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Salinity Stress Inhibits Bean Leaf Expansion by Reducing Turgor, Not Wall Extensibility[1]

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ABSTRACT

Treatment of bean (*Phaseolus vulgaris* L.) seedlings with low levels of salinity (50 or 100 millimolar NaCl) decreased the rate of light-induced leaf cell expansion in the primary leaves over a 3 day period. This decrease could be due to a reduction in one or both of the primary cellular growth parameters: wall extensibility and cell turgor. Wall extensibility was assessed by the Instron technique. Salinity did not decrease extensibility and caused small increases relative to the controls after 72 hours. On the other hand, 50 millimolar NaCl caused a significant reduction in leaf bulk turgor at 24 hours; adaptive decreases in leaf osmotic potential (osmotic adjustment) were more than compensated by parallel decreases in the xylem tension potential and the leaf apoplastic solute potential, resulting in a decreased leaf water potential. It is concluded that in bean seedlings, mild salinity initially affects leaf growth rate by a decrease in turgor rather than by a reduction in wall extensibility. Moreover, long-term salinization (10 days) resulted in an apparent mechanical adjustment, *i.e.* an increase in wall extensibility, which may help counteract reductions in turgor and maintain leaf growth rates.

Excess salinity adversely affects the growth of numerous glycophytic crop plants (11, 21). An important primary effect of mild salinization is a reduction in leaf growth, which can, in turn, directly contribute to reduced plant photosynthetic potential and yields (18). Since salt accumulates in the upper layers of the soil as a result of evapotranspiration, its effects on seedling growth can be particularly disturbing. The mechanism(s) by which salt reduces leaf area expansion during seedling growth has not been satisfactorily resolved. One possible mechanism is that the reduction in water potential in the root zone is transmitted via the xylem to the leaves, where cell turgor is correspondingly reduced. However, Bernstein (1), in a classic series of experiments, showed that the osmotic potential of leaf and root tissues adjusted in response to root media salinization, thus apparently preventing a decline in turgor potential. This conclusion was first questioned by Oertli (17) who hypothesized that salinization could lead to a buildup in cell wall (apoplast) osmotic potential, which would effectively reduce turgor inside the cell but would not be detected by assaying bulk leaf osmotic potentials. Unfortunately, difficulties in accurately measuring apoplastic solute potential have hindered investigations of this hypothesis (10). Recently, Termaat *et al.* (22) found that pressurization of the roots of salinized wheat and barley plants, while presumably restoring root and shoot turgor, did not restore long-term rates of leaf growth. They concluded that salt, rather than causing a reduction in turgor, induced a "message" which was transmitted from the root to the leaf and regulated leaf growth rate, possibly by an effect on cell wall properties.

The rate of cell enlargement (dV/dt) can be described by the equation:

$$dV/dt = m(P - Y) \quad (1)$$

where m is the wall extensibility, Y is a wall property reflecting the turgor threshold that must be exceeded in order for cell walls to expand, and P is the cell turgor (14). Thus, salinity stress could reduce leaf cell expansion rates by inducing reductions in wall extensibility as well as by reducing turgor. To test this, we have investigated the kinetics of changes in leaf wall extensibility in relation to bean leaf growth responses to salinity stress. In addition, we have examined the possibility that salinity-induced reductions in bean leaf growth rate are due to reduction in turgor. A major advantage of the bean leaf system used here is that leaf cell division can be completed during red light growth, prior to the initiation by white light of rapid cell expansion (23); thus, the effects of NaCl on leaf cell expansion alone can be studied.

MATERIALS AND METHODS

Plant Material. Bean plants (*Phaseolus vulgaris* L., cv Contender) were germinated and grown for 7 d in moistened vermiculite under 4 μE $m^{-2}s^{-1}$ of continuous RL[3] at 75% RH. On the 7th d, the seedlings were carefully transferred to hydroponic culture. Ten seedlings were held by their stems in polystyrene floats that suspended the roots in aerated 5 mM $CaCl_2$ (9, 13). Where indicated, a commercial source of soluble mineral nutrients was also added (0.75 g L^{-1} of Miracle-Grow 15-30-15 (NPK + trace elements) (Stern Nurseries Inc., Geneva, NY). Thus, leaf responses to salinization could be assayed with plants growing at different rates under high and low nutrient conditions. NaCl (50 or 100 mM) was usually added to hydroponic culture solution on day 10 after planting, 1 h prior to transfer to a growth chamber with 24 h fluorescent illumination (250 μE $m^{-2}s^{-1}$) at 25°C and 60% RH. For some longer term salinization experiments, plants were germinated in vermiculite moistened with 100 mM NaCl + 5 mM $CaCl_2$ and transferred to salinized (100 mM NaCl) nutrient solution at d 7.

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[3] Abbreviations: RL, dim red light; Ψ_w, bulk water potential; Ψ_π, bulk osmotic potential; Ψ_p, calculated bulk turgor potential; Ψ_t^{xyl}, negative pressure potential or tension of xylem solution; Ψ_π^{apo}, osmotic potential of apoplastic solution; Ψ_w^{apo}, water potential of apoplastic solution; RGR, relative growth rate; PEx, plastic extensibility of cell walls; WL, bright white light.

Leaf Growth. The area of marked primary leaves on each plant was determined periodically as the product of measured length and width, according to the regression equation of Van Volkenburgh and Cleland (23). Relative growth rates were calculated as percentage increase in area per hour. Upper epidermal impressions were taken from the leaves (23), and cell diameters were estimated using a microscope fitted with a micrometer scale eyepiece. Cell diameters are means of counts of five fields of vision on leaves of five separate plants.

Leaf Water Relations. Isopiestic thermocouple psychrometry was used to determine bulk leaf water potential (2, 3). Leaf discs (20 mm diameter) were cut and immediately transferred to Vaseline-coated chambers, which were closed and lowered into a water bath at 26°C. Distilled water was placed on the thermocouple ring and output was determined following equilibration (about 2 h). The chamber was then calibrated by using sucrose solutions. Finally, dry thermocouples were assayed to correct for heat of respiration (2, 25).

Discs were also collected from the primary leaf opposite to that used for water potential measurements; the discs were wrapped in aluminum foil, frozen on dry ice, and stored at −20°C. Ψ_π was determined by pressing frozen-thawed discs between wide-tipped forceps and collecting 8 μL of sap for assay in a Wescor 5100B vapor pressure osmometer. The osmometer was recalibrated after every pair of readings using commercial standards. Readings were converted to pressure units by assuming 40 mosmol kg^{-1} = 1 bar (or 0.1 mPa). Ψ_p was determined using the relationship: $\Psi_p = \Psi_w - \Psi_\pi$.

Ψ_t^{xyl} in shoots excised 4 cm below the primary leaf node was determined using a Scholander pressure chamber with a humidified chamber (12, 20). Following Ψ_t^{xyl} determinations, the protruding cut stem surface was washed with distilled water and blotted dry three times prior to raising the pressure in the chamber to 10 bars. At this pressure, apoplastic solution was exuded at the cut surface, and 10 μL were collected in approximately 2 min. Volume of sap in the stem xylem did not exceed 2 μL. The osmotic potential of apoplast exudate was assayed by isopiestic thermocouple psychrometry. A drop (5 μL) of sample was placed on the thermocouple ring and readings were taken after 80 min equilibration against distilled water and then calibrated against dilute sucrose solutions on filter paper discs at the base of the chamber. The water potential of the leaf apoplast solution could then be estimated using the relationship:

$$\Psi_w^{apo} = \Psi_t^{xyl} + \Psi_\pi^{apo}.$$

Thus, two separate methods, the pressure chamber and isopiestic thermocouple psychrometry, were used to determine the effect of root salinization on bulk leaf water potentials and, hence, indirectly on bulk turgor values. Determinations of bulk leaf water potential of growing tissues by isopiestic thermocouple psychrometry may be overly negative if wall relaxation occurs during the measurement period (2 h in these experiments). Previous reports (26) suggest that wall relaxation in bean leaves occurs between 6 and 12 h after incubation of discs in the psychrometer chamber. Moreover, Ψ_w values obtained here by thermocouple psychrometry were similar to those obtained using the rapid (5 min per measurement) pressure chamber method. Initial attempts at determining instantaneous turgor pressures of individual cells with a micro-pressure probe (8) were discontinued because of frequent clogging of the capillary tips.

Cell Wall Extensibility. Wall extensibility was assessed by measuring PEx with the Instron technique (5). PEx is not a direct measure of wall extensibility (m), but differences in PEx apparently provide a valid measure of differences in wall extensibility (for discussion, see Ref. 6). Leaf sections (15 × 5 mm) were cut adjacent and parallel to the main vein of the primary leaves (27). The sections were boiled for 5 min in methanol, cooled, and stored for Instron analysis using an Instron TM stress-strain analyzer (Instron Corp., Canton, MA). Prior to assay, sections were rehydrated for 3 to 5 min in water and then carefully clamped with 5 mm tissue between the clamps. Each section was extended at 0.3 cm min^{-1} until 15 g load was reached. The clamps were then returned to their original position and reextended to 15 g. The slope of the first extension between 10 and 15 g was extrapolated to give percentage of extension per 100 g load (*i.e.* total extensibility). The slope of the second extension gave elastic extensibility. PEx was determined as the difference between the two values (5) and is in units of percentage extension per 100 g applied load.

Statistics. Data are presented as means ± SE from one or more representive experiments where n = numbers of plants assayed. All experiments were repeated one or more times with similar results.

RESULTS

Effect of Mild Salinity Stress on the Rate of Light-Induced Bean Leaf Cell Enlargement. Seedlings were allowed to develop for a 10 d in RL and then transferred to WL in order to initiate rapid cell expansion. Leaf sizes were measured between 10 and 13 d after planting. Despite the presence of fully expanded cotyledons, seedlings grown with exogenous mineral nutrients produced larger leaves than those grown on 5 mM $CaCl_2$ alone (Fig. 1). In both cases, salinization of the root media at d 10 (zero h, Fig. 1) led to subsequent reductions in leaf size, which were associated with reductions in cell size. For example, mean diameters of upper epidermal cells were 24 ± 2 μm for leaves of

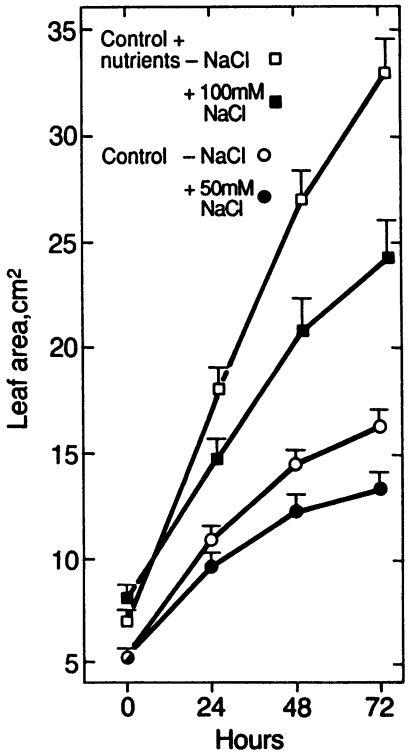

FIG. 1. Effect of salinization on leaf area. Bean seedlings were grown in RL for 7 d on vermiculite and for a further 3 d in solution culture (5 mM $CaCl_2$ ± mineral nutrients). Salinization with 50 or 100 mM NaCl was effected 1 h prior to induction of rapid leaf expansion by transfer to WL at d 10. $n \geq 10$. Leaf size is plotted as a function of time in WL. Vertical bars larger than symbols indicate SE. Treatments: control, no nutrients (○——○), control + nutrients (□——□); 50 mM NaCl, no nutrients (●——●); 100 mM NaCl + nutrients (■——■).

13 d plants salinized with 50 mM NaCl as compared with 28 ± 2 μm for nonsalinized plants.

Figure 2 shows that daily relative growth rates of leaves of nonsalinized plants with added mineral nutrients were higher than those for leaves of plants on 5 mM $CaCl_2$ alone. However, the overall developmental pattern was similar with or without added mineral nutrients, *i.e.* large increase in growth rate during the first 24 h after transfer from RL to WL, followed by progressive declines thereafter. Salinization of $CaCl_2$-grown plants with 50 mM NaCl decreased the initial white light-induced increase in growth rates, but did not alter the overall developmental pattern. The early stimulatory effect of WL on relative growth rates of leaves of plants grown with added mineral nutrients was almost completely inhibited by 100 mM NaCl.

Salinization and Leaf Cell Wall Extensibility. The Instron technique was used to determine whether the inhibition of leaf growth induced, by saline stress, could be due to an inhibition of the wall loosening process. The patterns of change in PEx during the 72 h period following transfer of control plants from RL to WL were similar to the pattern of changes observed in relative growth rates. Thus PEx values increased in the first 24 h following transfer to WL and then declined as shown earlier (24, 27) The PEx values for leaves of plants grown in mineral nutrient media were consistently slightly higher than the values observed in the slower growing, smaller leaves of plants grown on 5 mM $CaCl_2$ alone (Fig. 3, A and B). On the other hand, in both sets of plants, salinization failed to alter either the initial increase in wall extensibility observed after 24 h in WL, or the subsequent decrease in PEx observed between 24 and 72 h, even though the growth rate was modified by the salt stress. The only significant differences in PEx caused by salinization were the slightly higher values observed at 72 h in the salinized plants, in both low and high nutrient solutions (Fig. 3, A and B).

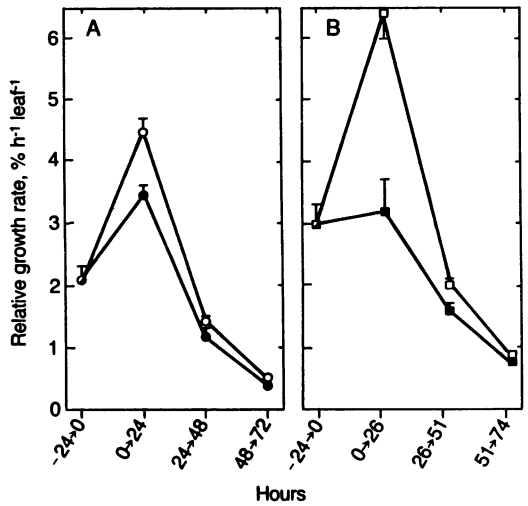

FIG. 2. Effect of salinization on leaf relative growth rates. A, No nutrients; B, plus nutrients. Conditions and symbols as in Figure 1. −24 → 0 indicates growth rate from d 9 to 10 in RL. The remaining intervals are all in WL.

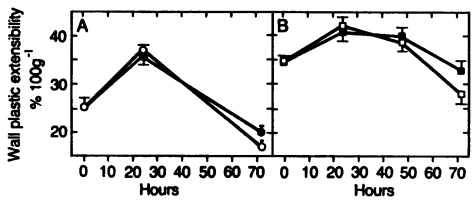

FIG. 3. Instron determination of leaf cell wall plastic extensibility. Leaf strips cut from plants treated as in Figure 1 were boiled in methanol and rehydrated in water prior to assay. A, No nutrients, ±50 mM NaCl; B, plus nutrients ± 100 mM NaCl.

In order to determine whether longer term salinization would reduce wall extensibility, one set of plants was germinated and grown in the presence of 100 mM NaCl plus nutrients for 10 d in RL. At this point the leaves were smaller than those of nonsalinized control plants. However, PEx values of the salinized plants were higher than those for nonsalinized plants. Furthermore, PEx increased to significantly higher values within 6 h of transfer of the saline-grown plants from RL to WL than those in equivalent plants grown for 10 d without any salinization (Table I). Saline-grown plants, transferred to nonsalinized solutions and WL coincidentally, showed only small additional increases in PEx values.

Although the transfer of salinized plants from RL to WL produced rapid and large increases in PEx, RGR increased toward control values only when the saline solution in the root medium was coincidentally removed. Clearly, therefore, even prolonged root salinization did not restrict leaf growth via an inhibitory effect on wall loosening, and other factors must be involved.

Salinization and Leaf Water Relations. If salt stress is not inhibiting leaf growth via a decrease in wall extensibility, it is likely to be acting via a reduction in turgor. Experiments were performed to test this hypothesis. Table II shows that in addition to affecting leaf growth (Figs. 1 and 2). salinization to 50 mM NaCl for 24 h had several effects on leaf water status. Ψ_π showed an adjustment to values 1.7 bars more negative 1 d after salinization to 50 mM NaCl. Ψ_w values were 3 bars more negative in salinized plants. Calculation of Ψ_P from the Ψ_π and Ψ_w values showed that Ψ_p declined by 1.2 bars in response to salinity. These trends were confirmed by estimating Ψ_w in an alternative manner. Table III shows that the tension in the leaf xylem (Ψ_t^{xyl}) was

Table I. *Effect of Germination and Growth of Bean Seedlings in 100 mM NaCl plus Nutrients for 10 d on Subsequent Light-Induced Changes in PEx and RGR*

Plants were germinated and grown for 10 d in RL ± 100 mM NaCl. At d 7 they were placed in hydroponic culture with nutrients. Some plants were placed in WL for 6 or 7 h immediately before harvest and assay of leaves on d 10; $n = 10$ for RGR; $n \geq 14$ for PEx.

NaCl during		Time in WL	PEx	RGR
0–10 d	6–7 h + WL			
mM	*mM*	*h*	*% 100 g⁻¹*	*% h⁻¹*
0			35 ± 1	
0	100[a]	7	39 ± 2	2.3 ± 0.1
0	0	7	40 ± 2	5.4 ± 0.9
100			42 ± 1	
100	100	6	52 ± 2	2.6 ± 0.3
100	0[b]	6	56 ± 2	4.1 ± 0.3

[a] Plants grown without NaCl, but salinized 1 h prior to transfer to WL. [b] Transferred to nonsalinized media 1 h prior to transfer to WL.

Table II. *Effects of 50 mM NaCl on Water Relations of Bean Seedling Leaves*

Ψ_w measured by isopiestic thermocouple psychrometry with leaf discs. Seedlings grown as in Figure 1 and assayed after 24 h in WL ± NaCl. Pooled means ±SE for two separate experiments; $n \geq 5$.

NaCl	Ψ_π	Ψ_w	Ψ_p
mM		*bars*	
0	−6.6 ± 0.2	−4.7 ± 0.6	+1.9 ± 0.6
50	−8.3 ± 0.1	−7.7 ± 0.3	+0.7 ± 0.2
	$\Delta\Psi_\pi = -1.7$	$\Delta\Psi_w = -3.0$	$\Delta\Psi_p = -1.2$

Table III. *Effect of Root Media Salinization for 24 h on Xylem Tension and Apoplastic Solute Potential*

Plants on 5 mM $CaCl_2$ in RL, salinized on d 10 with 50 mM NaCl, and transferred to WL for 24 h prior to excision of shoots 4 cm below primary node. Ψ_t^{xyl} determined with pressure chamber. Samples for Ψ_π^{apo} collected subsequent to repeated washing and blotting of cut stump and further pressurization of leaves to 10 bars; values determined by isopiestic thermocouple psychrometry. Ψ_w^{apo} is the sum of Ψ_t^{xyl} and Ψ_π^{apo}. Ψ_p is $\Psi_w^{apo} - \Psi_\pi$.

NaCl	Ψ_t^{xyl}	Ψ_π^{apo}	Ψ_w^{apo}	Ψ_π	Ψ_p
mM			*bars*		
0	−3.6 ± 0.4	−0.3 ± 0.1	−3.9	−6.6	+2.7
50	−5.7 ± 0.3	−0.8 ± 0.3	−6.5	−8.3	+1.8
	Δ = −2.1	Δ = −0.5	Δ = −2.6	Δ = −1.7	Δ = −0.9

2.1 bars more negative in salinized plants. Osmotic potentials of apoplastic sap, forced out of excised leaves under pressure, were 0.5 bar more negative as a result of salinization. Water potentials of the apoplastic solution (Ψ_w^{apo}), assumed to be at or near thermodynamic equilibrium with the cytoplasm[4], could then be determined from the equation:

$$\Psi_w^{apo} = \Psi_t^{xyl} + \Psi_\pi^{apo}.$$

Calculated values for Ψ_w^{apo} were 2.6 bars more negative as a result of salinization. This result is reasonably close to the 3.0 bars decline determined using isopiestic thermocouple psychrometry (Table II).

The Ψ_π^{apo} values are similar to those observed in leaf tissues by others (2, 12). The fact that Ψ_π^{apo} values are relatively more negative within 24 h of salinization supports Oertli's (17) hypothesis concerning apoplastic solute buildup. However, the possibility of contamination by damaged cells cannot be ruled out despite the precautions taken, and the overall contribution to reduced Ψ_w in salinized plants (≥0.5 bar) is relatively small, at least at 24 h postsalinization.

DISCUSSION

Reductions in the rate of cell expansion can result from changes in turgor and/or wall extensibility (14). Recent reports have suggested that leaf growth is reduced without any parallel reduction in turgor in both water- (15) and salt-stressed (22) plants, *i.e.* turgor loss is not the primary cause of the growth reductions. One might expect, therefore, that salinization should result in a reduction in wall extensibility.

We have assessed the effects of salinity on wall extensibility by using the Instron technique (5). The parameter PEx, is not a direct measure of wall extensibility (m), but is closely correlated (for discussion, see Refs. 5 and 6), so that a change in wall extensibility should result in a comparable change in PEx. Mild salinization (50 and 100 mM NaCl) reduced the light-induced growth rate of leaves by up to 50% with no comparable change in PEx (Fig. 3). In fact, the only effect was a slightly higher PEx in the salinized plants after 72 h in the light. We would conclude that mild salinity does not reduce bean leaf growth via an effect on wall extensibility. Termaat *et al.* (22) suggested that in wheat and barley leaves salinity inhibited growth via an indirect inhibition of wall extensibility, but no measurement of wall extensibility was actually made.

A second possibility is that the reduction in growth rate was due to a salinity-induced decrease in turgor. Turgor was not directly measured here but was calculated from the water and osmotic potentials of the leaves. Two separate techniques were used to measure leaf water potential, each of which has potential problems. For example, determinations of Ψ_w of leaf discs by isopiestic thermocouple psychrometry may give overly negative values, since wall relaxation (26) and consequent declines in water potential may occur during the measurement. However, Van Volkenburgh and Cleland (26) found that wall relaxation of bean leaf discs in the isopiestic psychrometer was minimal. Both methods gave comparable values for the water potential and showed that salinization resulted in a reduction of turgor of about 1 bar (Tables II and III). Since it is the turgor in excess of the yield threshold, Y, that governs cell enlargement, and this effective turgor may often be only 1 to 3 bars (7), a 1 bar decrease in turgor would be expected to have a major effect on the growth rate.

The conclusion that salinity reduces leaf growth primarily via a reduction in turgor must remain tentative at this time for two reasons. The first is that the evaluation of both wall extensibility and turgor are indirect. The techniques used could have unexpected artifacts, although both the Instron (5, 6) and the isopiestic psychrometer technique (2, 3, 25) have been extensively validated. The second is that the effect of salinization on the yield threshold has not yet been determined. Y has been found to decrease during light-induced leaf cell enlargement (26), and if Y were to change following salinization, it could alter the effective turgor and thus the RGR.

Reduced turgor as the mechanism of salt-induced inhibition of leaf growth is consistent with the rapid kinetics of growth inhibition and recovery upon addition and removal of NaCl to barley (16) and sunflower (19) plants. However, Termaat *et al.* (22) were unable to reverse the salt-induced inhibition of wheat leaf growth by a pressure applied to the roots (which was assumed to cause a comparable increase in leaf cell turgor). This might reflect a species difference, or it may be due to the fact that the pressure was applied only 3 d after the start of the salt stress, and by this time the ability of the cells to expand rapidly may have been reduced significantly. The necessary control, showing that removal of salt at this time could restore rapid expansion, was not included.

The adaptation of plants to prolonged salinity is of interest, since this is the condition that normally exists in the field. In these experiments, when plants were germinated and grown with 100 mM NaCl for 10 d, the PEx of the leaves was significantly higher than that of the nonsalinized controls (Table I). In addition, the increase in PEx upon illumination was twice as great in the salinized plants. As the increase in PEx in the light has been ascribed to light-induced proton efflux followed by acid-induced wall loosening (24), this increase could be due to an enhanced rate of proton excretion or an increased capacity of the walls to be loosened by the same wall pH (27). This mechanical adjustment (an increase in wall extensibility in response to stress) would aid in maintaining the rate of leaf cell enlargement, despite a reduced turgor. In combination with osmotic adjustment, it could help explain the ability of plants to live in saline environments. Mechanical adjustment has been reported previously by Bunce (4) for soybean leaves grown under different environmental conditions but apparently has not been reported previously for salinity stress.

[4] The Ψ_π^{apo} of leaf xylem sap would not be expected to be identical to that for the apoplastic solution surrounding the epidermal cells, but changes in the Ψ_π^{apo} of the leaf xylem sap and leaf apoplast would be expected to show similar responses to salinity.

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