Shade Effects on Salinity Tolerance of ‘Valencia’ Orange Trees on Rootstocks with Contrasting Salt Tolerance

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To gain insights into mechanisms of salt tolerance we studied the effects of shading during salinity stress using well-fertilized 2-year-old potted ‘Valencia’ orange trees on either Cleopatra mandarin (Cleo, relatively salt tolerant) or Carrizo citrange (Carr, relatively salt sensitive) rootstocks grown in Candler fine sand. We wanted to determine if shading could reduce the negative effects of salinity stress. Trees were grown either under 50% shadecloth or left unshaded in full sun light. Half the trees in sun and shade were salinized with 50 mM Cl– during two 9-week salinity periods in the spring and fall, interrupted by our normal 11-week summer rainy period, while the other half received no salinity treatment. The shade treatment generally reduced midday leaf temperature and evaporative demand while the salinity treatment reduced growth. In non-salinized trees, the shade effect increased midday photosynthesis and stomatal conductance but not leaf transpiration. Shade also increased leaf chlorophyll and water use efficiency of trees on both rootstocks and increased growth of trees on Cleo. Shade decreased Cl– concentrations in leaves of salinized Carr trees but had no effect on leaf or root Cl– of trees on Cleo. The growth reduction from salinity stress was actually greater for shaded than for sun-exposed trees. Shaded trees on both rootstocks had higher leaf Na+ than sun-exposed trees after the first salinity period and this shade-induced elevated leaf Na+ persisted after the second salinity period in trees on Carr. Although shading reduced Cl– accumulation in ‘Valencia’ on Carr, shading did not alleviate the negative effects of salinity on growth and Na+ accumulation in trees on either rootstock.

Salinity problems in Florida citrus can occur during the relatively dry spring and fall irrigation periods if irrigation water has a high salt content (Syvertsen et al., 1989). All commercial citrus trees are grafted on rootstocks that can regulate the amount of Cl– and/or Na+ accumulated in leaves (Levy and Syvertsen, 2004). Cleopatra mandarin rootstock is considered a Cl– excluder, whereas Carrizo citrange is considered a Cl– accumulator but also a Na+ excluder. The Cl– ion is considered to be a more important limitation than Na+ on citrus growth and yield (Bañuls et al., 1997). The accumulation of Cl– and, thus, relative salt tolerance, has been linked to tree growth (Castle and Krezdorn, 1975) and to tree water use (Moya et al., 1999, 2003; Syvertsen et al., 1989). However, the relationship between Cl– accumulation and water use in citrus is not universal because when water use was reduced during growth at elevated CO2, leaf Cl– was reduced only in relatively salt sensitive Carrizo seedlings but not in relatively salt tolerant Cleopatra (García-Sánchez and Syvertsen, 2006).

Salinity stress often occurs in conjunction with flooding, drought, and/or high temperature stress. Shade can improve physiological response of plants to drought (Duan et al., 2005) or to excess boron stress (Sotiropoulos et al., 2004) compared to unshaded plants. In citrus, 50% shade screens reduced excessively high leaf temperatures and evaporative demand at midday such that photosynthesis and leaf water use efficiency were increased above that of unshaded leaves (Syvertsen et al., 2003). Thus, one might think that salt stress should be reduced by shade. Increases in midday stomatal conductance (g) by shade, however, were accompanied by decreased evaporative demand such that leaf transpiration and whole-plant water use were unchanged (Jifon and Syvertsen, 2003a, 2003b). If Cl– uptake and transport in citrus are indeed linked to water use (Moya et al., 1999, 2003) and shade has little effect on water use, then shade should not have an effect on salt tolerance. Thus, we hypothesized that growing trees under shade should have little effect on leaf Cl– concentration under salinity stress.

We tested ‘Valencia’ orange trees grafted on two rootstocks with contrasting salinity tolerance, Cleopatra mandarin (relatively salt tolerant) and Carrizo citrange (relatively salt sensitive), to determine their physiological responses to salinity in sun and shade. These responses should yield insights into mechanisms of salinity tolerance in citrus. To mimic normal salinity patterns in Florida, the salinity treatment was applied during the irrigation periods in spring and fall with an intervening non-saline summer rainy period that leached any accumulated salts from the soil.

Materials and Methods

PLANT CULTURE AND TREATMENTS. The study was carried out at the University of Florida/IFAS Citrus Research and Education Center, Lake Alfred, FL (28.09°N, 81.73°W; elevation 51 m).
Two-year-old ‘Valencia’ orange (Citrus sinensis L. Osbeck) trees grafted on Cleopatra mandarin (Cleo, C. reticulata Blanco) or Carrizo citrange (Carr, C. sinensis L. Osb. × Poncirus trifoliate L.) were used in this experiment. Twenty uniform trees on each rootstock were grown outdoors in 5-L plastic containers filled with native Candler fine sand. The trees were watered three times per week with 1 L of soluble fertilizer solution (9N–2P–9K), Ca (NO$_3$)$_2$, and iron-chelate (6%) with an N concentration of 66 mg·L$^{-1}$. The 1-L volume of nutrient solution was enough to achieve leaching from the bottom of all containers.

The shade treatment was established from Apr. to Nov. 2003 by placing shade screens on top of 2.2-m-tall PVC frames constructed over the trees. Shade screens were Aluminet-50 (Polysack Plastic Industries, Nir Yitzhak, Israel), a spectrally neutral, aluminized polypropylene shade screen with a mesh size of 6 × 3 mm, which transmits about 50% of incident photosynthetically active radiation (PAR). Ten trees on each rootstock were placed under the shade and 10 trees served as an unshaded control. Two salinity treatments, 0 and 50 mm Cl$^-$ [NaCl and CaCl$_2$ (3:1) ~3600 ppm], were evaluated on five trees on each rootstock in both full sun and under shade. The salinity treatment was begun at the same time as the shade treatment but the salinity was applied during two 9-week dry periods, 23 Apr. to 24 June, and 18 Sept. to 21 Nov. At the beginning of each period, the salinity treatment was added in increasing increments of 15 mm Cl$^-$ per day during two consecutive irrigation days (to avoid osmotic shock) and on the third day, salinity was increased by 20 mm Cl$^-$ to reach the final concentration of 50 mm Cl$^-$. Although the shade treatment was maintained during the intervening typical summer rainy period (25 June to 17 Sept.), the previously salinized trees were irrigated only as necessary with the standard nutrient solution without salt. The experimental design was a two rootstock (Cleo and Carr) × two light intensities (unshaded and 50% shade) × two salt concentrations (0 and 50 mm Cl$^-$) × two light intensities (unshaded and 50% shade) factorial design with five replicate trees in each treatment.

**GAS EXCHANGE AND WATER RELATIONS.** Net gas exchange and water relations of leaves were measured on selected clear days near the end of each salinity period. Measurements were made on two leaves chosen from the mid-shoot area of each plant, giving 10 replicate leaves per treatment. Net assimilation of CO$_2$ ($A_{CO_2}$), stomatal conductance ($g_s$), and leaf transpiration ($E_l$) were determined with a LI-COR portable photosynthesis system (LI-6200; LI-COR Inc., Lincoln, NE) equipped with a well-stirred 0.25-L leaf chamber. Leaf temperature ($T_{lf}$) was measured using the thermocouple inside the gas exchange cuvette. Evaporative demand was measured as the difference (D) between the leaf and air water vapor pressures, assuming leaves were saturated at $T_{lf}$. Photosynthetic water use efficiency ($A_{CO_2}/E_l$) of leaves was calculated based on the equations of Von Caemmerer and Farquhar (1981). All environmental and gas exchange measurements were made in the morning from 1000 to 1200 hr. The measurement conditions within the cuvette are listed in Table 1. Leaf water potential, inversely related to leaf stress, was measured in the early afternoon (1300 to 1400 hr) using a Scholander-type pressure chamber (PMS Instrument, Corvallis, OR; Scholander et al., 1965) on similar leaves as those used for net gas exchange.

**CHLOROPHYLL ANALYSIS.** After gas exchange measurements, two leaf discs (0.45 cm$^2$ each) were sampled from the same leaves, avoiding major veins. Chlorophyll was eluted from the discs by submerging them in 2 mL of N,N-dimethyformamide in the dark for at least 72 h. Absorbances were read at 647 and 664 nm with a Shimadzu UV-vis spectrophotometer (Model UV2401PC, Shimadzu, Columbia, MD) and used to calculate total chlorophyll concentrations according to equations of Inskeep and Bloom (1985).

**LEAF ION CONCENTRATION AND GROWTH PARAMETERS.** At the end of each salinity period, five leaves per tree were used to analyze leaf Cl$^-$ and Na$^+$ concentration. Leaves were briefly rinsed with deionized water, oven-dried at 60 °C for at least 48 h, weighed, and ground to a fine powder. Samples were extracted with a 0.1 N solution of nitric acid and 10% acetic acid. Chloride concentration was measured using a silver ion titration chloridimeter (HBI Chloridimeter; Haake Buchler, Saddle Brook, NJ). Leaf Na$^+$ concentration was determined by a commercial laboratory (Waters Agricultural Lab, Camilla, GA). At the end of the experiment, root Cl$^-$ and Na$^+$ concentrations were also analyzed as above. Plants were harvested and total dry weights of leaves, stem, and roots were determined. Total leaf area was measured using a leaf area meter (LI-3000; LI-COR).

**STATISTICAL ANALYSIS.** Analysis of variance used two rootstocks × two shade levels × two salinity levels and five replicate plants per treatment. Treatment means were separated by Duncan’s multiple range test at $P < 0.05$ using SPSS statistical package (SPSS, Chicago). Linear regression was used to describe relationships between selected variables and analysis of covariance was used to compare slopes of relationships.

<table>
<thead>
<tr>
<th>Rootstock</th>
<th>Cover</th>
<th>Salt</th>
<th>$\text{PAR}$ (µmol m$^{-2}$·s$^{-1}$)</th>
<th>$T_{lf}$ (°C)</th>
<th>D (kPa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>V/Cleo</td>
<td>Unshaded</td>
<td>0S</td>
<td>1906 $^a$</td>
<td>37.0 a</td>
<td>3.4 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+S</td>
<td>1786 a</td>
<td>37.6 a</td>
<td>3.6 a</td>
</tr>
<tr>
<td></td>
<td>Shade</td>
<td>0S</td>
<td>788 b</td>
<td>34.4 b</td>
<td>2.5 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+S</td>
<td>735 b</td>
<td>35.3 b</td>
<td>3.0 b</td>
</tr>
<tr>
<td>V/Carr</td>
<td>Unshaded</td>
<td>0S</td>
<td>2050 a</td>
<td>37.8 a</td>
<td>3.5 a</td>
</tr>
<tr>
<td></td>
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<td>+S</td>
<td>1794 a</td>
<td>37.6 a</td>
<td>3.6 a</td>
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<td>Shade</td>
<td>0S</td>
<td>849 b</td>
<td>34.2 b</td>
<td>2.4 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td>+S</td>
<td>718 b</td>
<td>34.7 b</td>
<td>2.7 b</td>
</tr>
</tbody>
</table>

$^a$Within each column and each rootstock, values with the same letter are not significantly different at 5%.

$^{ns}$, ***Nonsignificant or significant at $P < 0.05$, 0.01, or 0.001, respectively.

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Table 1. Mid-morning (1000 to 1200 hr) photosynthetically active radiation (PAR), leaf temperature ($T_{lf}$), and leaf-to-air vapor pressure deficit (VPD) on a clear day in spring, (22 June 2003) after 9 weeks of shade and salinity treatments on 2-year-old ‘Valencia’ trees on Cleopatra mandarin (V/Cleo) or Carrizo citrange (V/Carr) rootstocks.
Results

TREE GROWTH AND LEAF CHLOROPHYLL. Although ‘Valencia’ trees on Carr in the sun tended to grow more total plant dry weight (TPDW) than those on Cleo, overall, trees on Cleo were larger (Fig. 1A). Non-salinized Cleo trees grew larger in the shade than in sun but TPDW was similar in shaded and unshaded Carr trees. Although salinity reduced growth of all trees, salinity reduced growth more in the shade than in sun (significant shade × salt interaction). The shoot to root dry weight ratio was not affected by any treatment (data not shown). Leaves of trees on Cleo had greater leaf dry weight/area, an index of leaf thickness, than those on Carr (Fig. 1B). Leaf thickness was generally decreased by shade but was only decreased by salinity in unshaded Carr trees. Chlorophyll concentrations in leaves were increased by shade and decreased by salinity (Fig. 1C). Leaf chlorophyll was not affected by rootstock.

MEASUREMENT CONDITIONS AND LEAF GAS EXCHANGE. At the end of the first 9 weeks of salinity treatment (spring salinization), shade reduced PAR about 58% and reduced mid-morning leaf temperature (Tmf) an average of 2.9 °C (from 37.5 to 34.6 °C; Table 1). Thus, shade also lowered evaporative demand (estimated by D) about 0.7 kPa, from an average of 3.5 kPa for sun-exposed leaves to 2.6 kPa for shaded leaves. ‘Valencia’ leaves on Carr had higher rates of photosynthesis than leaves on Cleo (Fig. 2A). Shade increased photosynthesis in non-salinized trees while salinity reduced photosynthesis in leaves on both rootstocks. Stomatal conductance was also reduced by salinity but increased by shade (data not shown). Leaf transpiration (E) was reduced by salinity but was unaffected by rootstock or...
shade treatment (Fig. 2B). There were significant differences in the two-way interaction shade × salt on A$_{CO_2}$ (Fig. 2A) and leaf water use efficiency (A$_{CO_2}$/E$_{lf}$) (Fig. 2C). In salinized trees, however, the already reduced gas exchange responses were not affected by shade. In the non-saline treatment, A$_{CO_2}$ and A$_{CO_2}$/E$_{lf}$ were significantly increased by shade. Salinity reduced A$_{CO_2}$ and A$_{CO_2}$/E$_{lf}$ in both unshaded and shaded leaves but reductions were greater in leaves on Cleo than on Carr. In salinized trees, however, the already reduced gas exchange responses were not affected by shade. At the end of the second salinity period (fall salinization), very similar responses to shade were recorded when PAR averaged 1302 and 614 μmol·m$^{-2}$·s$^{-1}$, T$_a$ averaged 34.6, and 32.3 °C and D averaged 3.0 and 2.4 kPa in the sun and shade, respectively. Again, the salt treatment reduced net gas exchange characteristics for trees on both rootstocks, and shading tended to increase both A$_{CO_2}$ and A$_{CO_2}$/E$_{lf}$ of non-saline trees on both rootstocks (data not shown). E$_{lf}$ was overall lower in the fall than in spring, however, as fall T$_a$ and D were lower and leaves aged.

When all gas exchange measurements across all treatments at the end of both salinity periods were analyzed together, there were strong correlations ($r > 0.87$, $P < 0.01$) between leaf temperature and D and consequently, strong negative relationships ($r < -0.52$, $P < 0.01$) between T$_a$ and g$_s$ (data not shown). Thus, high leaf temperatures increased evaporative demand and clearly lowered stomatal conductance regardless of the rootstock or salinity treatment.

**Chloride and Sodium Concentration in Leaves and Roots.** Leaves of salinized shaded trees had higher leaf Cl$^-$ concentrations than those on Cleo after both salinization periods but these differences were nonsignificant for shaded trees at the end of the first salinization period (Fig. 3). At the end of the spring salinization, leaf Cl$^-$ concentration was greater than at the end of the fall salinization that followed the leaching rainy period. Shade decreased leaf Cl$^-$ in salinized Carr at the end of both salinization periods. At the end of fall salinization, shaded Carr trees had significantly lower root Cl$^-$ concentration than unshaded trees.

Leaves of salinized shaded trees had higher leaf Na$^+$ concentration than those of unshaded trees on both rootstocks at the end of the spring salinization treatment (Fig. 3). Overall, leaf Na$^+$ and Cl$^-$ were lower after the rainy season and the fall salinization than after the spring salinization. Leaves on Carr trees had significantly lower leaf Na$^+$ concentration than those on Cleo at the end of the spring salinization under shade and at the end of the fall salinization in full sun. Shade increased leaf Na$^+$ in salinized trees except in Cleo at the end of the fall salinization. There was no rootstock or shade effect on root Na$^+$ concentration.

**Leaf Water Potential.** At the end of both salinization periods, afternoon leaf water stress was consistently increased (leaf water potential decreased) by salinity in leaves on both rootstocks under both light treatments (Fig. 4). Shade had no significant effect on leaf water stress at the end of the spring salinity period but at the end of the fall salinity period, shade increased leaf water stress in all trees except non-salinized trees on Cleo.

**Discussion**

**Effect of Shading on Non-Salinized Trees.** Shading trees with 50% screen cloth reduced mid-morning T$_a$ and D and resulted in higher photosynthesis and A$_{CO_2}$/E$_{lf}$ in non-salinized trees on both Cleo and Carr. Leaf transpiration, however, was not affected by shading. Although g$_s$ was higher in shaded leaves, the driving force for transpiration (D) was lower in shaded leaves and thus compensated for the higher g$_s$ such that E$_{lf}$ was not affected. The shade-induced increases in photosynthesis were not due to an increase in g$_s$ (Garcia-Sánchez et al., 2006) so high leaf temperatures were apparently more important than g$_s$ in limiting A$_{CO_2}$. Excessively high T$_a$ at high PAR also can lead to reductions of A$_{CO_2}$ in unshaded leaves due to an increase in photo inhibition (Jifon and Syvertsen, 2003b).

Consistent increases in mid-morning leaf gas exchange responses to lower T$_a$ and D from shade occurred during both measurement periods in non-salinized trees. In an experiment with young Murcott citrus trees, shading increased growth by increasing the leaf dry weight during a 3-month shade period (Medina et al., 2002). In our study, plant growth increased in shaded trees on Cleo but shaded trees on Carr had similar growth to those in full sun. Higher leaf gas exchange of shaded plants are typically only observed during the middle of the day, since PAR can be limiting in early morning and late afternoon (Medina et al., 2002; Syvertsen et al., 2003). Therefore, the positive effect of shading on A$_{CO_2}$ during midday hours may have been insufficient to increase the overall growth of trees on Carr. In addition, at the end of the experiment, leaves on Carr trees had higher leaf water stress in the shade than in sun-exposed conditions. This increase in leaf water stress, perhaps related to the higher mid-morning g$_s$ in the shade, could have negated any effect of shade on growth of trees on Carr.

**Effect of Shading on Salinized Trees.** At the end of both the spring and fall salinization periods, A$_{CO_2}$ of salinized trees was not enhanced by shading despite the fact that T$_a$ and D were consistently decreased. Since stomatal conductance was consistently increased by shade, the salinity-induced decrease in A$_{CO_2}$ was not primarily due to stomatal constraints but was more likely attributable to direct effects of Cl$^-$ and/or Na$^+$ toxicity (Garcia-Sánchez and Syvertsen, 2006; Storey and Walker, 1999). Leaf Cl$^-$ in salinized Carr was decreased by shade but apparently not enough to affect A$_{CO_2}$. Shaded leaves had higher leaf Na$^+$ concentration than unshaded leaves in trees on both rootstocks. Therefore, high Na$^+$ could have been responsible for negating any A$_{CO_2}$ response in shaded trees. In salinized ‘Valencia’ orange trees grafted on Troyer citrange or Cleopatra mandarin, A$_{CO_2}$ inhibition by salinity was more readily attributable to Na$^+$ toxicity than to Cl$^-$ toxicity (Lloyd et al. 1987).

Salinized trees on Cleo in sun had lower leaf Cl$^-$ than trees on Carr (Fig. 2), supporting salinity tolerance differences attributable to these rootstocks (Levy and Syvertsen, 2004). This well-known regulation of leaf Cl$^-$ concentration in citrus leaves has been associated with leaf transpiration and total water absorbed per plant (Moya et al., 1999, 2003), shoot root ratio (Storey and Walker, 1999), and efficiency of the root system for limiting Cl$^-$ uptake (Storey and Walker, 1999). In this experiment, the higher exclusion of Cl$^-$ from shoots of trees on Cleo than on Carr was more likely related to the ability of roots to restrict the movement of Cl$^-$ since their shoot:root ratio, leaf dry weight, and leaf transpiration were similar. In addition, shade decreased leaf Cl$^-$ concentration in leaves on Carr without changing leaf transpiration. Thus, leaf Cl$^-$ concentration was not necessarily closely linked to water use.

In unshaded trees, the overall growth reduction by salinity was greater for Carr than for Cleo trees (45% and 28%, respectively), reflecting their relative leaf Cl$^-$ concentrations in this study and in previous studies (García-Sánchez and Syvertsen, 2006; García-Sánchez et al., 2002). Growth reductions by salinity under shaded conditions, however, were greater than those in unshaded
conditions and were similar for trees on Cleo and Carr (55% to 59%). Negative effects of high salinity on strawberry fruit yield (Awang and Atherton, 1995), bean plants (Helal and Mengel, 1981), or melons (Meiri et al., 1982) were also greater under shaded conditions than in unshaded. In our study, the lower growth of salinized trees under shaded conditions than in full sun could have been due to the greater increase of the leaf Na\(^+\) concentration in shaded trees. This important effect of Na\(^+\) occurred in spite of the high Ca\(^{2+}\) in the salinity treatment as high Ca\(^{2+}\) can mitigate negative effects of Na\(^+\) (Gratten and Grieve, 1992).

Leaf Na\(^+\) concentration of salinized trees on Cleo tended to be higher than Carr at the end of the spring salinization period and this difference remained in unshaded trees at the end of the second period. Shade increased leaf Na\(^+\) in salinized Carr trees by the end of the second salinity period. Shading affected the Cl\(^-\) and Na\(^+\) concentration in different ways since leaf Na\(^+\) concentration was higher for shaded trees on both Cleo and Carr whereas leaf Cl\(^-\) concentration was lower for leaves and roots of shaded trees on Carr. We did not want to damage roots in the middle of the experiment so we did not sample root Na\(^+\) at the end of the first

Fig. 3. Effects of salinity (0S = 0 m\(\text{m} \) and +S = 50 m\(\text{m} \) Cl\(^-\)) and growing in sun or shaded conditions on mean (n = 5) Cl\(^-\) and Na\(^+\) concentration (mg·g\(^{-1}\) dry weight) in leaf and root tissues of 'Valencia' orange trees grafted on Cleopatra mandarin (V/Cleo) or Carrizo citrange (V/Carr). Data are from the end of the Spring or Fall salinity periods. Significant effects of rootstock, shade or salt treatments are denoted as P < 0.001 (***) or ***) or nonsignificant (ns). Different letters within each plate denote significant differences at P < 0.05 (Duncan’s test).
Salinity period. The decrease in $T_w$ by shade did not affect the final accumulation of Na\(^+\) in roots but must have increased root uptake since Na\(^+\) transport to leaves was apparently increased. Since shade consistently increased root growth in non-salinized trees on both rootstocks (García-Sánchez et al., 2006), a greater uptake of Na\(^+\) in shaded trees could have occurred through a transient increase in root growth that we did not measure at the end of the experiment.

In conclusion, citrus leaves growing in full sun experience high temperatures that decreased midday $A_{\text{CO}_2}$, $g_s$, and water use efficiency. Lowering leaf temperature by shading increased midday $A_{\text{CO}_2}$, $g_s$, and $A_{\text{CO}_2}/E_s$ but did not affect $E_w$. Shade did decrease Cl\(^-\) concentrations in leaves of salinized Carr trees but shade had no effect on Cl\(^-\) in Cleo. Salinity stress limited the positive effect of shading on net gas exchange of leaves on both rootstocks and negated any effects of shade on growth of 'Valencia' orange trees on Carr. In salt stressed trees, growth was reduced more under shade than in full sun and leaf Na\(^+\) was increased more than two-fold after the spring salinization period. Even though overall leaf Na\(^+\) concentrations were lower after the fall salinization period, Carr shade leaves still had twice the Na\(^+\) as sun leaves. Root Na\(^+\) in Cleo tended to be higher than in Carr roots and root Na\(^+\) was higher than leaf Na\(^+\) in both rootstocks. Although root Na\(^+\) was not significantly affected by shade, salinized root Na\(^+\) was consistently decreased by shade. Thus, the redistribution of Na\(^+\) from roots to leaves under shade conditions may have been responsible for the increase in leaf Na\(^+\). This idea is supported by our previous studies (García-Sánchez and Syvertsen, 2006) where patterns of changes in Na\(^+\) and Cl\(^-\) occurred in opposite directions in roots and leaves.

**Literature Cited**


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