Interactive Effects of Salinity and Substrate Phosphate on Soybean[1]

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ABSTRACT

Preliminary experiments at this laboratory indicated that salt injury of soybeans [*Glycine max* (L.) Merr.] is strongly dependent upon the inorganic phosphate (Pi) concentration in the substrate. Inorganic phosphate concentrations that are commonly used in nonsaline solution cultures were lethal to 'Kanrich' and 'Prize' cvs. in saline media. A solution culture experiment was conducted in the greenhouse to examine the interactive effects of salinity (−0.04, −0.24, and −0.44 MPa osmotic potential) and substrate Pi (0.02, 0.10, 0.20, and 0.30 mmol L^{-1}) on shoot and root growth, foliar injury, and tissue element concentration on five soybean cvs. ['Clark' (P-sensitive), 'Jackson' (salt-sensitive, P-tolerant), 'Lee' (salt-tolerant, P-tolerant), 'L63–1677' (P-tolerant), and Kanrich]. Increased Pi had no effect on growth under nonsaline conditions but in the presence of salinity it significantly reduced shoot and root growth of Clark and Kanrich cvs. only. High salinity (−0.44 MPa) in combination with Pi ≥ 0.10 mmol L^{-1} killed both Clark and Kanrich cvs. However, at 0.02 mmol L^{-1} Pi and high salinity, no foliar injury was found on Kanrich and only slight chlorosis was found on Clark. In contrast, no foliar injury was apparent on Lee in any treatment. Inorganic phosphate increased the severity of injury in L63–1677. Salinity greatly enhanced Pi accumulation in leaves and roots of Clark and Kanrich; whereas this effect was slight for the P-tolerant cvs. Lee, Jackson, and L63–1677. Injured Clark and Kanrich leaves contained abnormal amounts of P (400 to 800 mmol kg^{-1}, dry wt) indicating that the primary cause of injury was a salinity-induced Pi toxicity. Salinity also induced considerable foliar injury on Jackson; yet the onset and severity was independent of the substrate Pi concentration. Unlike the mechanism of foliar injury in Clark and Kanrich, we suspect injury in Jackson was caused by Cl toxicity. The striking adverse interaction between salinity and phosphate is a critical factor in solution culture studies of plant tolerance to salinity. These results further demonstrate that important genetic differences exist among cultivars that greatly affect their susceptibility to Pi toxicity.

Additional index words: ***Glycine max*** **L., Phosphate toxicity, Sodium, Chloride.**

INORGANIC phosphate (Pi) concentrations in nutrient solution cultures vary widely and are usually between one to three orders of magnitude higher than in soil solutions. High Pi concentrations in nutrient solutions are desirable because of the solutions' inability to replenish Pi absorbed by roots. Although Pi concentrations (0.2 to 2 mmol L^{-1}) usually found in nutrient solutions may be optimal for plant growth in the absence of salinity, the selected concentration may be toxic for some plants grown in saline media (Bernstein et al., 1974; Nieman and Clark, 1976; Cerda et al., 1977).

Bernstein et al. (1974) found that increased Pi concentrations increased salt injury in corn [*Zea mays* (L.)] and decreased salt tolerance. Ear weights from corn grown in the spring at −0.36 MPa osmotic potential (OP) decreased 80% when substrate Pi was increased from 0.05 to 2 mmol L^{-1}. However, increased Pi caused no visible effects on plants or yields in nonsaline treatments. Similar adverse interactive effects of salinity and substrate Pi were shown on corn by Nieman and Clark (1976).

More recently, Cerda et al. (1977) found that sesame [*Sesamum indicum* (L.)] yields increased as substrate Pi increased only in the absence of salinity (−0.04 MPa). At high salinity (−0.44 MPa), an increase in solution Pi concentration from 0.02 to 1.6 mmol L^{-1} decreased salt tolerance and caused necrosis of the leaf margins at the two highest Pi levels (0.8 and 1.6 mmol L^{-1}).

Soybeans [*Glycine max* (L.)Merr.] have been found to be extremely sensitive to salinity at relatively low nutrient solution Pi concentrations in preliminary studies conducted at our laboratory (Nieman et al., 1973; Nieman et al., 1974; Grattan and Maas, 1982). In the presence of −0.34 MPa NaCl + $CaCl_2$ salinity, 0.20 mmol L^{-1} substrate Pi killed 'Kanrich' and 'Prize' soybean cultivars whereas no injury was observed on −0.34 MPa treated plants at 0.02 mmol L^{-1} Pi and growth was only slightly reduced compared to the unsalinized controls.

Our objective was to examine the interactive effects of salinity and Pi on soybean growth, foliar injury, and elemental concentrations in both the leaves and roots of five different cultivars. Two of the cultivars selected vary widely in salt tolerance. 'Lee', a leaf Cl excluder, and 'Jackson', a leaf Cl accumulator, are classical salt-tolerant and salt-sensitive cultivars, respectively (Abel and MacKenzie, 1964; Abel, 1969). Two other cultivars that were selected have shown distinct differences in tolerance to 1.6 mmol L^{-1} Pi in solution cultures. 'L63–1677' has been classified as P-tolerant (Bernard, 1982, personal communication) and 'Clark' as P-sensitive (Howell and Bernard, 1961; Bernard and Howell, 1964). Lee and Jackson have also been classified as P-tolerant (Howell and Bernard, 1961). Kanrich was selected as a reference cultivar because of its sensitivity

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Table 1. Interactive effects of salinity and Pi on foliar injury of the various soybean cultivars.

Cultivar	Salinity (MPa)	Approximate day of incipient injury†								Foliar injury symptoms at harvest day
		Primary leaves				First trifoliate				
		P1	P2	P3	P4	P1	P2	P3	P4§	
Clark	−0.24 (S1)	-‡	20	15	13	-	20	18	16	No injury on P1 treatments. Severe interveinal chlorosis on primary and first trifoliates on all other Pi treatments. Some necrosis and leaf abscission of primary and first trifoliates in the P4 treatment.
Jackson	−0.24 (S1)	15	-	17	17	16	-	17	17	Distinct chlorosis and necrosis on the primary leaves of all P1 treatments only. General and interveinal chlorosis on primary leaves and first trifoliates of P3 and P4 treatments.
Kanrich	−0.24 (S1)	-	-	-	20	-	-	-	-	Interveinal chlorosis on primary leaves with slight necrosis along leaf margins on P4 treatments only.
Lee	−0.24 (S1)	-	-	-	-	-	-	-	-	No injury.
L63-1677	−0.24 (S1)	-	-	-	-	-	-	-	-	No injury.
Clark	−0.44 (S2)	20	10	9	8	20	13	12	12	Very slight to moderate chlorosis on primary and first trifoliates of all P1 treatments. Entire shoot died in all other Pi treatments.
Jackson	−0.44 (S2)	8	8	8	7	13	13	13	13	Chlorosis and necrosis on primary and first trifoliate leaf margins. General chlorosis on second trifoliate. Severity of injury variable and independent of Pi treatment.
Kanrich	−0.44 (S2)	-	15	13	10	-	17	17	16	No injury on P1 treatments. Severe necrosis and desiccation on other Pi treatments. Primary and first trifoliates abscissed. Youngest expanding trifoliates chlorotic.
Lee	−0.44 (S2)	-	-	-	-	-	-	-	-	No injury.
L63-1677	−0.44 (S2)	-	17	15	11	-	18	18	14	No injury on P1 treatments. Slight to severe chlorosis on primary and first trifoliates in the P2 treatment. Severe interveinal chlorosis on primary and trifoliate leaves of P3 and P4 treatments. Some necrosis along leaf margins.

† Refers to the number of days after salination was initiated that foliar injury was first observed.
‡ - Indicates absence of injury.
§ P1, P2, P3, and P4 refers to 0.02, 0.10, 0.20, and 0.30 mmol L^{-1} Pi treatments, respectively.

to interactive effects of salinity and Pi observed in preliminary experiments.

MATERIALS AND METHODS

Plant Culture. Soybean [*Glycine max* (L.) Merr. cvs. Clark, Jackson, Kanrich, L63-1677, and Lee] seeds were coated with 96% tetrachloro-p-benzoquinone (Spergon[3] seed protectant) and germinated in rolled paper towels saturated with a 0.5 mmol L^{-1} $CaSO_4$ solution in the laboratory on 16 Nov. 1982. Six days later, seedlings were transferred to the greenhouse and placed in 30-L containers filled with a 1:10 dilution of the following nutrient solution (Pi = 0.02 mmol L^{-1}). Seven-day-old seedlings were transplanted into 48, 190-L plastic drums filled with aerated nutrient solution consisting of 2.5 mmol L^{-1} $Ca(NO_3)_2$, 3 mmol L^{-1} KNO_3, 1.5 mmol L^{-1} $MgSO_4$, 50 μmol L^{-1} Fe (as sodium ferric diethylenetriamine pentaacetate), 23 μmol L^{-1} H_3BO_3, 5 μmol L^{-1} $MnSO_4$, 0.4 μmol L^{-1} $ZnSO_4$, 0.2 μmol L^{-1} $CuSO_4$, and 0.1 μmol L^{-1} H_2MoO_4 and either 0.02, 0.10, 0.20, or 0.30 mmol L^{-1} KH_2PO_4. Each drum contained five soybean seedlings, one of each cultivar. Large reservoirs were used to minimize changes in solution composition during the course of the experiment. The pH of the solution was maintained between 5.5 and 6.5 with H_2SO_4 and KOH. Inorganic phosphate concentrations in all drums were determined several times per week by the Bartlett (1959) modification of the Fiske-SubbaRow (1925) assay. KH_2PO_4 was added as needed to maintain the desired Pi concentrations above 0.01, 0.07, 0.17, and 0.26 mmol L^{-1} Pi for the 0.02, 0.10, 0.20, and 0.30 mmol L^{-1} Pi treatment, respectively. Salination began when plants were 10 days old. NaCl:$CaCl_2$ (2:1 on a molar basis) was added to the nutrient solution at a rate of 19 mmol L^{-1} day^{-1}, which reduced the osmotic potential (OP) of the nutrient solution 0.1 MPa day^{-1} to obtain the desired salinity.

Experimental Design. The 48 drums were divided into four replicated and completely randomized blocks. Each block contained three salinity treatments (−0.04, −0.24, and −0.44 MPa OP) each at four Pi concentrations (0.02, 0.10, 0.20, and 0.30 mmol L^{-1} KH_2PO_4). Hereinafter S0, S1, S2 and P1, P2, P3, P4 will denote the respective treatments above.

Environmental Conditions. Temperature and relative humidity fluctuated diurnally. The relative humidity in the greenhouse was uncontrolled and extreme temperature fluctuations were reduced by heaters and evaporative coolers. The average daily maximum and minimum temperature in the greenhouse during the course of the experiment was 30 and 19°C, respectively. All drums were wrapped with aluminum foil-faced fiberglass insulation (9 cm thick) to minimize temperature fluctuations in the culture media. Lighting was natural sunlight through glass.

Injury Observations. Visual observations were made daily on all plants. Injury symptoms and their severity, time of development, and location on the plant were recorded.

Harvest. All plants were harvested 22 days after salination began. Shoots were separated from roots and fresh weights were obtained. Roots were washed thrice, 60 s each, in separate 10-L quantities of deionized water. The shoots and roots were placed in paper bags and dried in an oven at 65°C. After dry weights were obtained, leaf blades were separated from stems and petioles. The leaves and roots from replicate treatments were composited, ground in a blender, and stored in glass vials for mineral analysis.

Plant Tissue Analysis. Sodium, K, Ca, and Mg were determined on nitric-perchloric acid digests of the tissue powder by atomic absorption spectrophotometry. Phosphorus was determined on the tissue digests by the molybdate-vanadate colorometric method (Kitson and Mellon, 1944). Chloride concentrations were determined on dilute nitric-acetic acid extracts of the dry-ground plant material by the Cotlove (1963) coulometric-amperometric titration procedure.

RESULTS

Foliar Injury. Distinct cultivar differences in type, severity, and time of injury development were observed. The approximate day incipient injury occurred and the description of injury for each treatment on the day of harvest are presented in Table 1.

[3] Mention of company names or products is for the benefit of the reader and does not imply endorsement, guarantee, or preferential treatment by the USDA or its agents.

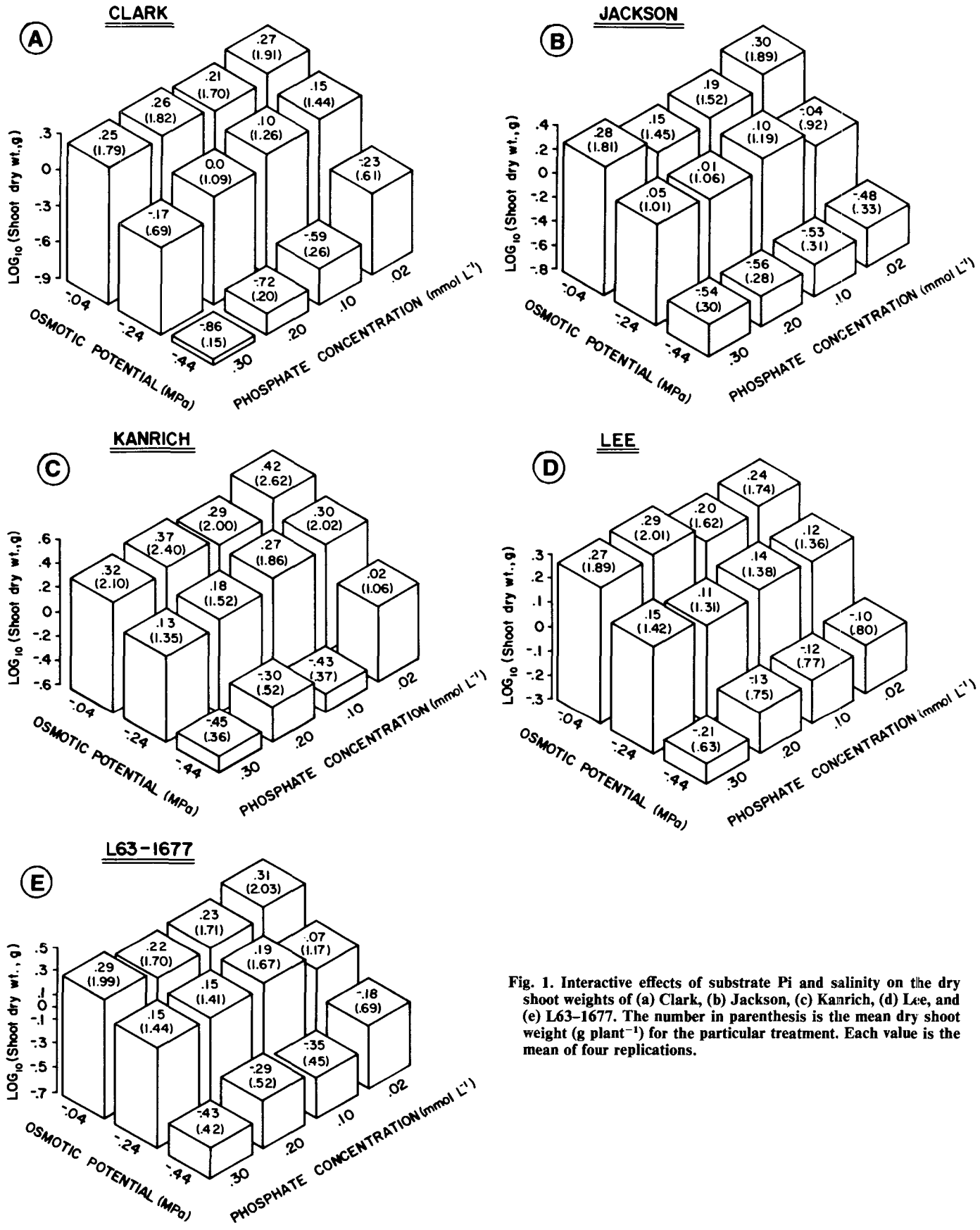

Fig. 1. Interactive effects of substrate Pi and salinity on the dry shoot weights of (a) Clark, (b) Jackson, (c) Kanrich, (d) Lee, and (e) L63–1677. The number in parenthesis is the mean dry shoot weight (g plant^{-1}) for the particular treatment. Each value is the mean of four replications.

Clark was the most sensitive cultivar to salinity in the presence of high Pi. Chlorosis developed on primary and first trifoliate leaves of the S2P4 treatment 8 and 12 days, respectively, after salination began. Later, necrosis developed along leaf margins and progressed towards the midrib as injury became more acute. After the trifoliates became considerably chlorotic, a characteristic hyponastic response developed. Finally, leaves became light brown and dried and eventually abscissed. Similar observations were noted on plants at two intermediate Pi concentrations (S2P2 and S2P3) but there the onset of injury was delayed. Plants grown at −0.44 MPa in combination with low Pi (S2P1), on the other hand, did not develop injury symptoms for 20 days. Very slight chlorosis was observed on both primary leaves and first trifoliates. At −0.24 MPa salinity (S1), injury symptoms developed after 13 days with high Pi and at increasingly later times as Pi concentrations were decreased. No injury or other unusual visual characteristics were observed on the S1P1 treated plants or on Pi treatments in the absence of salinity.

Kanrich was the second most sensitive cultivar to combined salinity and high Pi in the culture media. The type of injury was identical to that found on Clark, but symptoms developed later.

L63-1677 was only slightly sensitive to salinity in the presence of high Pi. Injury was absent on all S0 and S1 treatments as well as on S2P1 treated plants. Primary leaves of S2P4, S2P3, and S2P2 treatments became chlorotic 11, 15, and 17 days, respectively, after salination began. Necrosis along leaf margins of primary leaves and first trifoliates was evident on the day of harvest on both P3 and P4 treatments.

Table 2. Mean squares from analysis of variance of the $\log_{10}$ transformations of the plant dry weight of the various soybean cultivars.

Source of variation	Clark	Jackson	Kanrich	Lee	L63-1677
			Shoot		
Salinity	3.084***	2.491***	1.820***	0.650***	1.459***
error	0.026	0.014	0.012	0.007	0.016
Pi	0.226***	0.011	0.140***	0.001	0.007
Salinity × Pi	0.076***	0.015	0.044***	0.007	0.028
error	0.017	0.014	0.006	0.007	0.014
			Root		
Salinity	2.452***	1.304***	1.566***	0.466***	1.038***
error	0.024	0.018	0.024	0.007	0.016
Pi	0.249***	0.013	0.142***	0.001	0.015
Salinity × Pi	0.092***	0.014	0.046*	0.010	0.029
error	0.013	0.018	0.020	0.006	0.013

*,*** Statistical significance at the 5 and 0.5% confidence level, respectively.

Unlike the cultivars described above, Lee and Jackson never developed injury that was obviously attributed to an adverse salinity-Pi interaction. No injury was observed on Lee in any of the treatments. Jackson, on the other hand, developed injury symptoms at both salinity concentrations, but the severity of injury appeared independent of the substrate Pi concentration. Both the primary and first trifoliates became chlorotic on plants in the −0.44 MPa (S2) treatment 7 or 8 and 13 days, respectively, after salination began, regardless of Pi concentration. Necrosis developed along leaf margins of primary and first trifoliates 2 and 4 days after chlorosis appeared. Necrosis never developed on first trifoliates or primary leaves of P2, P3, and P4 treatments at −0.24 MPa salinity. The primary leaves of P1-treated plants, however, showed a unique type of injury on the day of harvest. Unlike injury described previously, necrosis occurred exclusively at the leaf apex. A distinct band of chlorotic tissue was contiguous to the necrotic tissue whereas the base of the leaf remained uninjured.

Shoot Growth. Figure 1 shows the interactive effects of salinity and substrate Pi on the shoot dry weights of the five soybean cultivars. Analyses of variance were performed on $\log_{10}$ transformations of the dry weights so that large nonsignificant differences from plants grown in nonsalinized treatments did not nullify small significant differences in saline treatments (Table 2).

Increased salinity in the growth media significantly ($\alpha \leq 0.005$) decreased the shoot dry weights of all cultivars. Increased Pi concentrations in the media had no significant effect on the shoot weights of Jackson, Lee, and L63-1677, but markedly decreased ($\alpha \leq 0.005$) those of Clark and Kanrich. The detrimental effect of increased Pi levels on shoot growth only occurred under saline conditions. This adverse interaction between salinity and Pi was highly significant ($\alpha \leq 0.005$). At moderate salinity (−0.24 MPa), the dry weights of Clark and Kanrich shoots decreased from 1.44 to 0.69 and from 2.02 to 1.35 g plant^{-1}, a reduction of 52 and 33%, respectively, as substrate Pi increased. At high salinity (−0.44 MPa), most Clark and Kanrich shoots died in the presence of 0.10 mmol L^{-1} Pi or higher. Consequently, dry matter yields from the highest Pi treatments were only 25 and 34% of those in the lowest Pi treatment for Clark and Kanrich, respectively.

Root Growth. The interactive effects of salinity and Pi on the dry weights of soybean roots were analogous to the effects on the shoot weights (Table 3). Salinity significantly ($\alpha \leq 0.005$) reduced root growth in all cultivars (Table 2). Increased Pi in the presence of salinity significantly ($\alpha \leq 0.005$) decreased the root

Table 3. Interactive effects of salinity and substrate Pi on the dry root weights of the five soybean cultivars. Each value is the mean of the four replications.

	Root dry weights (g plant^{-1})											
	−0.04 MPa				−0.24 MPa				−0.44 MPa			
Cultivar	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
Clark	0.38	0.38	0.38	0.39	0.28	0.22	0.14	0.13	0.15	0.06	0.06	0.03
Jackson	0.24	0.29	0.22	0.30	0.18	0.21	0.17	0.18	0.08	0.07	0.07	0.07
Kanrich	0.35	0.35	0.37	0.30	0.35	0.31	0.19	0.18	0.17	0.08	0.09	0.06
Lee	0.25	0.31	0.33	0.32	0.24	0.25	0.23	0.25	0.16	0.14	0.14	0.12
L63-1677	0.38	0.38	0.32	0.37	0.25	0.34	0.29	0.29	0.17	0.11	0.12	0.09

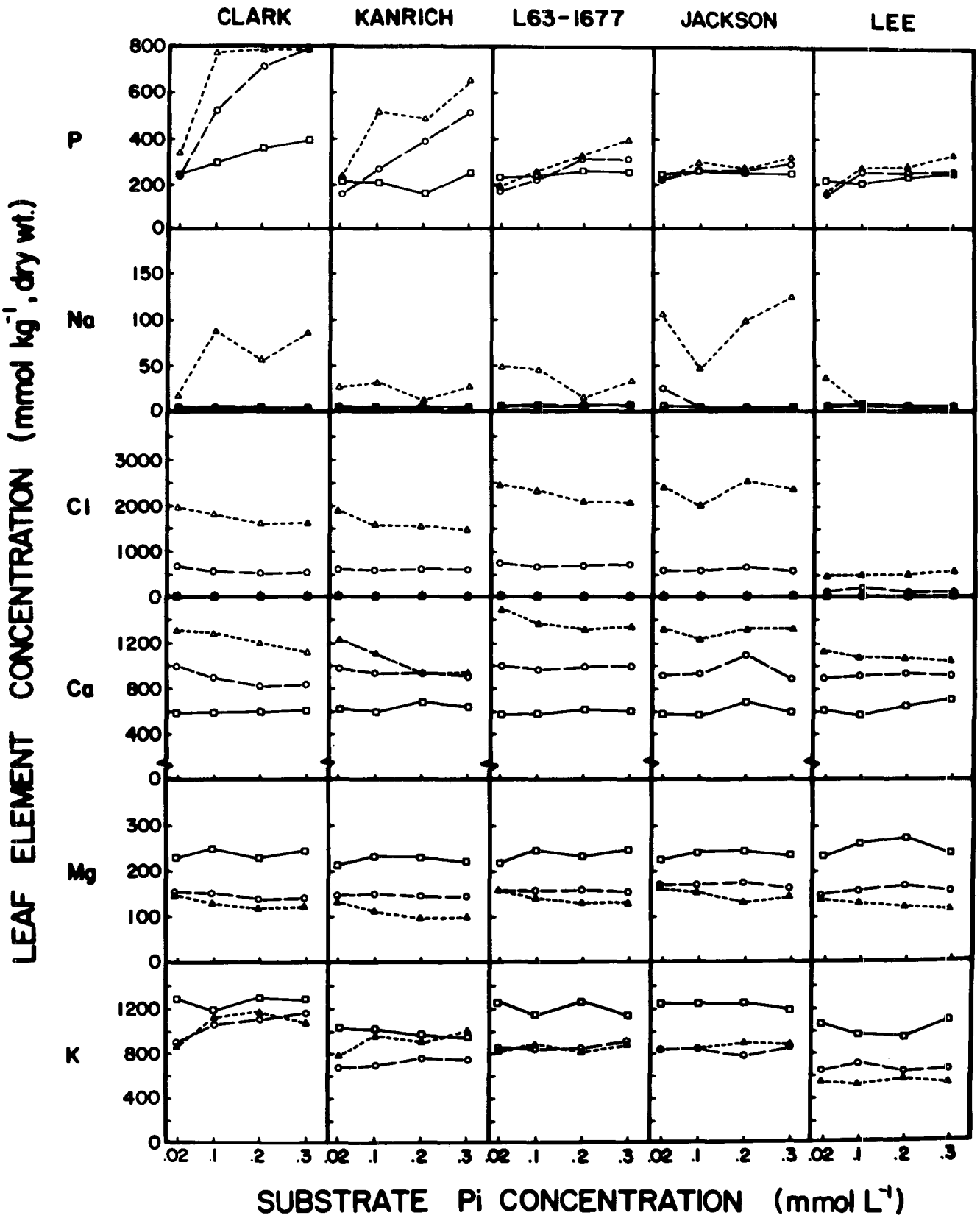

Fig. 2. Effect of substrate Pi in the presence or absence of salinity on leaf element concentration of the various soybean cultivars. S0 □——□, S1 ○——○, S2 △- - -△.

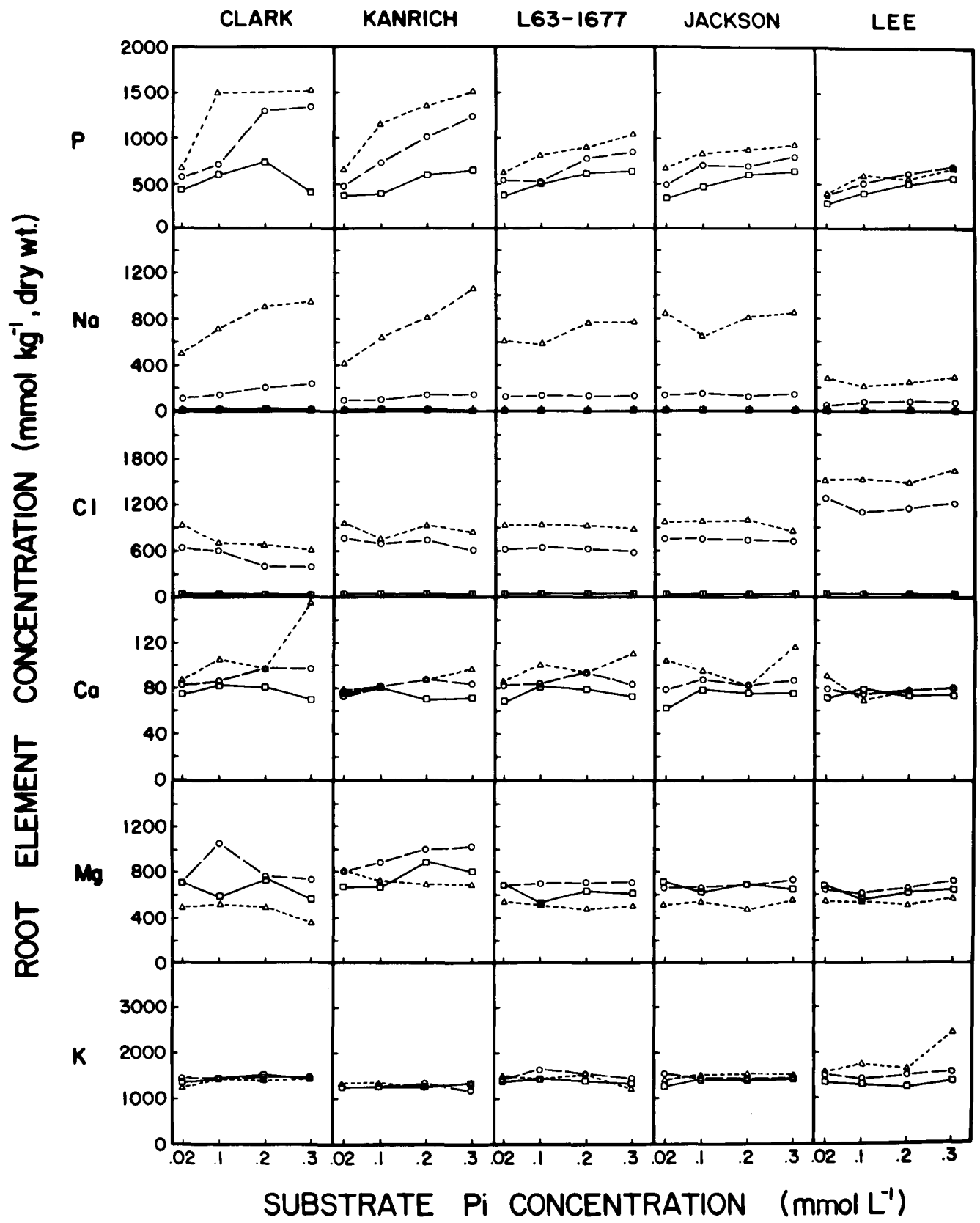

Fig. 3. Effect of substrate Pi in the presence or absence of salinity on root element concentration of the various soybean cultivars. S0 □——□, S1 ○——○, S2 △- - -△.

weights of Clark and Kanrich but had no effect on the other cultivars. A significant interaction confirmed the antagonistic effect of high Pi concentrations and salinity on Clark and Kanrich. At −0.24 MPa, Clark and Kanrich root weights decreased from 0.28 to 0.13 and 0.35 to 0.18 g plant^{-1}, respectively, as substrate Pi increased. At −0.44 MPa, the root weights of respective cultivars decreased from 0.15 to 0.03 and 0.17 to 0.06 g plant^{-1}. In the absence of salinity, no weight differences between Pi treatments were evident for any cultivar.

Leaf Element Concentrations. Leaf P concentrations of all cultivars increased as both substrate Pi and salinity increased, but the increase was much greater for Clark and Kanrich (Fig. 2). The P concentration in Clark reached a maximum (760 to 790 mmol kg^{-1} dry wt) with treatments of either −0.44 MPa salinity combined with ⩾ 0.10 mmol L^{-1} Pi or −0.24 MPa with 0.30 mmol L^{-1} Pi. The P concentrations in nonsalinized, low Pi (S0P1) control plants were similar for all cultivars (202 to 244 mmol kg^{-1} dry wt). Under nonsaline conditions, leaf P concentration in Clark increased from 244 to 384 mmol kg^{-1} dry wt as substrate Pi increased, but no substantial increase in leaf P occurred for any of the other cultivars.

Sodium analyses indicated that soybeans basically exclude Na from leaves. At −0.24 MPa salinity, Na was completely excluded from the leaves of all cultivars. At −0.44 MPa, only Lee effectively excluded Na from its leaves at P2, P3, and P4 treatments; whereas leaves of Clark and Jackson, in general, accumulated significant amounts of Na. Sodium accumulation in the leaves of Kanrich and L63–1677 plants at −0.44 MPa was intermediate.

Leaf Cl concentration increased substantially in all cultivars as salinity increased, although Lee accumulated significantly less than the others. Leaf Cl concentrations in Lee at −0.44 MPa were about the same as those in Clark, Kanrich, and Jackson plants treated at −0.24 MPa. In general, leaf Cl concentrations at −0.44 MPa were three or more times higher than those at −0.24 MPa. No distinct relationship between leaf Cl and substrate Pi was evident, although leaf Cl concentration decreased slightly with increased Pi at high salinity for Clark, Kanrich, and L63–1677.

Leaf Ca levels in all cultivars increased markedly with increased salinity in response to the added Ca in the saline substrate. However, differences in leaf Ca concentration between moderate and high salinity combined with either P3 or P4 levels were small in Kanrich. Leaf Ca appeared independent of the substrate Pi concentration except at −0.24 MPa for Clark and at −0.44 for Clark, Kanrich, and L63–1677, where increased substrate Pi decreased leaf Ca.

Salinity substantially reduced leaf Mg and K concentrations in all cultivars. At −0.44 MPa leaf Mg concentrations were approximately half those of the nonsaline plants. Although leaf Mg appeared to decrease further with increased substrate Pi, there was no indication of Mg deficiency in any treatment. The suppression of leaf K by salinity was more pronounced in Lee and Jackson than in Clark and Kanrich. Like Mg, K decreased most with the first −0.2 MPa addition of substrate salinity. Interestingly, −0.24 MPa suppressed leaf K in Kanrich more than did the −0.44 MPa. Substrate Pi had no consistent effect on leaf K.

Root Element Concentration. Although P concentrations in roots were about twice those in leaves, relative differences among treatments and cultivars were similar (Fig. 3). Unlike its effect on leaf P, however, increased substrate Pi in the absence of salinity increased root P in all cultivars, except for Clark at 0.30 mmol L^{-1} Pi. Salinity enhanced P accumulation in all cultivars at all Pi levels. The enhancement in Lee, however, was only slight. The effect of salinity on P accumulation in roots was most pronounced in Clark and Kanrich cultivars. Phosphorus concentrations in roots grown in −0.44 MPa solutions containing 0.3 mmol L^{-1} Pi were about threefold higher than those in the nonsaline, low-Pi control plants.

Unlike the leaves, the roots accumulated a substantial amount of Na. At all Pi levels, as salinity doubled, root Na more than doubled in all cultivars. Lee accumulated significantly less Na than the other cultivars. A strong synergistic effect between salinity and Pi increased root Na in Clark and Kanrich, but this relationship was not apparent in Jackson, Lee, or L63–1677. This relationship was evident only in the two cultivars most sensitive to the combination of salinity with increased substrate Pi.

Chloride concentrations were increased most by the first −0.2 MPa addition of salinity. Lee, the cultivar that accumulated the least amount of Cl in the leaves, accumulated the most Cl in the roots, about three times the amount found in leaves at −0.44 MPa. At −0.24 MPa, root Cl concentrations were 6 to 10 times those in leaves. Conversely, leaf Cl concentrations were about twice that of roots for the other cultivars treated at high salinity.

Salinity increased root Ca concentrations in all cultivars except Lee, but the increases were much less than those in leaves. No consistent relationship between root Ca and substrate Pi was evident.

At −0.24 MPa, salinity caused a slight increase in Mg concentration, but at −0.44 MPa, it decreased Mg concentrations. Inorganic phosphate levels had no consistent effect on Mg concentrations at any salinity level. Neither salinity nor Pi affected K concentrations in Clark, Jackson, Kanrich, and L63–1677. Increased salinity, however, increased K in Lee, particularly in the high Pi (0.3 mmol L^{-1}) treatment.

DISCUSSION

Although adverse interactive effects of salinity and substrate Pi have been reported previously on corn (Bernstein et al., 1974; Nieman and Clark, 1976) and sesame (Cerda et al., 1977), they were not nearly as severe as on Clark and Kanrich soybeans. At −0.44 MPa salinity, Pi concentrations above 0.1 mmol L^{-1} were lethal for these soybean cultivars; whereas corn and sesame grown at nearly the same OP were unaffected at Pi concentrations up to 0.5 and 0.8 mmol L^{-1}, respectively.

Substantial differences in tolerance to substrate Pi at high salinity were found among soybean cultivars. Clark was the most sensitive cultivar to increased Pi

in the presence of salinity followed in order by Kanrich > L63-1677 > Lee = Jackson.

Foliar injury observed on Clark and Kanrich cultivars appeared to be related more to excess Pi rather than to excess Na or Cl. These cultivars readily accumulated P in the leaves and were severely injured by Pi concentrations of 0.10 mmol L^{-1} or higher in saline media. Leaf P concentrations reached values 5 to 10 times higher than usually found in leaf tissues. Phosphate-tolerant cvs. L63-1677, Lee, and Jackson (Howell and Bernard, 1961) showed little or no differences in growth or injury among Pi treatments at a given OP and salinity only slightly increased P concentration in the leaves and roots. Salinity-induced P toxicity has been suggested as the primary cause of foliar injury and reduced growth in other crops (Bernstein et al., 1974; Nieman and Clark, 1976; Cerda et al., 1977). In Clark and Kanrich, neither Na nor Cl accumulation could be implicated as the major cause of foliar injury. In the S2P1 treatment, leaf Cl concentrations in uninjured Kanrich or very slightly injured Clark were greater than the concentrations in severely injured or dead leaves from the higher Pi treatments. Sodium concentrations in uninjured L63-1677 leaves were greater than in injured Kanrich leaves. Furthermore, leaf Na concentrations were less than 5% of the Cl concentrations. The only leaf element that correlated directly with foliar injury was P.

Salinity-induced Pi injury on soybeans has probably occurred in other studies but was not recognized as such. Shere et al. (1974) concluded that soybeans were highly sensitive to salinity and that they were less tolerant when grown in full-strength nutrient solution (1 mmol L^{-1} Pi) than in half-strength solution (0.5 mmol L^{-1} Pi). They suggested that the greater reduction in growth in full-strength solution could be due to a lower OP caused by the additional nutrient salts. The characteristic injury from salinity and high Pi (severe necrosis and defoliation of the older leaves) developed several days after salination to −0.2 MPa. In light of our experiment, the greater growth suppression in full-strength solution was more likely caused by increased substrate Pi. In fact, the data of Shere et al. (1974) show that shoot P concentration increased as salinity increased. This effect was more pronounced in the salinized full-strength solution (580 to 1480 mmol P kg^{-1} dry wt) than the salinized half-strength solution (480 to 870 mmol P kg^{-1} dry wt). Therefore their data, like ours, strongly suggest a salinity-induced P toxicity. Other workers have reported unusual injury on soybeans (cv. Hakucho) grown at −0.27 MPa in the presence of 1 mmol L^{-1} Pi (Nukaya et al., 1977; Nukaya et al., 1982). Although they did not attribute the injury to excessive Pi accumulation, the progression of injurious symptoms on their soybeans was very similar to ours.

Characteristic salinity-high Pi injury to soybeans has not been observed in some studies (Läuchli and Wieneke, 1979; Wieneke and Läuchli, 1979; Wieneke and Läuchli, 1980; Rathert and Doering, 1981; Roeb et al., 1982), presumably because the more tolerant cvs. Lee and Jackson were used.

For Clark and Kanrich, our data indicate that salinity enhanced Pi uptake and accumulation. The resultant excessive concentrations in the leaves produced foliar injury and subsequently reduced plant growth. The actual mechanism of injury warrants further research. We support the hypothesis that foliar injury was caused by phosphate that had accumulated to abnormal concentrations in the leaves and disrupted essential metabolic pathways. Although leaf P was the only element that directly correlated with injury, Na and Cl can not be entirely dismissed. Root Na increased in Clark and Kanrich with increased Pi. Perhaps Na plays a role in P uptake and/or transport. Chloride, on the other hand, may be partly responsible for injury if it, together with phosphate, lowered the solute potential of leaf cells to such an extent as to disrupt ideal water relations.

The mechanism of salinity injury in Jackson is undoubtedly different from the mechanism of salinity-induced Pi injury in Clark and Kanrich. The foliar injury and reduced growth observed in Jackson did not vary at either salinity as substrate Pi increased. Also, leaf P in Jackson increased only slightly as Pi increased in the presence of salinity. The suggested cause of foliar injury in Jackson is Cl toxicity from insufficient control of root Cl uptake and subsequent translocation to the leaves (Läuchli and Wieneke, 1979; Wieneke and Läuchli, 1979). We found that leaf Cl concentration in Jackson was much greater than in Lee. Conversely, root Cl in Jackson was considerably less than in Lee. Similar results have been observed by others (Läuchli and Wieneke, 1979; Roeb et al., 1982). Thus, leaf Cl exclusion in Lee has been suggested to be regulated by the roots (Läuchli and Wieneke, 1979). Evidently, leaf Cl concentration per se is not an adequate indicator for assessing foliar injury. For example, leaf Cl in L63-1677 treated at high salinity was essentially the same as in Jackson, yet injury was evident only on Jackson. Perhaps these two leaf Cl accumulators differ by their ability to sequester leaf Cl in vacuoles or exclude Cl from sensitive cytoplasmic sites.

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