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EFFECTS OF SALINITY ON BALDCYPRESS SEEDLINGS: PHYSIOLOGICAL RESPONSES AND THEIR RELATION TO SALINITY TOLERANCE

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Abstract: Growth and physiological responses of 15 open-pollinated families of baldcypress (*Taxodium distichum* var. *distichum*) subjected to flooding with saline water were evaluated in this study. Ten of the families were from coastal sites in Louisiana and Alabama, USA that have elevated levels of soil-water salinity. The other five families were from inland, freshwater sites in Louisiana. Seedlings from all families tolerated flooding with water of low (2 g l^{-1}) salinity. Differences in biomass among families became most apparent at the highest salinity levels (6 and 8 g l^{-1}). Overall, increasing salinity reduced leaf biomass more than root biomass, which in turn was reduced more than stem biomass. A subset of seedlings from the main greenhouse experiment was periodically placed indoors under artificial light, and measurements were made of gas exchange and leaf water potential. Also, tissue concentrations of Cl^-, Na^+, K^+, and Ca^{2+} were determined at the end of the greenhouse experiment. Significant intraspecific variation was found for nearly all the physiological parameters evaluated, but only leaf concentrations of Na^+ and Cl^- were correlated with an index of family-level differences in salt tolerance.

Key Words: *Taxodium distichum*, saltwater intrusion, salt tolerance, gas exchange, intraspecific variation, wetland restoration

INTRODUCTION

Among the most distinctive forested wetland tree species in the southern United States is baldcypress (*Taxodium distichum* var. *distichum* (L.) Rich.). Baldcypress occurs on sites with prolonged inundation or soil saturation in the southern Coastal Plain and throughout the Lower Mississippi Valley (Larsen 1980). The species is significant both because of its economic value and because of its dominance in many southern forested wetlands (Brown and Montz 1986, Conner 1988, Wilhite and Toliver 1990).

Like numerous other tree species, baldcypress has substantial genetic variation in attributes important from the perspectives of seedling production, commercial forestry, or horticulture. Such attributes include seed size, number of seeds per cone, first-year growth, and crown shape (Faulkner 1982, Dirr 1983, Faulkner 1985). There is also evidence of genetic variation in tolerance to various biotic and abiotic stresses.

For example, variation in leaf morphology seems to be an important factor affecting susceptibility to herbivory (Meeker and Goyer 1993) and, possibly, tolerance to different soil moisture regimes (Sharma and Madsen 1978). Genetic variation along a latitudinal gradient has been found in photoperiod response and in cold acclimation (Flint 1974).

One abiotic stress of particular concern to managers of coastal forests is salinity. Hydrologic modifications such as levees and canals, eustatic sea-level rise, land subsidence, and other factors have acted to allow salt water to intrude into many baldcypress-dominated swamps, particularly in southern Louisiana (Wicker et al. 1981, Templet and Meyer-Arendt 1988, Allen 1992). In addition to a host of other factors, such as altered patterns of flooding and sedimentation, nutria depredation, and vine damage (Conner 1988, Platt and Brantley 1990, Allen and Boykin 1991, Myers et al. 1995), elevated soil-water salinity may be a major factor inhibiting natural regeneration of baldcypress (Platt and Brantley 1990, but see Myers et al. 1995).

Although baldcypress is generally considered to be salt-sensitive (Brown and Montz 1986, Pezeshki et al. 1986, 1987), there is evidence of substantial intraspecific variation in salt tolerance. Pezeshki et al. (1990) and Yanosky et al. (1995) reported that mature stands or individuals of baldcypress have been found on sites exposed to substantial salinity stress, where many other baldcypress trees have died. The possibility that significant intraspecific variation in salt tolerance may exist is also suggested by Javanshir and Ewel (1993). Allen et al. (1994) and Pezeshki et al. (1995) both recently demonstrated that significant variation in response to salinity tolerance occurs among seedlings from open-pollinated families of baldcypress.

The existence of significant intraspecific variation in salt tolerance opens up the possibility of developing salt tolerant lines of baldcypress for use in coastal forest restoration. The task of screening very large numbers of seedlings for salinity tolerance is time-consuming and expensive. Measurements of physiological responses such as gas exchange, chlorophyll fluorescence, plant water status, or tissue nutrient concentrations, however, may prove to be effective as tools for screening large numbers of plants (Shannon 1979, Noble and Rogers 1992, Belkhodja et al. 1994).

The effectiveness of a physiologically-based approach to developing salt tolerant planting material depends on the existence of sufficient genetic variation in the traits of interest and on knowledge of how different genotypes respond to salinity stress (Noble and Rogers 1992). Thus, the specific objectives of this study were to (1) test for the existence of intraspecific variation in salt tolerance within baldcypress and (2) determine if differences in salt tolerance are related to differences in physiology.

MATERIALS AND METHODS

Plant Material

First-year seedlings from 15 open-pollinated families (hereafter referred to as families) were used in this experiment. Ten of the parent trees were from coastal locations in southern Louisiana and Mobile Bay, Alabama. Five other parent trees were from areas not subjected to brackish conditions. Approximate locations of the 15 trees, a summary of the salinity regimes in which the trees were found, and details on seed collection, processing and storage are provided in Allen (1994) and Allen et al. (1994).

Seedlings were grown until late June in 6.5-cm by 36-cm plastic pots filled with equal parts sand, vermiculite, and peat. They were then transferred into fiberglass tanks flooded with deionized water to approximately 5 cm above the soil surface. Prior to flooding, seedlings were fertilized every two weeks with 20-20-20 (N-P-K) water-soluble fertilizer. Seedlings were fertilized once after flooding with a combination of 20-20-20 (two parts) and a micronutrient fertilizer ('Liquid Iron,' Ferti-lome Products, Bonham, TX) by injecting the fertilizer solution into the pots. After a three-week flooding acclimation period, salt treatments were initiated.

Salinity Treatments

Five salinity treatments (0, 2, 4, 6, and 8 g l^{-1}, all with flooding to 5 cm above the soil surface) were prepared using a commercial seawater mix. The seawater mix had major ionic components in approximately the following percentages of dry weight: Cl (51%), Na (30%), Mg (4%), Ca (1%), and K (1%). Since baldcypress in coastal areas is commonly flooded, the 0 g l^{-1} treatment was considered to be the control.

Treatments were initiated in mid-July. Seedlings were exposed gradually by raising the salinity in the tanks by 1/4 of the final treatment concentration each week for four weeks. After reaching final salinity treatment levels on 6 August, treatments were maintained until final harvest in late October/early November. Further details on the environmental conditions in the greenhouse and tanks are provided in Allen et al. (1994).

A split-plot design was used, with salinity level as the main plot treatment and family as the subplot effect. Main plots were arranged in a complete randomized block design with three blocks. Each block con-

sisted of 5 tanks (plots). Each tank contained 12 seedlings of each family, for a total of 180 seedlings per tank and 2,700 seedlings in the whole experiment.

Gas Exchange and Leaf Water Potential Measurements

In mid-August and again in mid-September, 225 seedlings (3 seedlings/family/salinity level) were removed from the greenhouse and placed under controlled conditions in a laboratory. Seedlings were placed in tanks with the same flooding depth and salinity level as they were in the greenhouse. A combination of fluorescent and incandescent lighting yielded approximately 400–450 $\mu mol\ m^{-2}\ s^{-1}$ PPFD at the top of the plants. Photoperiod was 14 hr of daylight. Temperature and relative humidity conditions remained fairly constant at approximately 25–26 °C and 40–50%, respectively. Seedlings were acclimated to the laboratory conditions for at least 48 hr prior to initiation of measurements. All measurements were made between 1000 and 1600 h and were typically completed over a three-day period.

Net photosynthesis (A) and stomatal conductance (g_w) were measured using a portable, open gas exchange system (LCA-3; Analytical Development Company, Hoddesson, England). The seventh fully expanded leaf of each seedling was detached and immediately placed in the chamber. Leaf temperatures were between 24.0 and 26.5 °C, and PPFD was between 460 and 500 $\mu mol\ m^{-2}\ s^{-1}$. Following the gas exchange measurement, leaf area was measured using a Li-Cor (Lincoln, NE, USA) Model LI-3000A leaf area meter. Immediately after the measurement of leaf area, the leaf water potential was measured using a pressure chamber (Model 1002, PMS Instrument Co., Corvallis, OR, USA). Early morning ("predawn") measurements of leaf water potential were also made on a small subsample of seedlings from four families ($n = 6$–10 per salinity treatment) during each of the two sample periods.

Leaf, Stem, and Root Biomass

During the harvest, all living seedlings were separated into roots, stems, and leaves. They were dried at 70 °C to a constant weight for biomass measurements.

Tissue Analyses

Cl^-, Na^+, K^+ and Ca^{2+} concentrations in leaf, root, and stem tissue were determined for a subset of seedlings at the time of the harvest (late October–early November). Three seedlings/family/salinity level ($n = 225$) were selected. For analysis of Na^+, K^+, and Ca^{2+} concentrations, oven-dried leaf, root, and stem tissues were ground in a Wiley Mill with a 20 mesh screen, digested in HNO_3, and filtered. Na^+ and K^+ concentrations were analyzed by flame emission spectrophotometry, and Ca^{2+} concentrations were analyzed by flame absorption spectrophotometry. Cl^- concentrations were measured using a digital chloridometer, following extraction in distilled water.

Data Analyses

The General Linear Models (GLM) procedure (SAS Institute, Inc. 1988) was used to test for differences among salinity treatments (main plot effects), families (subplot effects), and salinity × family interactions at 0.05 level of significance. Physiological responses were evaluated using measurements from August and September combined. Because significant linear correlations were found between initial height and the biomass variables evaluated, initial height of each seedling was used as a covariate and least-square means were compared. Natural log transformations were made on all biomass response variables except root weight ratio.

In an effort to further quantify overall salinity tolerance, an index incorporating relative responses of individual families to high and low salinity levels was calculated. The 'Potential Survival Index' (PSI) was calculated as described in Allen et al. (1994). The PSI was an attempt to assess future survival by combining first-year survival with a measure that we believed was indicative of the likelihood of future survival (leaf area). The index has a maximum value of 10,000, and higher PSI values are indicative of better relative performance.

Analyses of variance were used to test for differences in the gas exchange, water potential, and tissue concentrations of Cl^-, Na^+, K^+ and the Na^+/K^+ and Na^+/Ca^{2+} ratios among salinity treatments, families, and salinity × family interactions. Where significant differences were found, means were separated using Tukey's studentized range test. In addition, the SAS Correlation (CORR) procedure was used to test for linear correlations between physiological measurements and PSI values.

RESULTS

Biomass

There were significant differences among families for leaf, stem, and root biomass (Table 1). In general, families from brackish locations had greater biomass than families from inland locations at the highest salinity levels (Table 2). Differences were most pro-

Table 1. Analysis of covariance table for biomass variables.

Variable	F Value			
	Salinity d.f. = 4	Family d.f. = 14	Salinity × Family d.f. = 56	Initial Height (Covariate) d.f. = 1
Leaf Biomass (g dry wt)	398.24*	11.15*	3.61*	222.80*
Stem Biomass (g dry wt)	107.46*	7.71*	1.66*	1128.67*
Root Biomass (g dry wt)	213.38*	3.68*	2.15*	798.35*
Root Weight Ratio (root biomass/total biomass)	35.83*	4.86*	1.80*	50.78*

* Significant at 0.001 level.

nounced at 6 g l^{-1}, where families from brackish locations had twice as much leaf biomass, 17% greater stem biomass, and 55% greater root biomass than families from freshwater sources.

At 6 g l^{-1}, Family FA2 clearly stood out, with the greatest mean stem and root biomass, the second greatest leaf biomass, and the highest percent total biomass relative to the 0 g l^{-1} treatment (95%). Other outstanding families at this salinity level include FA3, SG2, FA1, and VE2—all from brackish locations. Several of these families did not perform as well at 8 g l^{-1} (relative to average performances for all families), suggesting that families had different tolerance thresholds. The best biomass-producing families at 8 g l^{-1} were CB3, FA2, FA3, and CB2—again all from brackish locations.

There were significant interactions between salinity and family for leaf, stem, and root biomass (Table 1), also indicating that families responded to salinity treatments in different ways. An example of the differences in response of four families can be seen in the data presented in Table 2. Two families (CB3 and SG2) showed similar and essentially linear declines in leaf biomass with increasing salinity. Another family (FA2) maintained relatively high leaf biomass up to the 6 g l^{-1} treatment before apparently crossing a tolerance threshold between 6 and 8 g l^{-1}, and the fourth family (BO2) appeared to cross a tolerance threshold between 4 and 6 g l^{-1}.

Salinity affected shoot biomass more than root biomass at intermediate salinity levels, resulting in an increase in root weight ratio (root biomass/total plant biomass). Mean root weight ratio peaked at 0.34 in the 4 g l^{-1} treatment and declined at higher salinities to the point where, at 8 g l^{-1}, it was not significantly different from the 0 g l^{-1} treatment (Figure 1). Within

Table 2. Mean leaf (L), stem (S), and root (R) biomass (g dry wt) by salinity and family.

Family	Salinity (g l^{-1})														
	0			2			4			6			8		
	L	S	R	L	S	R	L	S	R	L	S	R	L	S	R
Brackish Sources															
CB2	2.9	4.2	2.9	2.2	3.9	3.2	1.3	3.2	2.3	1.4	2.6	1.4	0.2	2.3	1.3
CB3	2.4	3.7	2.4	1.8	3.6	2.4	1.2	2.4	1.9	0.8	2.5	1.7	0.5	2.3	1.4
FA1	2.7	4.6	2.9	2.6	4.3	2.8	1.6	3.5	2.5	0.6	3.1	1.7	0.2	2.3	0.9
FA2	2.2	3.3	2.0	2.0	3.6	2.4	1.9	3.3	2.7	1.3	3.4	2.4	0.2	2.4	1.4
FA3	2.8	4.5	3.1	2.3	4.1	2.8	2.0	3.5	2.9	1.1	2.8	2.1	0.3	2.6	1.3
FA4	2.1	3.6	2.1	2.5	4.3	3.1	1.7	2.8	2.3	0.4	2.3	1.2	0.1	1.9	0.9
PB1	0.9	1.6	1.3	0.8	1.7	1.1	0.6	1.6	1.1	0.2	2.0	1.3	0.0	1.9	0.8
SG2	1.9	3.3	2.3	1.7	3.5	2.6	1.2	2.8	2.3	0.8	3.1	2.0	0.2	2.1	1.0
VE2	2.1	3.7	2.8	2.2	4.3	3.0	1.4	3.0	2.8	0.7	2.6	2.0	0.2	2.1	1.1
VE3	2.5	4.9	3.2	2.7	5.1	3.8	1.7	3.4	3.0	0.4	2.6	1.5	0.1	2.5	1.0
Mean	2.3	3.7	2.5	2.1	3.8	2.7	1.5	2.9	2.4	0.8	2.7	1.7	0.2	2.2	1.1
Freshwater Sources															
BO2	2.1	3.2	2.2	1.4	2.1	1.7	1.3	2.2	1.7	0.1	2.0	0.9	0.0	1.8	0.8
LS1	2.1	3.4	2.5	1.9	3.8	2.9	0.9	2.8	2.1	0.2	2.5	1.3	0.1	2.2	1.0
PR1	1.1	2.6	1.5	1.3	2.4	1.7	0.8	2.2	1.8	0.2	1.9	0.8	0.1	2.1	0.9
SW1	2.4	3.8	2.2	1.8	3.2	2.0	1.9	3.3	2.4	0.6	2.4	1.1	0.2	1.9	0.9
SW2	2.3	4.4	2.3	2.3	3.9	2.6	1.8	3.4	2.6	0.7	2.7	1.5	0.1	2.1	0.8
Mean	2.0	3.5	2.1	1.7	3.1	2.2	1.3	2.8	2.1	0.4	2.3	1.1	0.1	2.0	0.9
Overall Mean	2.2	3.7	2.4	2.0	3.6	2.5	1.4	2.9	2.3	0.6	2.6	1.5	0.2	2.2	1.0

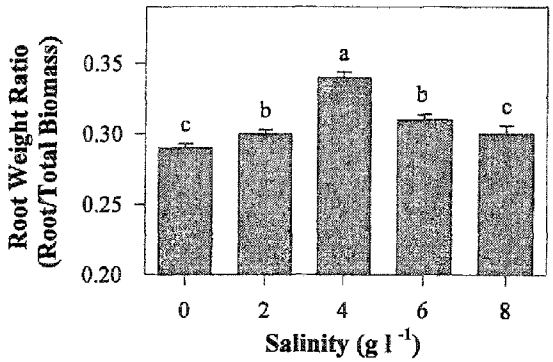

Figure 1. Mean root weight ratio (root biomass/total biomass; ± 1 s.e.) for all 15 families. Means with the same letter above the bar are not significantly different as determined by Tukey's studentized range test (α = 0.05).

the shoot, leaf biomass was much more affected than stem biomass. Stem biomass at 8 g l^{-1} was 59% of the 0 ppt mean, but leaf biomass at 8 ppt was only 7% of the mean for the 0 g l^{-1} treatment. Stem biomass, in fact, changed less in response to salinity than root biomass.

Gas Exchange

The means of net photosynthesis (A) and stomatal conductance (g_w) for the 15 families combined each declined substantially with increasing salinity (Figures 2a and b). The means for A and g_w at 8 g l^{-1} were less than 30% of the corresponding values for the freshwater controls. A similar pattern of decline was observed for both of the gas exchange measures. There was an initial and significant ($P \leq 0.05$) drop between 0 and 2 g l^{-1}, no significant differences between the 2 and 4 g l^{-1} treatments, and significant declines among the 4, 6, and 8 g l^{-1} treatments.

Substantial variation among the 15 families was found for A and g_w. Differences in overall family means (i.e., across salinities) were significant for both variables, but salinity × family interactions were not (Table 3). An example of the variation observed

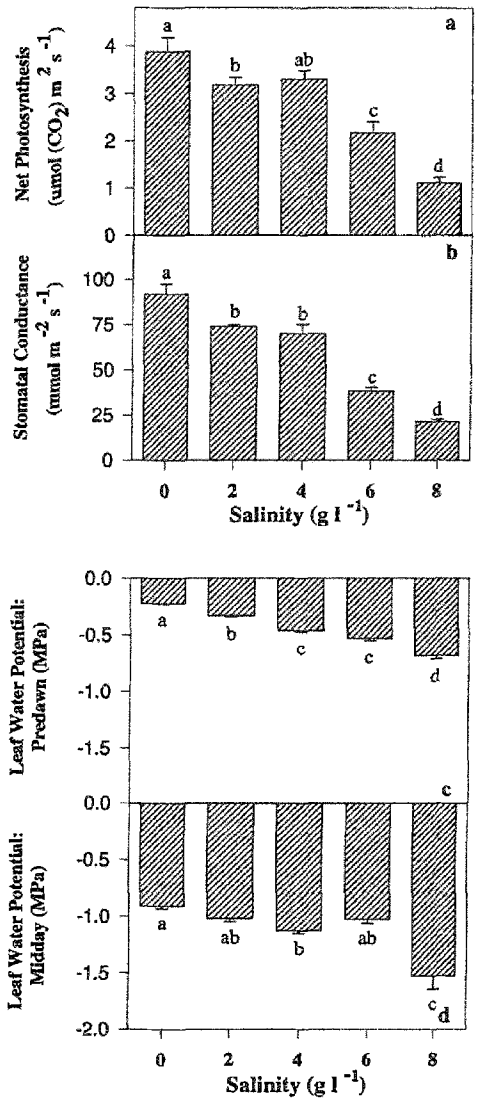

Figure 2. Mean gas exchange and leaf water potential (± 1 s.e.) for all 15 families: (a) net photosynthesis, (b) stomatal conductance, (c) predawn leaf water potential, and (d) midday leaf water potential. Within each graph, means with the same letter above the bar are not significantly different as determined by Tukey's studentized range test (α = 0.05).

Table 3. Analysis of variance table for gas exchange and water potential variables.

	Salinity (d.f. = 4)[1]			Family (d.f. = 14)			Salinity × Family (d.f. = 56)		
Variable	MSE	F	P	MSE	F	P	MSE	F	P
Gas Exchange									
A	53.59	76.93	0.001	4.68	2.33	0.028	1.47	0.84	0.763
g_w	0.036	80.36	0.001	0.001	2.63	0.014	0.0006	1.07	0.384
Water Potential									
Midday	251.95	33.75	0.001	14.03	0.80	0.657	14.57	0.93	0.607
Predawn	19.95	210.55	0.001	0.79	8.31	0.002	0.27	2.85	0.035

[1] Degrees of freedom apply to all variables except predawn leaf water potential, which has 4 d.f. for salinity, 3 d.f. for family, and 9 d.f. for salinity × family.

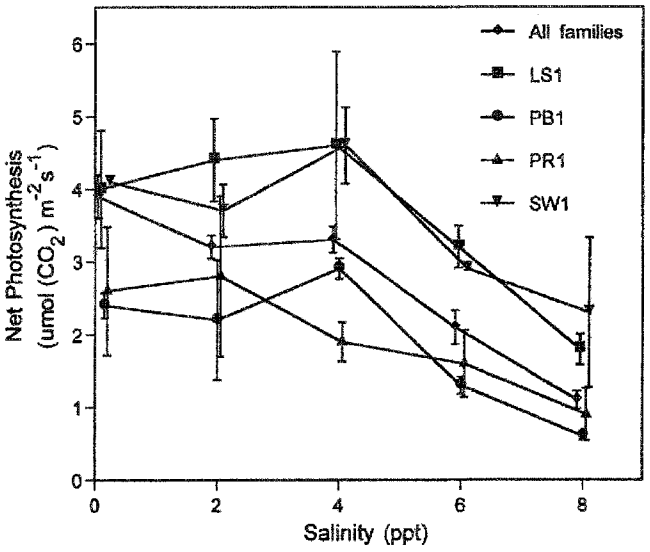

Figure 3. Mean net photosynthesis (± 1 s.e.) by salinity level for all 15 families combined and for four selected families. Means have been slightly offset on the *x*-axis to allow clearer differentiation of error bars.

among families is depicted in Figure 3 for net photosynthesis. Some families (e.g., LS1 and SW1) maintained rates of photosynthesis consistently above the overall mean, while others (e.g., PB1 and PR1) had consistently below-average photosynthetic rates. Variation was also high within families. Some individual seedlings in the 6 and 8 g l^{-1} treatments maintained rates of photosynthesis as high as the overall mean for the 0 g l^{-1} controls. No consistent pattern was apparent in the means for the families from brackish locations compared to those from freshwater locations, and differences between the two sources were not significant for either of the gas exchange variables.

Leaf Water Potential

Mean predawn leaf water potentials for the four families evaluated ranged from −0.22 MPa for the 0 g l^{-1} treatment to −0.68 MPa for the 8 g l^{-1} treatment (Figure 2c). The mean declined by approximately 0.07 to 0.15 MPa with each 2 g l^{-1} increase in salinity, and differences among treatments were significant with the exception of 4 and 6 g l^{-1}. Differences among families and the family and salinity × family interaction were significant for the predawn sample (Table 3), but the differences were apparent only at 6 and 8 g l^{-1}.

A less consistent trend was observed in the midday leaf water potential measurements. Mean midday leaf water potential decreased only slightly as salinity increased from 0 to 6 g l^{-1} but was much lower in the 8 g l^{-1} treatment (Figure 2d). The low mean leaf water potential at 8 g l^{-1} was due in large part to a number of leaves with unusually low potentials (in the range of −2.5 to −3.4 MPa). The high variability at 8 g l^{-1} is evident in the large standard error, which is more than three times that of any other salinity treatment. In contrast to the predawn sample, family and salinity × family interactions were not significant for midday leaf water potential (Table 3).

Tissue Ion Concentrations

Concentrations of Na^+ and Cl^- in leaf, stem, and root tissue increased significantly with increasing salinity (Figures 4a and 4b). Cl^- accumulated to the highest concentrations in leaf tissue, whereas Na^+ concentrations were nearly equal in leaf and root tissue (Figures 4a and 4b). Both Na^+ and Cl^- continued to accumulate as salinity increased.

The mean concentration of K^+ dropped substantially between 0 and 2 g l^{-1} and remained relatively stable with further increases in salinity. There were some important changes in concentrations in K^+ among the different tissues, however. Leaf concentrations increased steadily as salinity increased above 2 g l^{-1}, whereas K^+ concentrations declined further in the root tissue (Figure 4d). The differential pattern of K^+ concentrations in the three organs is reflected strongly in the Na^+/K^+ ratio (Figure 4f). The Na^+/K^+ ratio for leaves remained relatively stable across the 2 to 8 g l^{-1} salinity treatments, while it increased substantially in stems and especially roots (Figure 4f). Ca^{2+} concentrations changed less than the other ions (Figure 4c). The most notable change was in the root Na^+/Ca^{2+} ratio, which increased significantly at higher salinities (Figure 4e).

Family differences were less frequently significant than differences among salinity treatments (Table 4). The most consistent differences among families are in Na^+ and Cl^- concentrations. In Figure 5, the means of Na^+ and Cl^- concentrations of the three families believed to be the most salt tolerant (CB3, FA2, and FA3) are compared with the means for all 15 families by tissue type. Na^+ concentrations were consistently lower for the three tolerant families, while Cl^- levels were not different overall. The differences in Na^+ concentration were most apparent in the shoots and particularly in the leaves (Figure 5), where the mean Na^+ concentration for Families CB3, FA2, and FA3 was 34% lower than the overall mean.

The differences in Na^+ concentrations were even more pronounced at the highest salinity levels (Figure 5). Also, at the highest salinity levels, differences in Cl^- concentrations in shoot tissues became apparent. At 6 g l^{-1}, Cl^- concentrations for the top three families were 20% lower in the leaf tissue than the overall mean and 25% lower in the stems.

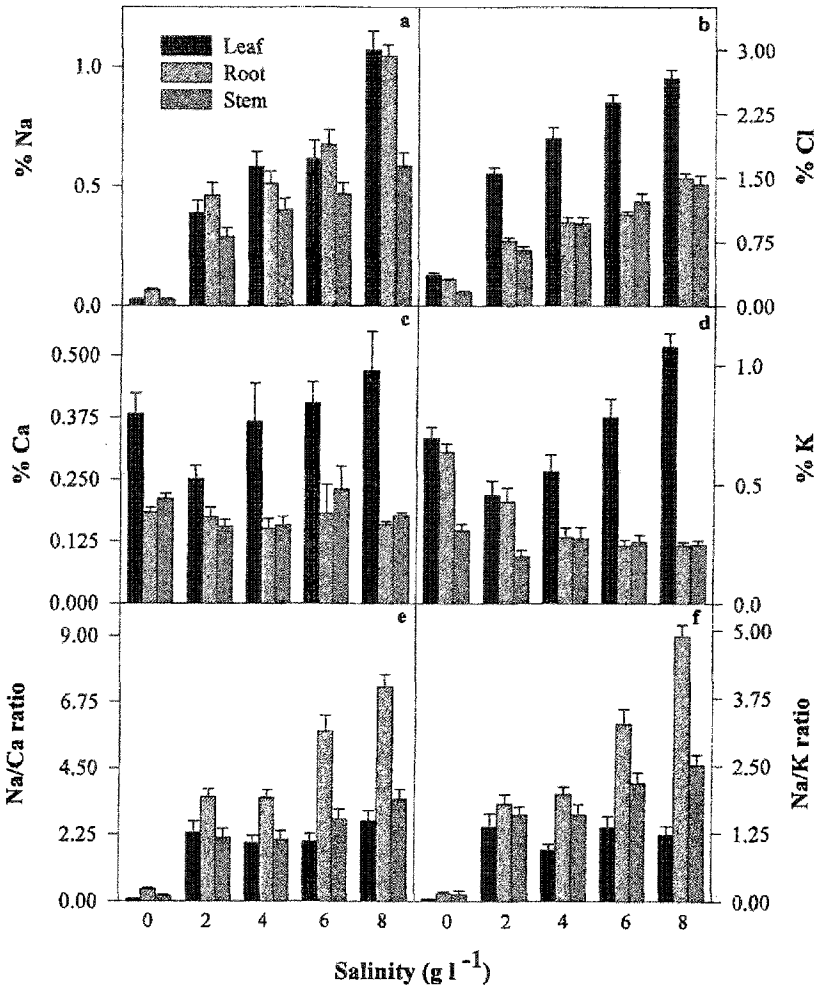

Figure 4. Means (± 1 s.e.) by salinity level and tissue type for concentrations of (a) Na^+, (b) Cl^-, (c) Ca^{2+}, (d) K^+ , (e) Na^+/Ca^{2+}, and (f) Na^+/K^+ ratios.

Relationship Between Physiological Responses and Potential Survival Index

Linear correlations between gas exchange and the Potential Survival Index (Allen et al. 1994) were not significant (Table 5 and Allen 1994). There were, however, significant linear correlations between tissue concentrations of ions in leaf tissue and PSI, most notably for Na^+ and Cl^-. All significant correlations were negative (Table 5), indicating that high ion concentrations were associated with low salt tolerance.

DISCUSSION

Overall Seedling Responses

As salinity increased from 0 to 4 g l^{-1}, an increasing proportion of total seedling biomass was partitioned to roots, a response previously observed in baldcypress (Javanshir and Ewel 1993). Low level (2 g l^{-1}) salinity actually promoted root growth in 9 of the 15 families. Increased partitioning to roots may act to provide the plant with a greater surface area for uptake of water (Shannon et al. 1993). Because many soils have non-uniform salinity conditions (Thomson 1988, Tanji and Karajeh 1993), the increased surface area enhances the possibility of roots encountering zones of lower salinity. The value of having some portion of the root system in low salinity zones has been demonstrated in split-root studies (Zekri and Parsons 1990). Increased partitioning to roots may also yield other benefits, such as greater production of cytokinins. Waisel and Breckle (1987) suggested that maintaining a high number of root primordia (sites for cytokinin production) may enable the plant to endure higher salinity, possibly by counteracting elevated ABA concentrations.

Biomass partitioning to roots decreased at salinity levels above 4 g l^{-1}. A possible explanation for this phenomenon is suggested by the large increases in both the Na^+/K^+ and Na^+/Ca^{2+} ratios in the roots that occurred between the 4 and 6 g l^{-1} treatments. The

Table 4. Analysis of variance table for leaf, root, and stem ion concentrations.

	Salinity (d.f. = 4)			Family (d.f. = 14)			Salinity × Family (d.f. = 56)		
Variable	MSE	F	P	MSE	F	P	MSE	F	P
Cl^-—Leaf	16.62	147.34	0.001	0.31	1.95	0.064	0.14	1.06	0.435
Cl^-—Root	7.91	32.06	0.001	0.08	1.10	0.508	0.08	1.10	0.333
Cl^-—Stem	10.46	13.34	0.001	0.35	2.32	0.028	0.27	1.49	0.042
Na^+—Leaf	4.89	28.71	0.001	0.31	3.08	0.005	0.12	1.40	0.091
Na^+—Root	5.44	15.57	0.001	0.07	0.75	0.714	0.07	0.85	0.747
Na^+—Stem	1.95	11.66	0.002	0.13	2.94	0.007	0.08	1.38	0.086
K^+—Leaf	1.85	2.18	0.162	0.18	2.07	0.049	0.11	0.78	0.835
K^+—Root	1.27	7.04	0.010	0.06	0.87	0.598	0.06	1.06	0.399
K^+—Stem	0.07	0.60	0.673	0.03	1.14	0.367	0.03	0.99	0.509
Ca^{2+}—L	0.27	1.01	0.455	0.12	1.07	0.419	0.13	0.90	0.666
Ca^{2+}—R	0.01	0.16	0.954	0.07	1.19	0.335	0.03	1.00	0.487
Ca^{2+}—S	0.05	0.76	0.580	0.02	0.79	0.673	0.02	0.85	0.746
Na^+/K^+—L	12.90	3.01	0.086	2.20	2.28	0.031	1.13	1.04	0.425
Na^+/K^+—R	138.70	36.57	0.001	1.58	1.66	0.123	1.15	0.70	0.934
Na^+/K^+—S	36.85	12.73	0.001	1.20	2.00	0.057	1.06	0.92	0.635
Na^+/Ca^{2+}—L	40.22	5.88	0.017	4.55	1.07	0.426	2.75	0.87	0.716
Na^+/Ca^{2+}—R	297.48	18.58	0.001	5.94	0.99	0.488	4.44	1.08	0.365
Na^+/Ca^{2+}—S	68.74	7.29	0.009	6.36	1.81	0.088	4.21	1.50	0.037

Na^+/K^+ ratio in the root tissue increased from 1.9 to 3.3 between 4 and 6 g l^{-1}; the Na^+/Ca^{2+} ratio increased from 3.5 to 5.7. The degree of ion imbalance represented by these high ratios is likely to have caused severe disruption of root metabolic functions.

Declines in A and g_w with increasing salinity have been reported in a number of previous studies on baldcypress (Pezeshki and Chambers 1986, Pezeshki et al. 1987, 1990). In general, however, the declines observed for each salinity level were less in the present study than those reported previously. Pezeshki et al. (1987), for example, reported mean values of A at 2 and 4 g l^{-1} that were 69% and 64% of a flooded control, respectively. Corresponding percentages from the current study are 82% and 85%.

One reason why observed declines in A and g_w may have been lower in this study than in previous reports is the relatively low light levels in which gas exchange measurements were made in this study. Light levels (PPFD) at the top of the plants in most of the earlier studies of baldcypress were reported to be between 1100 and 1200 μmol m^{-2} s^{-1} (Pezeshki et al. 1986, 1987), compared to 400 to 450 μmol m^{-2} s^{-1} in this study. It is unlikely that lower light levels fully account for the differences with previous reports, however, because the light saturation level for baldcypress is reportedly around 590 μmol m^{-2} s^{-1} (K. McLeod, Savannah River Ecology Laboratory, pers. comm.), suggesting that light levels in the current study were approximately 78% to 85% of the light saturation level for baldcypress.

Salinity-related declines in A of baldcypress and other species have been attributed to both stomatal and non-stomatal factors (Pezeshki et al. 1987, 1989). In the current study, evidence for the relative importance of stomatal versus non-stomatal factors is not conclusive, but non-stomatal factors seem to be more important. Net photosynthesis declined roughly in proportion to stomatal conductance, initially suggesting an important role for diffusional limitations to photosynthesis. Internal concentrations of CO_2, however, did not change substantially in relation to salinity levels (Allen 1994), a result also reported by Pezeshki et al. (1988). Therefore, the decline in g_w may be playing a much greater role in limiting water loss than in limiting A (Wong et al. 1979, Thomson 1988).

The possible importance of non-stomatal factors is also suggested by the large increases in leaf concentrations of Na^+ and Cl^- with increasing salinity, both of which may cause direct toxicity to leaf tissue (Greenway and Munns 1980, Marschner 1986). The mean leaf Na^+/K^+ ratio did not change appreciably as salinity increased above 2 g l^{-1}. The values of the ratio calculated for 2 g l^{-1} and above (0.9 to 1.4), however, were on the upper end of those reported by Pezeshki et al. (1988), who found a strong negative correlation between Na^+/K^+ ratio and A. In general, Na^+/K^+ ratios of less than 1 are thought to be necessary for normal cell function in glycophytes (Wyn Jones et al. 1979). Thus, the role of ion imbalances may also be an important factor limiting photosynthesis in baldcypress. The energetic costs of maintaining relatively stable Na^+/K^+ and Na^+/Ca^{2+} ratios in the leaf tissue may have also been an important non-stomatal limitation on A.

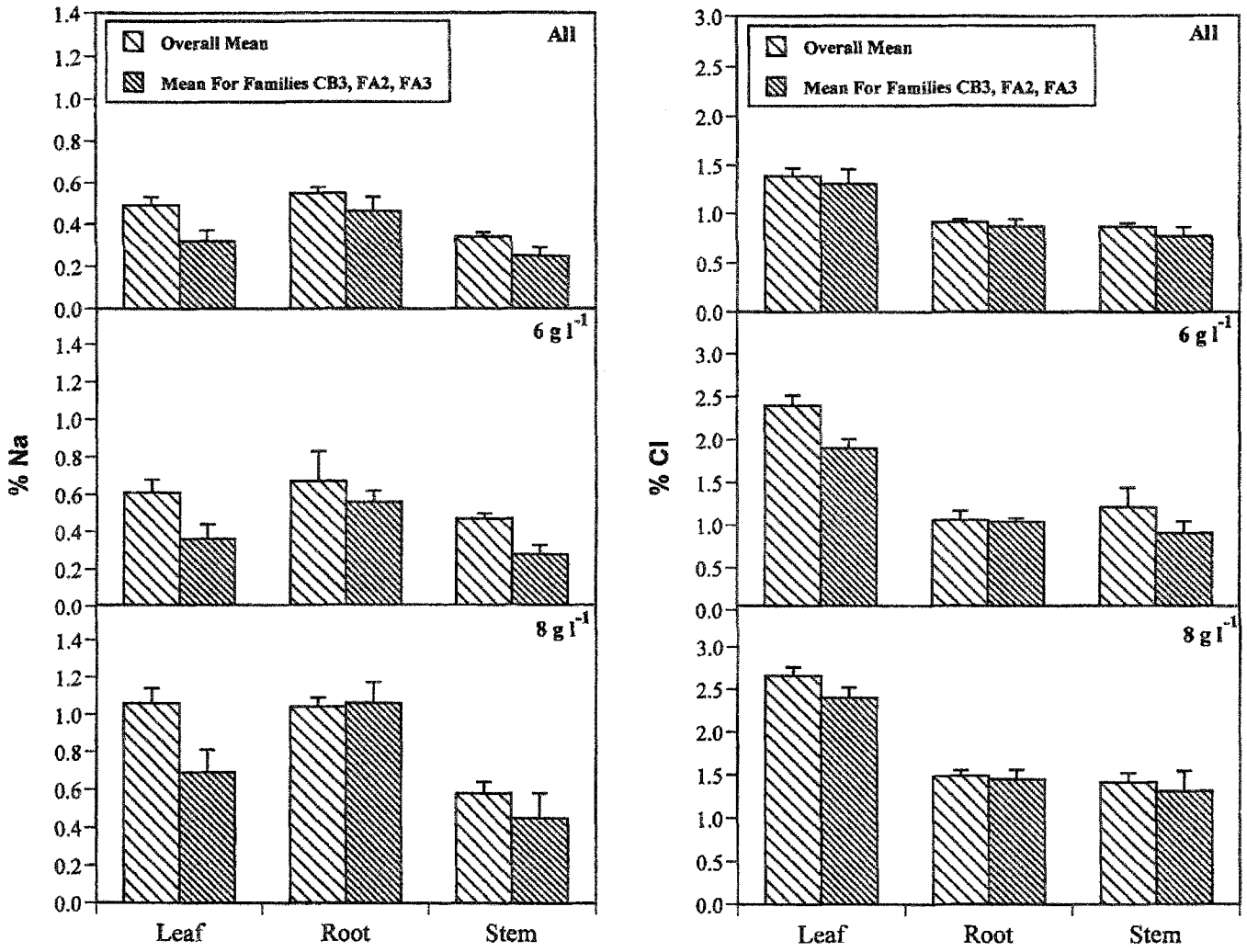

Figure 5. Means (± 1 s.e.) by tissue type and salinity level for Na^+ and Cl^- concentrations for all 15 families combined and for Families CB3, FA2, and FA3 combined. Families CB3, FA2, and FA3 had the highest Potential Survival Index values (Allen et al. 1994).

Intraspecific Variation

Substantial family-level variation was found for all measures of salt tolerance (e.g., biomass; also leaf area and PSI, Allen et al. 1994) and for all measures of gas exchange and water potential with the exception of midday water potential. There was no clear indication, however, that the variation in most physiological factors observed was related to the salt tolerance of the 15 families. Linear correlations between these variables and the PSI tolerance index were not significant. When overall means for the variables were compared, the more tolerant families did not consistently rank high or low—instead they tended to rank at intermediate levels.

The clearest relationship between patterns of family-level variation and salt tolerance was found for tissue concentrations of Na^+ and Cl^- in the shoots. Correlation coefficients for leaf concentrations and tolerance indices were consistently negative, indicating that salt tolerance in baldcypress may be related to the ability to exclude greater amounts of Na^+ and Cl^- from the shoots. Differential abilities to exclude Na^+ and/or Cl^- are often invoked as explanations for intraspecific variation in salt tolerance (Thomson 1988, Maas 1993, Ashraf and Fatima 1995), and exclusion of both Na^+ and Cl^- seems to be the most plausible explanation for differential tolerance in baldcypress.

The characteristic of ion exclusion has proven to be a useful selection criterion for some (but not all) species (Noble and Rogers 1992, Munns 1993). In the case of baldcypress, the ability to exclude Na^+ and Cl^- from shoot tissue is the most promising physiologically-based selection criterion of those evaluated. Ion exclusion from shoots, however, is a "broad" selection criterion that is likely to be the result of several integrated physiological functions (Noble and Rogers

Table 5. Linear correlation coefficients (r) and P values for relationships between selected physiological measures and an index of salt tolerance.

Variable		Potential Survival Index r	P
Net Photosynthesis			
A (0)[1]		0.06	0.81
A (2)		−0.32	0.25
A (4)		0.15	0.59
A (6)		−0.19	0.50
A (8)		0.20	0.47
Leaf Tissue Ion Concentrations and Ratios			
Na^+	(all)	−0.82	<0.01
Cl^-	(all)	0.10	0.72
Na^+/K^+	(all)	−0.40	0.13
Na^+/Ca^{2+}	(all)	−0.44	0.10
Na^+	(6)	−0.55	0.03
Cl^-	(6)	−0.88	<0.01
Na^+/K^+	(6)	−0.36	0.19
Na^+/Ca^{2+}	(6)	−0.25	0.36

[1] Numbers in parentheses are salinity levels; "all" represents all salinity levels combined.

1992). Both Noble and Rogers (1992) and Munns (1993) stated that breaking down the ion exclusion characteristic into its component parts could enhance its usefulness in selection for salt tolerance.

Noble and Rogers (1992), citing previous reports, list control of uptake at the root plasmalemma and tonoplasts of the cortex, accumulation and release of ions from the stele to the xylem, reabsorption of ions by xylem parenchyma cells, phloem translocation, and compartmentation in older leaves as possible mechanisms of ion exclusion. Another possibility that could explain intraspecific differences in ion exclusion is earlier formation of Casparian bands in tolerant genotypes (Thomson 1988). The identification of specific mechanisms responsible for intraspecific variation in ion exclusion capacity would seem to be an important research priority and one with great potential for producing gains in salt tolerance of baldcypress.

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