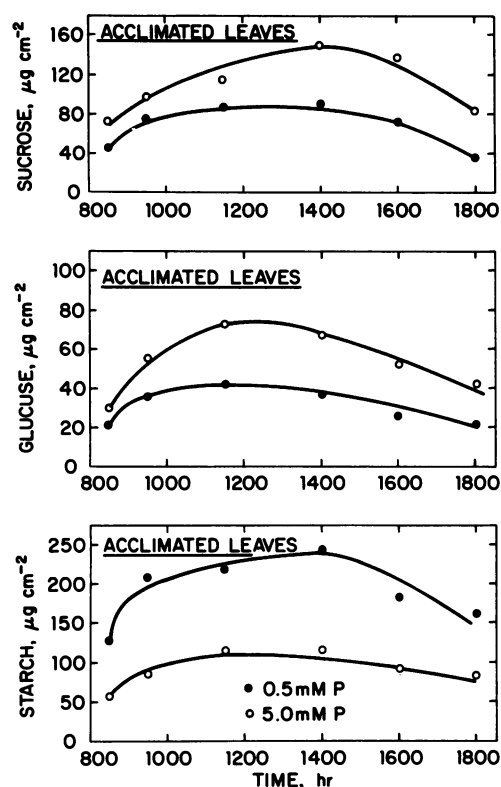
FIG. 5. Sucrose, glucose, and starch levels in stress-acclimated cotton leaves during dehydration. Data were pooled from three experiments with duplicate measurements at each time point in each experiment. SE were 11% or less of the mean values reported. Leaf water potentials were 6.4 ± 1.0 bars at the start of the photoperiod and 22.5 ± 1.1 bars by 2100 h.

prevent the buildup of starch that occurs in stress-acclimated cotton leaves (2, 3).

DISCUSSION

The effects of P fertility on partitioning of carbon between sugars and starch in cotton are in accordance with prior data obtained from isolated chloroplasts (8), leaf discs (9), and whole plants (6). High P resulted in higher concentrations of glucose and sucrose (Figs. 4 and 5), but did not significantly alter the leaf turgor-leaf water potential relationships (Fig. 1). The increased sugar levels could contribute only about 0.4 bar to the leaf osmotic potential, based on calculations of cellular volumes and the attendant sugar concentrations (2, 3). This 'osmotic adjustment' due to high P is similar to the amount shown in Figure 1. Radin (12) recently reached a similar conclusion with regard to suboptimal levels of P.

Phosphorus fertility influenced water use efficiency on a single leaf basis in acclimated plants (Fig. 3). Lower leaf conductances and higher photosynthetic rates were characteristic of plants grown on 5.0 mM P. Radin (12) demonstrated that P deficiency causes stomata of cotton to begin closing at higher leaf water potentials when compared to the stomatal response of plants grown on more typical P levels (0.05 versus 0.5 mM). The present experiments along with those of Radin (12) clearly demonstrate that P fertility level exerts an effect on stomatal response to stress.

Phosphorus-induced changes in water use efficiency were also mediated through increased photosynthetic capacity (Figs. 2 and 3). In acclimated plants, high P levels resulted in higher photosynthetic rates and lower leaf conductances at most leaf water potentials. The inhibition of photosynthesis at high leaf water

potentials as a consequence of stress acclimation was not as great in these experiments as was previously observed (2, 3). This disparity may be due to differences in the growing media used in the experiments.

High P did inhibit the accumulation of starch normally associated with stress acclimation in cotton (Fig. 5; Refs. 2, 3). Because high P reversed the effects of stress acclimation on starch accumulation, the data indicate that intracellular Pi levels may have mediated responses to acclimation. In this regard, P uptake by plants is severely depressed by water stress (5, 7, 16), which could have a marked effect on carbon partitioning, and perhaps photosynthesis, in plants subjected to periods of water deficit. Based on the present experiments and those reported earlier (2, 3), the following explanation can be offered to account for the large accumulation of starch in stress-acclimated cotton leaves. During periods of water stress, P uptake is suppressed resulting in lower cellular Pi levels which lead to starch accumulation (6, 8, 9, 11). Use of high P fertility levels mitigates the effects of stress on P uptake resulting in more 'normal' intracellular Pi levels, thus accounting for the inhibition of starch accumulation in the acclimated leaves (Fig. 5).

Regulation of carbon partitioning between sucrose and starch is mediated by cellular Pi levels (8, 9, 11). Species differ with respect to cytoplasmic sucrose-P-synthase activity in relation to intracellular Pi concentration (10). Consequently, partitioning of carbon into soluble and insoluble fractions in response to water stress may be different among species, thus accounting for differences in the acclimation response to water stress. Although no well-defined interspecific variation in P uptake during stress appears to exist, this could also have a bearing on stress acclimation by virtue of the P effects on carbon partitioning as observed in these experiments.

In summary, stress acclimation in cotton greatly increases leaf starch levels. This change can be prevented if nutrient P is maintained at very high levels. It is suggested that water stress cycles which induce acclimation interfere with P uptake or maintenance of adequate tissue P levels. Thus, P fertility as well as N fertility (13-15) can alter plant responses to stress.

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