Sodium Chloride Concentration Affects Early Growth and Nutrient Accumulation in Taro

Steven Hill, Robert Abaidoo, and Susan Miyasaka¹

Agronomy and Soil Science Department, University of Hawaii at Manoa, Honolulu, HI 96822

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Abstract. The growth and nutrient accumulation responses of taro [*Colocasia esculenta* (L.) Schott, cv. Bun long] to varying sodium chloride concentrations were studied in an aerated hydroponic system. Vegetative propagules were grown at seven levels of NaCl (0, 5, 10, 20, 40, 60, and 80 mM) for 43 days. We estimated the NaCl tolerance threshold (95% of maximum growth) to be at 4.9 mM solution NaCl. Relative dry-matter yield decreased 1.6% per mM increase in solution NaCl above 4.9. These values for tolerance threshold and response slope led us to classify this taro cultivar as sensitive to salinity. As solution NaCl levels increased, Na concentration in petiole and root tissues increased, but not in lamina (leaf blade) tissues. This implies the existence of an effective mechanism for excluding excess Na, in spite of a lack of tolerance to solution NaCl in terms of growth response. Chloride concentration increased in all plant tissues with increasing solution NaCl levels; the greatest increase occurred in petiole tissue, and the lowest in lamina tissue, indicating some ability to partition Cl levels within the plant. Tissue concentrations of Ca and Mg, but not of K, were reduced by high solution NaCl levels.

Salinity is a constraint to agricultural production on some coral atoll islands in the Pacific Ocean, where the aroid (family Araceae) taro is a staple food. Taro is grown primarily for its starchy corm, and secondarily for leaves and petioles consumed as a potherb.

On low elevation atolls, rainfall maintains a precarious freshwater lens, which is subject to saltwater intrusion during droughts or storms (Bruce, 1987). Lack of tolerance to salinity may be a factor for declining interest in taro production in favor of imported food, and for cultivation of swamp taro (*Cyrtosperma* Griff.), another edible aroid that appears to have some salinity tolerance (Manner, 1993).

The effects of salinity on taro growth and nutrient accumulation are not well known. Some variability in tolerance among aroid genera (Manner, 1993) and within the genus *Colocasia* (Chang et al., 1984) has been observed. The primary response mechanisms of taro to high rhizosphere salt concentrations are largely unknown.

Response to salinity can be evaluated by a conceptual model (Bolarin et al., 1991; Maas and Hoffman, 1977), consisting of a Y-intercept (expected productivity under nonsaline conditions), with a tolerance threshold (high-

est salt concentration that has no significant effect on growth), and a negative linear growth response beyond the threshold. Maas and Hoffman (1977) used the two parameters of threshold and slope to classify many plant species into categories ranging from sensitive to tolerant to salinity.

Plants vary in degree of tolerance and in mechanisms of response to saline root environments. Complex whole-plant-level responses controlled by multiple gene loci are more important than simpler intracellular responses (Cheeseman, 1988). Examples of whole-plant responses include: 1) Na (Ashraf et al., 1986) and Cl (Abel and MacKenzie, 1964) exclusion, or reduced uptake and shunting to specialized cells; and 2) accelerated K uptake (Flowers et al., 1977).

By definition (Maas and Hoffman, 1977), growth (dry-matter accumulation) of sensitive plants is reduced by excess salinity. Hence, the effects of varying plant size on nutrient accumulation in plants must be separated from direct effects of solution NaCl on nutrient accumulation. When treatment applications affect plant size, many resultant mineral accumulation patterns are explicable by the mineral dilution hypothesis (Jarrell and Beverley, 1981). A small plant would be expected to have a higher mineral concentration than a larger plant of equal age, because of less dilution by carbon fixation, but the same or lower mineral content. Any variation from this pattern would imply the existence of a factor other than mineral dilution.

The objectives of this work were to: 1) by measuring its growth response, quantitatively determine the sensitivity of one taro cultivar to varying salinity levels (NaCl hydroponic solu-

tion concentration); and 2) identify potential salinity response mechanisms, principally through analysis of nutrient accumulation responses to solution NaCl.

Materials and Methods

Plant culture. Vegetative propagules (setts), consisting of lower petiole and upper corm tissue of 'Bun long' taro, were harvested and planted in a vermiculite rooting medium 7 d prior to placement in a hydroponic solution. The experiment was conducted during Mar. and Apr. 1995, at lat. 21°N and long. 157°, in a greenhouse at the Univ. of Hawaii at Manoa.

Setts were washed to remove vermiculite and selected for uniform size before transplanting. At transplanting, they were blocked according to fresh mass (20–30, 30–40, and 40–50 g/sett), since larger setts tend to produce faster-growing plants with a greater tolerance to environmental stresses than plants from smaller planting setts.

Setts were supported by plastic latticed racks located directly above 10 L of aerated nutrient solution (Miyasaka et al., 1993) in polyethylene buckets. Macronutrients were provided from analytical grade chemicals in the following millimolar (mM) concentrations: nitrate-nitrogen (N), 2.7; ammonium-N, 0.3; P, 0.1; K, 1.2; Ca, 1.0; Mg, 0.4; Na, 0.04; S, 0.7; and Cl, 0.08. Micronutrients were provided in the following micromolar (μM) concentrations: Mn, 2; B, 6; Zn, 1; Cu, 0.5; Mo, 0.1; and Fe as FeEDDHA, 10. The standard solution was amended with seven levels of NaCl (0, 5, 10, 20, 40, 80, and 160 mM), representing 0.3, 0.9, 1.4, 2.5, 4.5, 7.6, and 13.5 dS·m⁻¹ conductivity, respectively. Conductivity was measured with a conductivity bridge (Model 31; Yellow Springs Instruments, Yellow Springs, Ohio).

After 1 week, the 160 mM treatment was replaced with a 60 mM (6.1 dS·m⁻¹) treatment, because the setts failed to grow. Two plants of the 60 mM treatment and one plant from the 80 mM treatment were also replaced 3 d after transplanting because they appeared to be dying. The nutrient solution was completely renewed after 4 weeks. Plants were observed weekly for distress symptoms and maintained pest-free.

Sampling. Plants were removed from the nutrient solution 43 d after transplanting, rinsed once in tap water, then three times in deionized water. Plants were separated into lamina, petiole, corm, and root. Lamina area, including necrotic tissue, was determined with a leaf area meter (LI-3100; LI-COR Inc., Lincoln, Nebr.). All plant parts were subsequently dried in a forced-air oven at 65 °C to constant mass.

Total dry matter is the sum of lamina, petiole, and root dry mass. Corm dry matter was not included in our analysis because corm mass increased little beyond that initially present.

Plant components were ground separately to pass through a 1-mm mesh. Samples from the 60 and 80 mM treatments were bulked for nutrient analysis because of the small quantity of available tissue. Subsamples of the ground

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¹To whom reprint requests should be addressed.

material were ashed in a muffle furnace and analyzed for Ca, Mg, K, P, Mn, Zn, Cu, Fe, and Na in 1 M HCl using an inductively coupled plasma spectrometer (Model 6500; Perkin-Elmer Inc., Norwalk, Conn.) (Isaac and Jones, 1972). Boron was analyzed using the azomethine-H method (Wolf, 1974).

Chloride was extracted in boiling water (Johnson et al., 1958), and analyzed by high-pressure liquid chromatography (Model DX-500; Dionex Corp., Sunnyvale, Calif.), using an anion exchange column (IonPac AS4A-SC), a guard column (IonPac AG4A-SC), and an anion suppressor (ASRS-1), all manufactured by Dionex Corp. The eluant contained 22 mM boric acid and 22 mM sodium borate. At a flow rate of 2.0 mL·min⁻¹, Cl eluted in ≈1.7 min.

Experimental design and statistical analysis. Solution containers were arranged in completely randomized blocks with four replications per block for dry-mass responses. Three replications were randomly selected for nutrient analyses. Analysis of variance (ANOVA) and regression procedures were conducted using Statistix statistical analysis software (Analytic Software, St. Paul, Minn.).

Simple linear regressions from 0, 5, 10, and 20 mM of solution NaCl, all to 60 mM, were computed. The regression with the highest adjusted R^2 (0.94, using points only from 10 to 60 mM of solution NaCl) was selected to characterize the negative linear growth response phase of Maas and Hoffman's (1977) model. We defined the tolerance threshold as the solution NaCl concentration at which dry-matter accumulation predicted by the regression slope would be equivalent to 95% of the mean dry-matter accumulation for the 0 mM treatment.

Simple linear regressions were computed to determine the effect of NaCl on plant nutrient concentration and content, based on data including only the 0 to 40 mM solution NaCl treatments. Since the dried tissue from the 60 and 80 mM treatments was bulked by treatment, hence not replicated, these treatments were excluded from the regression analysis. Nutrient content was calculated by multiplying nutrient concentration by the dry mass of the corresponding plant part.

Results and Discussion

Visual symptoms. Marginal lamina necrosis in the 20 mM treatment, and lamina cupping and crinkling in the 40 mM treatment, were observed. The 60 and 80 mM treatments caused necrosis of entire older laminae and pronounced crinkling of younger laminae.

Fosberg (1949) observed widespread taro chlorosis in a survey of Pacific Basin atoll vegetation. We did not observe chlorosis at any NaCl treatment level in our experiment. We agree with Fosberg's speculation that the chlorosis he observed was due to micronutrient deficiency. Atoll soils are commonly deficient in Fe (Hart and Widdowson, 1987). Schreiner and Nafus (1993) clearly established an association between low soil Fe and chlorosis in taro.

Plant growth. Both final dry mass of all plant parts (lamina, petiole, root) and lamina area decreased with increasing levels of solution NaCl (ANOVA $P < 0.01$) (data not shown). In accordance with the model of Maas and Hoffman (1977), death occurred at the point where the negative growth response reached zero final dry mass (Fig. 1, two of four plants at 80 mM NaCl died before harvest). Our model, based on Maas and Hoffman (1977) provided a salinity threshold value of 4.9 mM NaCl and a beyond-threshold slope of 1.6% decrease in relative final dry matter (Fig. 1).

Using the corresponding electrical conductivity values for mM of NaCl, to conform to the methods used by Maas and Hoffman (1977), we determined that 'Bun long' is in the least tolerant category. Our aerated hydroponic conditions were close to ideal for water and nutrient availability relative to soil conditions. Although our data are not from a field trial, as called for by Maas and Hoffman (1977), the growth response would probably have been worse in a field experiment; therefore, our classification of 'Bun long' as sensitive to salinity is reasonable.

Nutrient accumulation in plant tissues. We used simple linear regressions of nutrient concentration and content to assess the general trends in nutrient accumulation under conditions of increasing levels of solution NaCl (Table 1). Only symbols (+ for positive slope, $P < 0.05$; - for negative slope, $P < 0.05$; and 0 for nonsignificant regression) were used, as

we do not wish to imply that a simple linear regression is necessarily the best fit for all of the nutrient accumulation responses. The purpose of using simple linear regression analyses was to screen out nutrient accumulation responses explicable by Jarrell and Beverley's (1981) nutrient dilution hypothesis.

Lamina Na concentrations remained fairly constant with increasing solution NaCl level (Tables 1, 2). Exclusion of Na may have been more effective at intermediate NaCl solution levels than at higher levels (Table 2). In contrast, Na concentration in petioles and roots increased with increasing solution NaCl levels, consistent with the hypothesis of Jarrell and Beverley (1981) (Tables 1, 2). Thus, excess Na was excluded from laminae, but not from petioles and roots, at higher solution NaCl levels.

Sodium exclusion from upper plant parts has been associated with salt tolerance in barley (*Hordeum* spp.) (Huang and Redmann, 1995) and corn (*Zea mays* L.) (Cerde et al., 1995). However, considering our classification of cv. Bun long as sensitive to salinity, Na exclusion from laminae does not seem to confer tolerance to this cultivar.

Chloride increased significantly in concentration in all plant parts with increasing solution NaCl, with greatest effect in petioles, and least in laminae (Tables 1, 2). In contrast, Cl content increased only in the petiole with increasing solution NaCl (Table 1), indicating that Cl is sequestered there.

Fig. 1. Effects of NaCl solution concentration on percent total relative dry matter of taro plants, where 100% = total mean dry matter at 0 mM solution NaCl. Data are fitted to our model; r^2_{adj} for linear phase = 0.94.

Table 1. Summary of simple linear regressions for effects of solution NaCl on nutrient concentration (concn) and content in taro plant parts.^a

Nutrient	Lamina		Petiole		Root	
	Concn	Content	Concn	Content	Concn	Content
Na	0	-	+	0	+	0
Cl	+	0	+	+	+	0
K	+	-	+	0	+	0
Ca	-	-	-	-	-	-
Mg	-	-	-	-	-	-
Mn	+	+	+	+	+	0

^aSymbols indicate that slope was nonsignificant (0), positive and significant at $P \leq 0.05$ (+), or negative and significant at $P \leq 0.05$ (-).

Table 2. Effects of concentration of solution NaCl on concentrations of selected nutrients in lamina, petiole, and root tissues of taro.^z

NaCl (mM)	Tissue nutrient concn					(µg·g ⁻¹)
	(mg·g ⁻¹)					
	Na	Cl	K	Ca	Mg	
<i>Lamina</i>						
0	0.080	0.179	2.31	2.23	0.510	116
5	0.073	1.69	2.96	2.29	0.473	125
10	0.047	1.38	2.47	2.46	0.513	134
20	0.040	2.07	2.66	2.24	0.437	161
40	0.070	2.57	3.12	1.93	0.363	328
60 ^y	0.050	1.20	3.46	1.33	0.35	362
80 ^y	0.050	n.d. ^x	3.10	1.46	0.41	366
Significance ^w P =	0.023	0.004	0.005	0.066	0.0002	0.00001
<i>Petiole</i>						
0	0.080	0.34	4.57	1.40	0.307	22.0
5	0.143	1.69	7.66	1.56	0.360	22.0
10	0.170	3.01	7.32	1.56	0.350	24.7
20	0.450	3.85	8.43	1.38	0.237	23.3
40	0.463	5.69	11.4	1.32	0.253	71.0
60 ^y	0.330	9.62	10.2	0.69	0.320	126.0
80 ^y	0.490	6.32	9.16	0.68	0.290	124.0
Significance ^w P =	0.003	0.008	0.016	0.00001	0.0003	0.00001
<i>Root</i>						
0	0.07	0.22	3.18	0.74	1.14	4.00
5	1.23	0.22	3.62	0.673	1.10	5.00
10	1.96	2.20	2.32	0.71	1.10	6.33
20	2.30	2.76	2.63	0.637	1.03	6.00
40	1.93	3.55	7.34	0.423	0.54	14.3
60 ^y	2.58	n.d. ^x	5.08	0.360	0.27	131.0
80 ^y	3.60	n.d. ^x	3.55	0.390	0.35	327.0
Significance ^w P =	0.00001	0.00001	0.00001	0.00001	0.0004	0.0004

^zMean of three samples.

^ySamples were bulked for tissue analysis.

^xNo data, insufficient sample material for analysis.

^wANOVA results are for 0 to 40 mm solution NaCl treatments only.

The concentration of K increased significantly with increasing solution NaCl in all tissues (Table 2), whereas K content decreased or remained constant (Table 2), in accordance with the nutrient dilution hypothesis (Jarrell and Beverley, 1981).

Solution NaCl did not have a significant effect on lamina and petiole K : Na ratios. A K : Na ratio >18 (mass basis) was maintained in laminae and petioles at all treatment levels (Table 3). Wyn Jones et al. (1979) claimed that a critical K : Na ratio of 1 was necessary to maintain normal metabolic processes in plants not adapted to saline conditions. Hue and McCall (1989) determined that the critical ratio for macadamia (*Macadamia integrifolia* Maiden & Betcher) was 2.5. Given the contrast in lamina accumulation responses for Na and K (Tables 1, 2) maintenance of high K : Na ratios may be explained solely by Na exclusion, as opposed to accelerated K uptake.

Calcium and Mg concentrations were significantly reduced by high solution NaCl levels (Tables 1, 2), suggesting a competition effect of Ca and Mg vs. Na. Calcium never fell below the critical foliar level of 7 mg·g⁻¹ determined by Miyasaka (1979) in a 7-week hydroponic experiment with 'Lehua maoli' taro. Leaf blade Mg levels also never fell below a critical level of 1.4 mg·g⁻¹ for 4-week-old hydroponically grown 'Bun long' (Austin et al., 1994).

Calcium and Na competition in tissue accumulation was observed in field bean relatives (*Phaseolus* spp.) by LaHaye and Epstein (1971), and Mg and Na competition was observed in maritime pine (*Pinus pinaster* Ait.) seedlings (Saur et al., 1995), but neither interaction was observed in rice (*Oryza sativa* L.) (Yeo and Flowers, 1985).

One potentially important difference between conditions in our experiment and those of agronomic interest is that saline soils in the Pacific Basin tend to be very high in available Ca (Bruce, 1987; Fosberg, 1949; Manner, 1993). LaHaye and Epstein (1971), using an experimental apparatus similar to our own, found that additional solution Ca conferred additional tolerance of solution Na in *Phaseolus* spp.

Manganese concentration and content in laminae and petioles increased significantly ($P < 0.05$) with increasing solution NaCl (Tables 1, 2). High rhizosphere Cl concentrations can induce accelerated Mn uptake (Khattack and Jarrell, 1989).

Manganese toxicity, characterized by marginal lamina chlorosis and necrosis, with necrotic spots or freckles across the laminae in 'Bun long' (Miyasaka, personal communication), was not detected in our experiment. Lamina Mn levels (Table 2) were well below the threshold toxic concentration of 13 mg·g⁻¹ for 'Bun long' (Miyasaka, personal communication).

Table 3. Effects of solution NaCl concentration on the K : Na mass ratio in taro tissues (elemental basis).^z

NaCl (mm)	Lamina	Petiole	Root
0	29.2	63.0	43.9
5	41.3	55.8	3.43
10	53.5	43.5	1.19
20	68.2	19.2	1.15
40	50.2	24.7	3.80
60 ^y	69.2	31.0	1.97
80 ^y	62.0	18.7	0.99
Significance ^x P =	0.058	0.075	0.00001

^zMean of three samples.

^ySamples were bulked for tissue analysis.

^xANOVA results are for 0 to 40 mm solution NaCl treatments only.

Concentrations of P, Fe, Zn, Cu, and B increased, and contents remained stable or decreased, as dry-matter production declined with increasing solution NaCl (data not shown). These observations support the nutrient dilution hypothesis of Jarrell and Beverley (1981). This strongly implies that inhibition of growth was solely responsible for the accumulation responses observed for those nutrients.

Conclusion. The salinity threshold level and response slope values for dry-matter accumulation suggest that 'Bun long' is sensitive to rhizosphere NaCl. Its ability to manipulate Na levels in lamina tissue (exclusion) and Cl levels in the petiole (sequestration), demonstrates that 'Bun long' actively responds to elevated salinity. For the salinity responses of taro to be properly understood, similar research is required with additional cultivars to establish the nature and extent of genetically determined tolerance to rhizosphere NaCl. Some of this work should be carried out at varying Ca : Na ratios in nutrient solution to determine the effects of relative Ca abundance on salinity tolerance.

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