

# Growth and Nutrition of Baldcypress Families Planted Under Varying Salinity Regimes in Louisiana, USA

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## ABSTRACT

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Saltwater intrusion from the Gulf of Mexico is one important factor in the destruction of baldcypress (*Taxodium distichum* (L.) Rich.) swamps along the Louisiana Gulf Coast, USA. Recent restoration efforts have focused on identification of baldcypress genotypes with greater tolerance to saline conditions than previously reported. To date, salt tolerance investigations have not been conducted under saline field conditions. In 1996, therefore, three plantations were established with 10 half-sib genotype collections of baldcypress in mesohaline wetlands. Tree survival and growth were measured at the end of two growing seasons, and foliar ion concentrations of Na, Cl, K, and Ca and available soil nutrients were measured during the 1996 growing season. In general, soil nutrient concentrations exceeded averages found in other baldcypress stands in the southeastern United States. Seedlings differed among sites in all parameters measured, with height, diameter, foliar biomass, and survival decreasing as site salinity increased. Average seedling height at the end of two years, for example, was 196.4 cm on the lowest salinity site and 121.6 cm on the highest. Several half-sib families maintained greater height growth increments (ranging from 25.5 to 54.5 cm on the highest salinity site), as well as lower foliar ion concentrations of K, Cl, and Ca. Results indicate that genotypic screening of baldcypress may improve growth and vigor of seedlings planted within wetlands impacted by saltwater intrusion.

**ADDITIONAL INDEX WORDS:** *Salt tolerance, restoration, provenance testing, coastal swamp forests, reforestation, forest tree improvement, wetland, Taxodium distichum.*

## INTRODUCTION

Along the Gulf Coast of Louisiana, saltwater intrusion into freshwater wetlands is responsible for the destruction of baldcypress (*Taxodium distichum* (L.) Rich.) and water tupelo (*Nyssa aquatica* L.) communities (ALLEN, 1992; PEZESHKI *et al.*, 1990; WICKER *et al.*, 1981). Saltwater intrusion and associated negative effects may be combated in at least two ways: (1) the restoration of natural hydrologic patterns and/or (2) the identification, and subsequent planting, of species or genotypes of vegetation tolerant to saline conditions. Projects aimed at complete hydrologic restoration are highly unlikely in coastal Louisiana due to logistic, economic, and social considerations (ALLEN, 1994). In contrast, partial hydrologic restoration, in the form of freshwater river diversions, has met with some success (BOYER *et al.*, 1997). Likewise, ALLEN *et al.* (1994a) suggests that projects aimed at salt tolerance improvement in forest tree species may be justifiable,

since tree species possess a broad range of genetic variation in salt tolerance. PEZESHKI *et al.* (1990) and ALLEN *et al.* (1994b) suggest that selection of individual baldcypress trees with acceptable form and vigor from large forests impacted by saltwater intrusion may prove beneficial. Several studies have shown that baldcypress selected from brackish-water sources have better general performance based upon physiological and morphological characteristics than those from freshwater sources (ALLEN *et al.*, 1994b; 1997).

Other studies have investigated treatment-level (CONNER, 1994; JAVANSHIR and EWEL, 1993; OMRAN *et al.*, 1979; PEZESHKI *et al.*, 1987; 1988; MCLEOD *et al.*, 1996) and family-level responses (KRAUSS *et al.*, 1996; 1998; in press) of baldcypress to salinity. To our knowledge, published studies addressing intraspecific variation in baldcypress under saline field conditions do not exist. If genotypes of baldcypress possessing greater tolerance to saline field conditions can be identified, then perhaps forest restoration projects within degraded swamps, coupled with partial hydrologic restoration, may be conducted with a higher degree of success.

The purpose of this study was to field test survival, growth, and foliar nutrient levels of half-sib collections of baldcypress seedlings planted on three sites within degraded coastal

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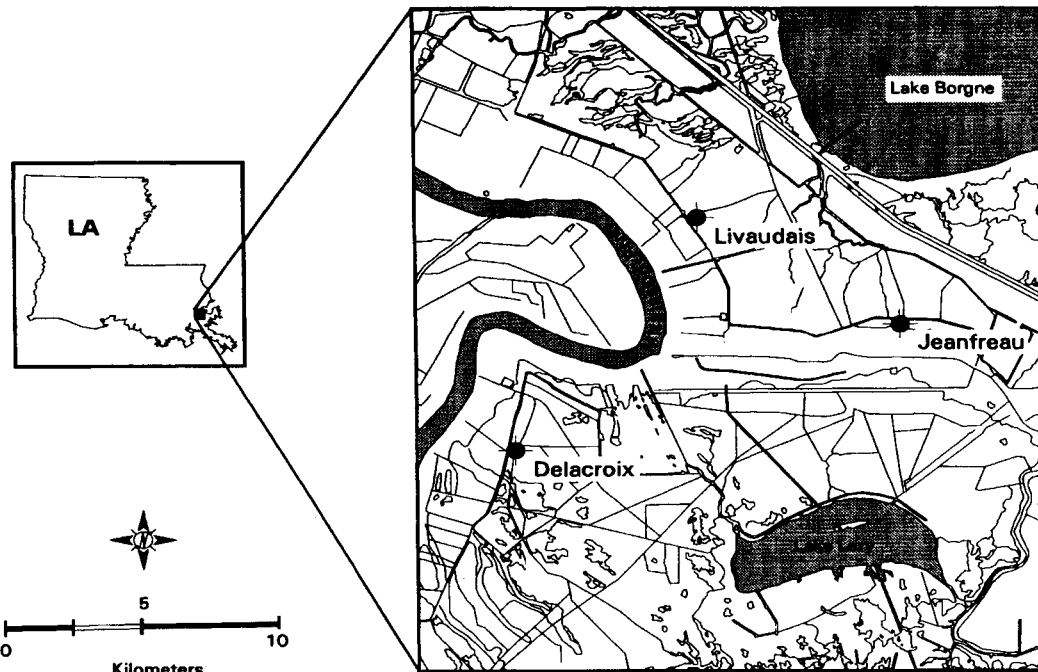


Figure 1. Location of baldcypress field plantations near Chalmette, Louisiana. The waterway depicted just southwest of Lake Borgne is the Mississippi River-Gulf Outlet, which is primarily responsible for saltwater intrusion into the study area. Base map from the U.S. Geological Survey 1:100,000 hydrography layer (USGS National Wetlands Research Center, Lafayette, LA).

swamp forests. In addition, we evaluated soil nutrient composition within these plantations and related limitations to the general performance of baldcypress.

## METHODS

### Study Sites

Three study sites with histories of saltwater intrusion were located to the southeast of New Orleans, Louisiana. Sites were chosen based on aerial photographs and visual indicators of salinity regime, accessibility, and site availability. Two sites, henceforth referred to as the Jeanfreau, or JEA, site (N 29°53', W 89°49') and the Livaudais, or LIV, site (N 29°55', W 89°53'), were located in St. Bernard Parish near Chalmette, Louisiana. The other site, henceforth referred to as the Delacroix, or DEL, site (N 29°50', W 89°58'), was located in the northeast corner of Plaquemines Parish (Figure 1).

Historically, hydrologic patterns on all sites were dominated by seasonal discharge from the Mississippi River, precipitation, winds, and tidal influx from Lake Borgne, a nearby brackish-water embayment (ROUNSEFELL, 1964; WICKER *et al.*, 1982). The 1961 construction of the Mississippi River-Gulf Outlet increased salinity to the area and drastically altered vegetative associations, which were historically dominated by baldcypress and water tupelo (WICKER *et al.*, 1982). During the 1996 growing season, however, the DEL site supported a vegetative association of saltmeadow cordgrass (*Spartina patens* (Ait.) Muhl.) and traces of marsh morning-glory (*Ipomea sagittata* Poir. in Lam.), the JEA site was dominated by

water grass (*Echinochloa walteri* (Pursh) Heller) and deerpea (*Vigna luteola* (Jacq.) Benth.), and the LIV site supported canary grass (*Phalaris angusta* Nees. Ex Trin.) and smartweed (*Polygonum* sp. L.) early in the season and deerpea beginning in July. All sites were located within or adjacent to "ghost forests"—salt-impacted wetlands containing dead standing baldcypress.

Soils on the JEA and LIV sites are of the Barbary series (thermic Typic Hydraquents), poorly drained, and contain a high mineral content. Such soils are indicative of impounded freshwater areas and are often found adjacent to the more organic Clovelly series, which form under brackish-water conditions (TRAHAN *et al.*, 1989). The Clovelly series (thermic Terric Medisaprists) prevails on the DEL site (NRCS, IN PRESS). The 22-year average annual rainfall for the region is 151 cm, with average daily temperatures ranging from a low of 5.9 °C during winter months to a high of 32.4 °C during summer months (TRAHAN *et al.*, 1989).

### Plant Material

Baldcypress plant material was collected from the same parent trees or from parent trees within the same source stands described by ALLEN (1994) and ALLEN *et al.* (1994b). For the purposes of this study, seedlings collected from the same parent tree will be referenced as belonging to the same half-sib "family". Family as used in this study, hence, does not refer to the taxonomic designation but rather to the forest tree improvement definition by ZOBEL and TALBERT (1984,

p. 26) of "individuals that are more closely related to each other than to other individuals in a population . . .".

A total of eight brackish-water source collections of baldcypress and two freshwater source collections (*i.e.*, SW1 and SW2) were evaluated. All brackish-water source collections were made from parent trees remaining within stands established prior to impact from saltwater intrusion. The potential salt tolerance of families FA1, FA2, CB3, SG2, VE2, SW1, and SW2 was previously tested under controlled conditions, with families FA2 and CB3 demonstrating the greatest degree of salt tolerance and families SW1 and SW2 the least (ALLEN *et al.*, 1994b; 1997). Families FA7, FA8, and SG3 were previously untested for relative salt tolerance.

After collection, seeds were allowed to air-dry on tables for three weeks, separated from cones, soaked for five minutes in 70% ethyl alcohol, rinsed twice in tap water, rinsed once in deionized water, mixed with wet sand containing a commercial Captan fungicide, and stored in plastic bags between 4 and 8 °C for a nine week stratification period (see KRAUSS *et al.*, 1998). Seeds were then planted in germination flats and placed at the Louisiana State University Agricultural Center greenhouse facility for a period of approximately 50 days. Seedlings were transplanted into 656 ml plastic 'Deepots' (Stuewe and Sons, Inc., Corvallis, OR), and containers were filled with two parts Jiffy-Mix (Canadian sphagnum peat and vermiculite, West Chicago, IL) and one part sand. A water-soluble 20-10-20 NPK fertilizer (Scotts-Peters Professional, Allentown, PA) was applied weekly for five weeks at an average rate of 20.5 g L<sup>-1</sup> of water volume followed by one application of a slow-release 18-6-12 NPK fertilizer (Osmocote, Marysville, OH) at a rate of 5 g L<sup>-1</sup> of soil volume. All seedlings were maintained under healthy growing conditions throughout the 1995 growing season.

Acclimation treatments were initiated prior to establishment of plantations in an effort to avoid or reduce the possibility of acute stress mortality caused by sudden exposure to salinity. In October of 1995, seedlings were flooded to 5 cm above the soil surface for approximately 60 days, at which time a commercial seawater mix ('Forty Fathoms Marine Mix', Marine Enterprises Inc., Baltimore, MD) was used to bring water salinities up to 1.2 g L<sup>-1</sup> for a period of 14 days, then up to 2.4 g L<sup>-1</sup> for an additional 10 day period. Pots were allowed to drain for three days prior to being transported to their respective field sites.

In January of 1996, a total of 1200 nine-month-old baldcypress seedlings were selected based upon superior growth form and planted on the three sites. Each site contained 40 seedlings from each of 10 families for a total of 400 seedlings per site. Initially, seedlings averaged 87.2 cm ( $\pm 11.4$  s.d.) in height across all sites and were planted on a 1 × 1 m grid, with ten blocks per site consisting of four-tree family row plots arranged in a randomized, complete block design. Blocks were placed perpendicular to apparent hydrologic gradients.

Since signs of nutria (*Myocastor coypus* Molina) were abundant on all sites, each seedling was protected by a 91 cm tall polypropylene tree protector (TreePro Inc., West Lafayette, IN) supported by a 1.5 m tall by 1.3 cm diameter polyvinylchloride (PVC) pipe. Tree protectors have been successful in

preventing damage to tree seedlings by nutria (ALLEN, 1995; PLATT and BRANTLEY, 1990; ALLEN and BOYKIN, 1991; MYERS *et al.*, 1995).

### Experimental Measurements

Free soil water salinity and temperature were measured periodically from the center of each block (10 locations per site). Measurements were taken seven times beginning in February, 1996, using a combined temperature and conductivity meter (YSI Model 33 S-C-T meter, Yellow Springs, OH) and measured less frequently throughout the 1997 growing season. Most often, a hole had to be dug until the shallow water table was reached (*cf.*, PENFOUND and HATHAWAY, 1938). Water table depths were recorded to the nearest cm and measured from the top of the water surface to the soil surface.

In July of 1996, soil samples were collected from the center of each block on all three sites. All samples were taken from the 15–25 cm soil depth in an attempt to sample root zone soil conditions. Soil samples were analyzed through the Soil Testing Laboratory at the Louisiana State University Agricultural Center. Tests for exchangeable base cation nutrients (Na, K, Ca, Mg), phosphorus, pH, and organic matter were performed. For exchangeable base cations, soils were extracted with 1 M ammonia acetate. Extracts were analyzed with induction coupled plasma (ICP) instrumentation (THOMAS, 1982). Available P was determined by the "Bray 2" method (BRAY and KURTZ, 1945). Levels of pH were measured by use of a pH meter (MCLEAN, 1982), and percent readily oxidizable organic matter was determined by the Walkley-Black Procedure (WALKLEY, 1947; NELSON and SOMMERS, 1982).

Initial height and diameter measurements were taken from all seedlings immediately after planting and were re-measured at the end of the 1996 and 1997 growing seasons. All height measurements were recorded to the nearest cm. Diameter measurements were taken to the nearest tenth of a cm at 4 cm above the soil line using a vernier caliper. The use of positive growth parameters as an indicator of stress tolerance has been cautioned, since individuals with the greatest amount of tolerance to a particular stress often maintain the least amount of growth (CHAPIN, 1991). An evaluation of height growth increment, on the other hand, is probably an appropriate response variable under these conditions. Herbaceous plant competition is intense in salt-impacted coastal wetlands (MYERS *et al.*, 1995), and trees that do not grow tall may not survive the competition imposed by less desirable vegetation. In an effort to incorporate both growth and survival into one indicator of family-level performance, however, a modified version of ALLEN *et al.* (1994b)'s Potential Productivity Index (PPI) was calculated as follows:

$$(S_L/S_H) \times [(D^2H_L/D^2H_H) \times 100]$$

where S was percent survival, D was seedling diameter, and H was seedling height. The subscript L stands for the low salinity, or DEL, site and H stands for the high salinity, or LIV, site.

On each site, 25% of all seedlings were destructively sampled at the end of the 1996 growing season to attain estimates

Table 1. A comparison of the chemical properties of soils on DEL, JEA, and LIV sites on a dry weight basis ( $\pm$  SE). All samples were collected 15–25 cm below the soil surface. Site-level differences were significant for all parameters ( $P \leq 0.0035$ ).

Site	P ( $\text{cmol kg}^{-1}$ )	Na ( $\text{cmol kg}^{-1}$ )	K ( $\text{cmol kg}^{-1}$ )	Ca ( $\text{cmol kg}^{-1}$ )	Mg ( $\text{cmol kg}^{-1}$ )	OM (%)	pH
DEL	0.3 (0.02)	11.2 (0.7)	0.8 (0.03)	7.0 (0.2)	8.6 (0.3)	5.2 (0.09)	5.18 (0.07)
JEA	0.6 (0.06)	4.4 (0.6)	1.2 (0.08)	5.6 (0.5)	8.3 (0.8)	4.3 (0.32)	6.52 (0.08)
LIV	0.5 (0.02)	21.9 (1.0)	1.1 (0.03)	8.3 (0.0)	10.7 (0.3)	5.5 (0.20)	6.20 (0.05)

of leaf biomass among sites and families. One row of trees from each block was randomly selected for harvest. During sampling, individual canopies were severed below the live crown and placed in plastic bags, stored at room temperature for a period no longer than two days, and stored between 2–4 °C for two days. Foliage was separated from shoots, placed in paper sacks, and dried at 70 °C to a constant weight.

Dried leaf material from each seedling was ground in a Wiley mill (40  $\mu\text{m}$  mesh) and chemically analyzed by the Louisiana State University Agricultural Chemistry Department. For determination of K, Na, and Ca, samples were digested in a microwave digester and analyzed using an ICP (Leeman Labs, PS-3000, Lowell, MA; procedure AOAC, 1995). Cl concentrations were determined through a calorimetric process in which the samples were diluted to 200 ml with deionized water, mixed with a hot water bath shaker for 20 min, and placed in an auto-analyzer (Bran-Luebbe, Buffalo Grove, IL) (Dave Wall, LSU Agricultural Chemistry Department, Personal communication).

### Statistical Analysis

The statistical design was a combination of a split-plot, with one randomization restriction, and a nested design, with blocks nested within sites. The general linear model (GLM) of the SAS System (SAS INSTITUTE, INC., 1989) was used to analyze differences in final growth increment at the end of the 1997 season. Height and diameter data were normalized using a non-parametric linear rank transformation, where growth was calculated as a percent of the pre-season value. Standard parametric transformations were not successful in conforming data to a normal distribution. Analysis of covariance, with initial height as the covariate, was used to identify differences in leaf biomass by site and family at the end of the 1996 growing season. Analysis of variance for survival (both years) was determined through the use of the GLM model as well, but after an arc sin transformation. A Tukey's studentized range test ( $\alpha = 0.05$ ) for individual parameters of survival, height, diameter, leaf biomass, PPI, and tissue ion concentration was used to identify site and family rank when a significant difference was detected by the GLM analysis.

## RESULTS

### Site Physical Parameters and Soil Composition

Free soil water salinity was highest on the LIV site throughout the experiment, where it averaged 2.0  $\text{g L}^{-1}$  during the 1996 growing season, but rose as high as 4.2  $\text{g L}^{-1}$  in August, 1996, and as high as 15.0  $\text{g L}^{-1}$  in September, 1997.

Salinities averaged 0.5 and 1.2  $\text{g L}^{-1}$  for the DEL and JEA sites, respectively, during the first growing season and changed only slightly during the 1997 growing season. Most saltwater pulses occurred at the end of the respective growing seasons and remained fairly low during active growth periods from March through August.

Mean water temperature for all sites during the 1996 growing season ranged from a low of 13.0 °C in March to a high of 26.9 °C in August. During the same growing season, mean water tables were significantly lower on the LIV site (–12.3 cm; a negative number indicates a water level below the soil surface) than on the DEL (–0.6 cm) and JEA sites (–2.4 cm); however, soil water deficiency was never a limiting factor on any of the sites since soils remained wet to the surface throughout both growing seasons. Water level reached its maximum (56.6 cm) on the DEL site during January of 1996 when a local freshwater diversion allowed for direct water flow from the Mississippi River.

Available soil nutrients varied significantly among sites, with P, Na, K, Ca, and Mg averaging 0.5, 12.5, 1.0, 7.0, and 9.2  $\text{cmol kg}^{-1}$ , respectively (Table 1). The range of nutrient concentrations among the three sites was small, with the exception of Na, which ranged from a low of 4.4  $\text{cmol kg}^{-1}$  on the JEA site to a high of 21.9  $\text{cmol kg}^{-1}$  on the LIV site. In general, all sites contained high concentrations of those nutrients tested, had fairly high levels of organic matter, and were acidic (Table 1).

### Site-Level Response

Survival at the end of the 1996 growing season was 99.5, 93.0, and 86.4%, respectively, for the DEL, JEA, and LIV sites and 98.3, 92.7, and 17.7%, respectively, at the end of the 1997 growing season (Table 2). All measured parameters, except survival, on the DEL and JEA sites showed an increase throughout both growing seasons (Tables 2 and 3). Due to meristem dieback and mortality, average seedling height on the LIV site was only 121.6 cm by the end of the 1997 growing season as compared to 196.4 and 165.9 cm on the DEL and JEA sites, respectively (Figure 2). In addition to height growth superiority, seedlings on the DEL site appeared more vigorous (e.g., more leaf area, less foliar leaf and tip burn) than seedlings on either the JEA or LIV sites throughout both years.

Site-level differences in diameter growth were significantly greater on both the DEL site and the JEA site than the LIV site at the end of 1997 (Tables 3 and 4). Throughout the 1996 growing season, seedlings on the DEL site maintained more than double the leaf biomass of seedlings on the JEA site and

Table 2. Mean seedling survival by family for DEL, JEA, and LIV sites at the end of two growing seasons.

Family	1996 Survival (%)			1997 Survival (%)		
	DEL	JEA	LIV	DEL	JEA	LIV
FA1	100.0	82.5	91.7	100.0	86.7	23.3
FA2	100.0	100.0	75.0	100.0	100.0	22.2
FA7	100.0	90.0	95.0	100.0	90.0	13.3
FA8	100.0	90.0	80.0	100.0	90.0	16.8
VE2	100.0	90.0	85.0	100.0	93.3	20.0
SG2	100.0	95.0	87.5	100.0	93.3	13.3
SG3	97.5	94.9	88.9	96.7	93.3	22.2
CB3	100.0	97.5	86.1	93.3	96.7	22.2
SW1	97.5	95.0	86.5	93.3	93.3	16.7
SW2	100.0	95.0	87.9	100.0	90.0	7.4
Mean	99.5a	93.0ab	86.4b	98.3a	92.7a	17.7b

Site differences were significant ( $F_{2,27} = 9.66$ ;  $P = 0.0007$ ) and family-level differences were not significant ( $F_{9,240} = 0.50$ ;  $P = 0.8721$ ) for 1996. Likewise, site-level differences were significant ( $F_{2,27} = 359.37$ ;  $P \leq 0.0001$ ) for 1997, but family-level differences were not ( $F_{2,239} = 0.57$ ;  $P = 0.8173$ ). Mean values for site followed by the same letter within a year are not significantly different at the 0.05 level.

more than three times the average leaf biomass of seedlings on the LIV site (Table 3).

With the exception of K, analysis of tissue ion concentrations within baldcypress leaves differed significantly among sites (Table 5). Seedlings on the LIV site had greater foliar ion concentrations than seedlings on the DEL and JEA sites (Figure 3), with foliar Cl approximately 1.8 times greater. Foliar concentrations of Na and Ca were 0.54 and 0.77%, respectively, on the LIV site, 0.26 and 0.66%, respectively, on the JEA site, and 0.11 and 0.64%, respectively, on the DEL site. Accordingly, a significant linear relationship existed between the individual site's free soil water salinity at the time of collection and foliar Na concentrations ( $r^2 = 0.4411$ ;  $P < 0.0001$ ), Ca concentrations ( $r^2 = 0.1767$ ;  $P < 0.0001$ ), and Cl concentrations ( $r^2 = 0.6076$ ;  $P < 0.0001$ ). Foliar concentrations of K were not linearly correlated with salinity ( $r^2 = 0.0016$ ;  $P = 0.5053$ ). Significant site-level differences in tissue Na/K ratios and Na/Ca ratios were observed (Table 5,

Table 3. Mean seedling height and diameter increment ( $\pm$  SE) at the end of the 1997 growing season and mean seedling leaf biomass ( $\pm$  SE) at the end of the 1996 growing season by family for the DEL, JEA, and LIV sites.

Family	Height (cm)			Diameter (cm)			Leaf Biomass (g dry wt)				
	DEL	JEA	LIV	Family	DEL	JEA	LIV	Family	DEL	JEA	LIV
SW1 <sup>a</sup>	112.1 (6.3)	87.6 (2.9)	44.0 (8.6)	SG2 <sup>a</sup>	4.75 (0.21)	3.51 (0.14)	1.58 (0.16)	SG2 <sup>a</sup>	16.5 (1.4)	7.2 (0.9)	5.0 (1.0)
SW2 <sup>ab</sup>	118.2 (3.9)	80.5 (2.7)	54.5 (13.5)	FA7 <sup>a</sup>	3.68 (0.22)	3.05 (0.15)	1.16 (0.17)	SW1 <sup>a</sup>	13.6 (1.8)	5.0 (1.3)	5.4 (1.3)
VE2 <sup>abc</sup>	113.7 (4.3)	80.8 (3.7)	30.2 (8.8)	SW2 <sup>a</sup>	4.31 (0.20)	2.98 (0.13)	1.40 (0.05)	FA1 <sup>a</sup>	18.8 (1.7)	6.8 (1.7)	3.6 (0.7)
FA2 <sup>bc</sup>	103.9 (4.1)	76.5 (3.3)	37.3 (5.8)	CB3 <sup>a</sup>	4.53 (0.23)	3.53 (0.13)	1.44 (0.18)	SG3 <sup>a</sup>	17.9 (3.0)	7.5 (1.0)	5.9 (1.3)
SG2 <sup>c</sup>	110.9 (4.3)	67.7 (3.8)	28.3 (8.8)	FA2 <sup>a</sup>	4.28 (0.23)	3.51 (0.12)	1.33 (0.20)	CB3 <sup>a</sup>	15.0 (2.1)	10.0 (1.2)	5.4 (0.7)
FA7 <sup>cd</sup>	102.1 (4.5)	78.3 (3.8)	25.5 (10.1)	SW1 <sup>a</sup>	3.74 (0.24)	2.98 (0.18)	1.31 (0.15)	VE2 <sup>a</sup>	17.2 (1.5)	6.0 (1.5)	5.6 (1.0)
FA1 <sup>cd</sup>	117.7 (7.3)	81.5 (4.4)	28.0 (5.7)	VE2 <sup>a</sup>	4.31 (0.23)	3.24 (0.12)	1.35 (0.17)	FA8 <sup>a</sup>	13.3 (2.2)	6.8 (1.4)	2.3 (1.0)
CB3 <sup>cd</sup>	103.4 (5.2)	68.6 (3.2)	33.3 (7.0)	SG3 <sup>a</sup>	4.08 (0.22)	3.80 (0.16)	1.78 (0.16)	SW2 <sup>a</sup>	13.6 (1.0)	8.1 (1.1)	5.4 (1.1)
FA8 <sup>cd</sup>	103.3 (6.0)	77.5 (4.1)	26.4 (5.5)	FA8 <sup>a</sup>	3.63 (0.25)	3.40 (0.22)	1.10 (0.12)	FA7 <sup>a</sup>	10.2 (1.2)	6.2 (0.9)	3.5 (0.7)
SG3 <sup>d</sup>	101.0 (5.6)	72.3 (3.7)	35.0 (6.9)	FA1 <sup>a</sup>	4.60 (0.22)	3.31 (0.16)	1.17 (0.13)	FA2 <sup>a</sup>	17.8 (2.1)	7.3 (1.2)	4.1 (0.9)
Mean	108.7a	77.1b	33.1c		4.19a	3.33a	1.36b		15.4a	7.1b	4.6c

Mean values for site and/or family followed by the same letter for a particular response variable are not significantly different at the 0.05 level. Intra-specific differences were determined by the average response of a particular family across all three study sites (Site  $\times$  Family effects were not significant for the above parameters—see Table 4).

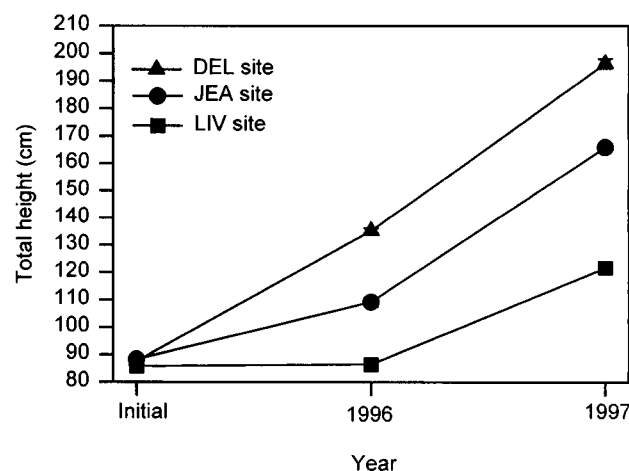


Figure 2. Mean height (cm) for baldcypress seedlings planted on the DEL, JEA, and LIV sites for the 1996 and 1997 growing seasons. Vertical lines representing standard errors of the mean are barely visible.

Figure 3). In general, ratios remained constant within a particular site, with Na remaining less abundant in leaf tissue than K and Ca. On the LIV site, however, foliar Na concentrations exceeded K concentrations by nearly 14% (Figure 3).

### Family-Level Response

Family-level variation in survival was not significant at the end of either the 1996 or 1997 growing seasons (Table 2), but was significant for height (Table 4). The site  $\times$  family interaction proved non-significant for both height and diameter increments (Table 4). Height growth increment by family ranged from 101.0 cm to 118.2 cm on the DEL site, 67.7 cm to 87.6 cm on the JEA site, and 25.5 cm to 54.5 cm on the LIV site (Table 3). Calculations of PPI did reveal significant intraspecific differences ( $F_{9,45} = 2.58$ ;  $P = 0.0210$ ), however, rankings changed only slightly from those presented for height in Table 3. The major difference involved family SW1

Table 4. General linear model analysis of variance for final height and diameter at the end of the 1997 growing season and for leaf biomass at the end of the 1996 growing season for seedlings planted on the DEL, JEA, and LIV sites.

Source of Variation	Height				Diameter			Leaf Biomass		
	df	MSE	F Value	P > F	MSE	F Value	P > F	MSE	F Value	P > F
Site	2	1.90e5	34.85	0.0001	2.48e8	14.20	0.0001	2907.17	140.06	0.0001
Block(site)—er. a	27	5457.0	—	—	1.75e7	—	—	20.76	—	—
Family	9	3668.2	3.96	0.0001	3.61e6	1.09	0.3745	33.39	1.54	0.1347
Site × Family	18	873.5	0.94	0.5292	2.21e6	0.67	0.8408	24.50	1.13	0.3237
Family × Block(site)—er. b	240	927.4	—	—	3.32e6	—	—	21.69	—	—

Height and diameter data were transformed and analyzed as a percent of pretreatment size. Initial height as a covariate was not significant for leaf biomass analysis

(PPI = 3456.9), which had a PPI significantly less than family SW2 (PPI = 24023.1). The total among-family range in calculated PPI values was 21639.9.

Family-specific diameter increments ranged from 3.63 to 4.75 cm on the DEL site, 2.98 to 3.80 cm on the JEA site, and 1.10 to 1.78 cm on the LIV site (Table 3). Intraspecific variation in diameter growth was significant at the end of the 1996 growing season but was not significant by the end of the 1997 growing season, presumably due to variation caused by butt swell. At the end of the 1996 growing season, family-level differences for total leaf biomass were not significant (Table 4).

Intraspecific variation in foliar ion concentrations were significant for analyses of K, Cl, and Ca (Tables 5 and 6). In addition, the site × family interactions were significant for Na and Cl, reflecting differences in among-family ion uptake with increases in salinity (Figure 4). Foliar ion concentrations of K ranged from 0.42 to 0.73%, concentrations of Cl ranged from 1.45 to 1.88%, and concentrations of Ca ranged from 0.63 to 0.72% among half-sib families across all sites (Table 6). Na concentrations differed by family only on the higher salinity, LIV site, and Cl concentration differed by family on both the DEL and LIV sites. Families FA2 and SG2 had lower foliar concentrations of Cl than did family SW2 across all sites. Family-level differences in Na/K ratios were significant (Tables 5 and 6), indicating a cellular ion imbalance within

foliage among families. Across all sites, family SW2 had the highest observed Na/K ratio (0.78; Table 6) and family FA8 had the lowest (0.37). This imbalance differed significantly with increases in salinity.

## DISCUSSION

### Site Physical Parameters and Soil Composition

In general, soil nutrient levels in the present study (Table 1) were found to be high compared to data from other studies (BROADFOOT, 1976; COULTAS and DUEVER, 1984). BROADFOOT (1976) found that on 28 possible soil types supporting baldcypress, P, Na, K, Ca, and Mg averaged the equivalent of 0.03, 0.34, 0.27, 9.0, and 3.77 cmol kg<sup>-1</sup> soil, respectively. Mean P, Na, K, and Mg levels were higher in the present study than those reported by BROADFOOT (1976). Concentrations of Ca, on the other hand, averaged 2.0 cmol kg<sup>-1</sup> less in the present study. COULTAS and DUEVER (1984) cited three other studies, all of which reported lower soil nutrient concentrations for typical baldcypress stand associations than reported in this study.

The pH level was slightly more acidic for soils on the DEL site and slightly more basic for soils on the JEA and LIV sites in relation to averages from BROADFOOT (1976). XU and LONG (1983) found the optimal pH for baldcypress growing in the Pearl River Delta, China, to be 6.1, which is only

Table 5. General linear model analysis of variance for foliar ion concentrations of seedlings planted on the DEL, JEA, and LIV sites at the end of the 1996 growing season.

Source of Variation	df	Na			Cl <sup>1</sup>			K		
		MSE	F Value	P > F	MSE	F Value	P > F	MSE	F Value	P > F
Site	2	4.29	94.23	0.0001	47.43	189.09	0.0001	0.11	1.25	0.3032
Block(site)—er. a	27	0.05	—	—	0.25	—	—	2.27	—	—
Family	9	0.06	1.70	0.0915	0.86	4.84	0.0001	0.29	5.42	0.0001
Site × Family	18	0.09	2.63	0.0005	0.37	2.10	0.0070	0.07	1.40	0.1329
Family × Block(site)—er. b	217	0.03	—	—	0.18	—	—	11.48	—	—

Source of Variation	df	Ca			Na/K			Na/Ca		
		MSE	F Value	P > F	MSE	F Value	P > F	MSE	F Value	P > F
Site	2	0.45	19.14	0.0001	17.98	65.29	0.0001	6.18	64.82	0.0001
Block(site)—er. a	27	0.02	—	—	0.28	—	—	0.10	—	—
Family	9	0.03	2.08	0.0329	0.49	2.91	0.0029	0.09	1.34	0.2195
Site × Family	18	0.02	1.59	0.0652	0.33	1.97	0.0126	0.11	1.64	0.0517
Family × Block(site)—er. b	217	0.01	—	—	0.17	—	—	0.07	—	—

<sup>1</sup> Degrees of freedom for Family × Block(site) were only 114 due to lack of sufficient sample quantities for some seedlings

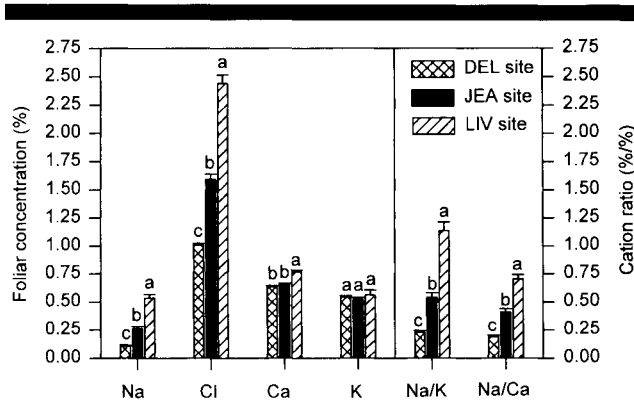


Figure 3. Mean tissue ion concentrations (%) and cation ratios (%/%) for seedlings growing on the DEL, JEA, and LIV sites in August, 1996. Vertical lines represent standard errors of the mean. Groupings were determined by using a Tukey's Studentized Range Test, with sites followed by the same letter for a particular ion being significantly different at the 0.05 level.

slightly different from average pH ranges reported by BROADFOOT (1976).

Although this study indicates that survival and growth of baldcypress seedlings and subsequent regeneration on plantation sites were probably not limited by deficiencies of soil nutrients tested, caution is suggested for two reasons. First, maximum potential growth responses were not quantified by fertilization treatments. MYERS *et al.* (1995) found nearly a two-fold increase in diameter growth for fertilized as compared to unfertilized treatments under similar wetland conditions. The relationship between regeneration success and nutrient deficiencies are difficult to assess, since historic site nutrition status present during original stand regeneration can not be quantified. Second, MYERS *et al.* (1995) incorporated a large portion of nitrogen in their fertilizer experiments; nitrogen levels were not quantified in this study.

Mature baldcypress commonly occur under low levels of salinity in coastal areas (PENFOUND and HATHAWAY, 1938; HARLOW and HARRAR, 1969; CHABRECK, 1972). The degree to which measured salinities impacted the growth of baldcypress on plantation sites is negatively correlated but remains unclear. Data from other studies indicate that salinity should be around  $6 \text{ g L}^{-1}$  (under non-competitive, controlled-environment conditions) for much of the growing season to impose a suitable stress intensity for salt tolerance screening (ALLEN, 1994; ALLEN *et al.*, 1994b; 1997). Although the two experimental sites were covered with baldcypress snags, free soil water salinity was not high within plantations during the 1996 growing season. Salinity was slightly higher for the 1997 growing season, but the highest salinities, which occurred in September and October of 1997 on the LIV site, probably had little effect on growth of seedlings during that year. A similar trend was discovered by ALLEN *et al.* (1994b), where it was apparent that salinities responsible for mortality of baldcypress swamps were quite different historically in some cases than those reported for the growing season stud-

ied. Higher salinities could, however, have had a greater effect on survival than growth in the present study.

### Site-Level Response

Researchers have developed lists, primarily by observation, of tree species with enough tolerance to salt to be used in afforestation and reforestation projects on salt-affected lands. These studies were conducted outside of the United States and with species other than baldcypress (GOGATE *et al.*, 1984; FIRMIN, 1968; SHRIVASTAVA *et al.*, 1988; BECKMANN, 1991). Studies specific to baldcypress, however, indicate that this species maintains adequate growth when subjected to low levels of salinity under field conditions (XU and LONG, 1983; MYERS *et al.*, 1995).

Survival and growth of baldcypress seedlings varied significantly among the three sites in the present study, all of which differed in salinity, hydrologic, and vegetative regimes. XU and LONG (1983), on the other hand, found that baldcypress and pond cypress (*Taxodium distichum* var. *nutans* (Ait.) Sweet) appeared to be relatively salt resistant and maintained adequate growth with soil salinities as high as  $0.38\%$  ( $\sim 3.8 \text{ g L}^{-1}$ ). A negative relationship between soil salinity and growth did exist for both *Taxodium* species. MYERS *et al.* (1995) found that baldcypress growing in Manchac Wildlife Management Area, Louisiana, were not limited in survival by water salinities at least as high as  $2.8 \text{ g L}^{-1}$  after hurricane passage. Variation in survival in the present study does not agree with observations made by MYERS *et al.* (1995), since there were significant differences in seedling survival during both growing seasons among sites at different mean salinity concentrations. In addition, survival at the end of the 1997 growing season was as low as 17.7% on the high salinity site but averaged 95.5% on the other two sites (Table 2).

Growth in this study appeared limited by the combinations of vegetation, salinity, and hydrologic regime present on each study site. Height and diameter growth was far superior on the DEL site, which had the lowest salinity (Table 3). In addition, floodwaters were abundant on the DEL site during winter months and somewhat less abundant on the other two sites. This agrees with CONNER and FLYNN (1989), who found survival and height growth in baldcypress seedlings to be higher under intermittently and permanently flooded conditions, and DICKSON and BROYER (1972), who found that height and top dry weight of baldcypress had increased markedly from unsaturated to saturated to saturated-aerated treatments. An intermittently flooded condition prevailed on the JEA site as well; however, growth appeared influenced both by salinity and vegetative competition during the 1996 growing season. Seedlings on the JEA site maintained greater height growth and leaf biomass than seedlings on the LIV site, where the water table was lower, vegetative competition was more intense, and free soil water salinity was higher throughout the growing season. MYERS *et al.* (1995) reported greater height growth for baldcypress seedlings growing under more intense vegetative competition (*i.e.*, unmanaged treatments) than managed treatments. Since height growth in the present study was least on the LIV site, which had the

Table 6. Combined mean tissue ion concentrations and cation ratios by family for seedlings growing on DEL, JEA, and LIV sites.

Family	Foliar Concentration (%)					Cation Ratio (%/%)					
	Na	Family	Cl	Family	K	Family <sup>1</sup>	Ca	Family	Na/K	Family	Na/Ca
SG3 <sup>a</sup>	0.351	SW2 <sup>a</sup>	1.884	FA8 <sup>a</sup>	0.730	VE2 <sup>a</sup>	0.717	SW2 <sup>a</sup>	0.778	SG3 <sup>a</sup>	0.507
FA7 <sup>a</sup>	0.324	FA8 <sup>ab</sup>	1.797	SW1 <sup>ab</sup>	0.645	FA1 <sup>a</sup>	0.715	FA7 <sup>a</sup>	0.742	SW1 <sup>a</sup>	0.479
SW2 <sup>a</sup>	0.321	SW1 <sup>ab</sup>	1.712	VE2 <sup>abc</sup>	0.632	FA8 <sup>a</sup>	0.714	FA1 <sup>a</sup>	0.725	FA7 <sup>a</sup>	0.452
FA8 <sup>a</sup>	0.300	SG3 <sup>ab</sup>	1.637	FA2 <sup>abcd</sup>	0.574	SG3 <sup>a</sup>	0.696	SG3 <sup>a</sup>	0.725	SW2 <sup>a</sup>	0.448
FA1 <sup>a</sup>	0.296	CB3 <sup>ab</sup>	1.631	FA1 <sup>abcd</sup>	0.545	FA2 <sup>a</sup>	0.691	CB3 <sup>ab</sup>	0.657	FA1 <sup>a</sup>	0.411
SW1 <sup>a</sup>	0.291	FA1 <sup>ab</sup>	1.610	SG3 <sup>abc</sup>	0.517	SG2 <sup>a</sup>	0.685	SG2 <sup>ab</sup>	0.598	CB3 <sup>a</sup>	0.402
SG2 <sup>a</sup>	0.268	VE2 <sup>ab</sup>	1.593	SG2 <sup>abc</sup>	0.484	FA7 <sup>a</sup>	0.681	SW1 <sup>ab</sup>	0.561	SG2 <sup>a</sup>	0.387
VE2 <sup>a</sup>	0.255	FA7 <sup>ab</sup>	1.540	FA7 <sup>abc</sup>	0.470	SW2 <sup>a</sup>	0.678	FA2 <sup>ab</sup>	0.454	FA8 <sup>a</sup>	0.375
FA2 <sup>a</sup>	0.253	FA2 <sup>b</sup>	1.471	SW2 <sup>bc</sup>	0.438	CB3 <sup>a</sup>	0.634	VE2 <sup>ab</sup>	0.425	FA2 <sup>a</sup>	0.360
CB3 <sup>a</sup>	0.242	SG2 <sup>b</sup>	1.450	CB3 <sup>d</sup>	0.419	SW1 <sup>a</sup>	0.625	FA8 <sup>b</sup>	0.367	VE2 <sup>a</sup>	0.349

<sup>1</sup> Although family-level variation was statistically significant, a Tukey's Studentized Range Test failed to detect significant family separations. Mean values by family for a particular ion and/or ion ratio followed by the same letter are not significantly different at the 0.05 level

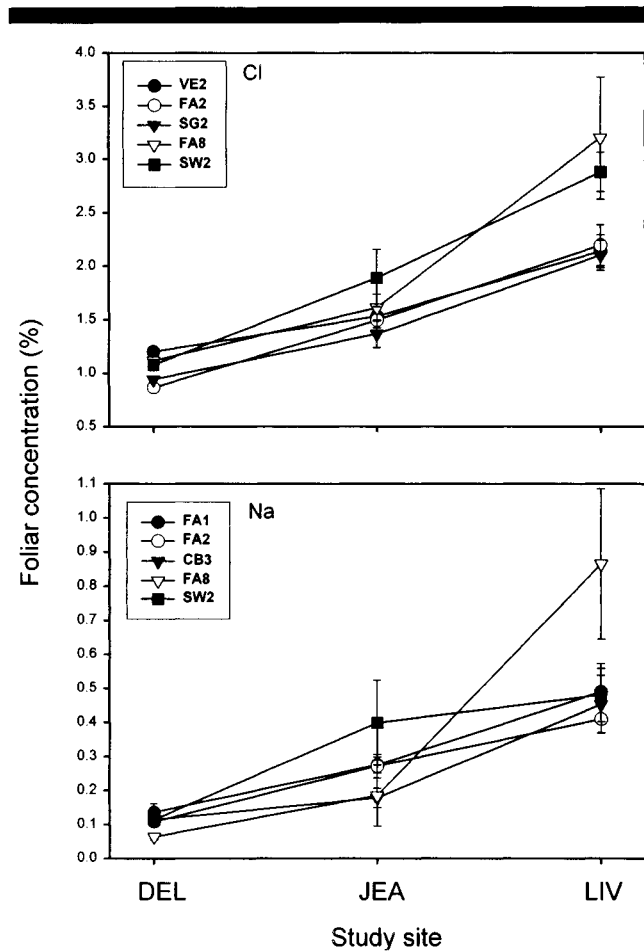


Figure 4. Intraspecific differences in foliar ion concentrations (%) of Cl and Na. Differences were significant for Cl on the DEL site ( $F_{9,80} = 6.71$ ;  $P < 0.0001$ ) and for both Cl ( $F_{9,61} = 2.77$ ;  $P = 0.0087$ ) and Na ( $F_{9,63} = 2.30$ ;  $P = 0.0267$ ) on the LIV site. Vertical lines represent standard errors of the mean.

greatest amount of competition, factors other than vegetative competition (e.g., salinity, water level) explain these differences.

ALLEN *et al.* (1997) found that as salinity increased, foliar concentrations of both Na and Cl increased accordingly, with Cl concentrations exceeding Na. Results from the present study (Table 5, Figure 3) indicate a similar phenomenon, since foliar concentrations of both Na and Cl increased significantly as site salinity increased. Increased Na and Cl ions within leaf tissue at the levels reported adds a considerable stress to baldcypress planted within salt-impacted wetlands, since both ions have been shown to cause direct ion toxicity in glycophytes (GREENWAY and MUNNS, 1980). With this increase in foliar Na and Cl, K and Ca concentrations remained relatively constant. The consistency in foliar K concentration among all sites and in foliar Ca concentration between the DEL and JEA sites led to increases in both the Na/K and Na/Ca ratios (Figure 3). The inability of cells to maintain a balance between foliar ion components, a relationship also demonstrated by ALLEN *et al.* (1997), may have led to reduced growth on the JEA and LIV sites relative to the DEL site. ALLEN *et al.* (1997) discovered foliar Na/K ratios between 0.9 and 1.4 with an increase in salinity above  $2 \text{ g L}^{-1}$  for fertilized seedlings under controlled growth conditions. PEZESHKI *et al.* (1988) also reported an increase in Na/K ratios up to 1.10 for the  $8 \text{ g L}^{-1}$  salinity treatment. WYN JONES *et al.* (1979) suggests that Na/K ratios less than 1 are necessary for normal cellular function in glycophytes. Since the mean Na/K ratio for baldcypress planted on the LIV site exceeded this value (i.e., 1.14; Figure 3), increased stress on this site may be associated with both an increased ion load and an ion imbalance.

#### Family-Level Response

Results from this investigation correspond with at least two other field studies addressing intraspecific variation under saline conditions for forest tree species (THOMSON, 1988; BIDNER-BARHAVA and RAMATI, 1967). THOMSON (1988), by conducting field trials evaluating the salt tolerance of a number of gum species (*Eucalyptus* sp.) in Australia, found intraspecific variation in survival and growth. Intraspecific climatic zone groups identified as salt-tolerant tended to have



less reduction in growth at higher soil salinities (THOMSON, 1988). Likewise, baldcypress families performing well in up to  $4 \text{ g L}^{-1}$  salinity under controlled conditions (ALLEN *et al.*, 1994b; 1997) performed similarly under field conditions in the present study relative to other families at comparable salinity levels. In addition, differences in individual tree morphology, similar to the present study, were noted for a number of *Eucalyptus*, *Pinus*, and other forest tree species planted under saline conditions in the Negev Desert, Israel (BIDNER-BARHAVA and RAMATI, 1967). ALLEN *et al.* (1994b) found that the most tolerant seedlings, based on biomass and salt tolerance indices, tended to have less dieback of the apical meristem and subsequent refoliation. Based on foliar biomass measurements, seedlings did not partition leaf growth differently at the family-level through one growing season in the present study, but did show greater leaf biomass on sites with lower salinity (Table 3).

ALLEN (1994) and ALLEN *et al.* (1994b) demonstrated significant intraspecific variation in baldcypress biomass, leaf area, tolerance index values, morphological patterns, physiological patterns, and tissue Na and Cl concentrations. In general, the 10 half-sib families from brackish-water seed sources maintained a greater level of growth in treatments as high as  $8 \text{ g L}^{-1}$  than the five families from freshwater seed sources. ALLEN *et al.* (1997) also found significant intraspecific variation in net photosynthesis and stomatal conductance. In contrast, results from the lower salinities tested in this study agree with PEZESHKI *et al.* (1995) and KRAUSS *et al.* (IN PRESS), who found no conclusive evidence, based on an evaluation of root elongation, that genotypes with the greatest amount of tolerance to multiple concentrations of salt will always be found in brackish-water seed sources. In fact, only two freshwater seed sources were evaluated in this study (*i.e.*, SW1 and SW2) and both were among the top performers under saline field conditions as quantified by height growth increment. PPI calculations confirmed the superiority of family SW2 even though 1997 survival on the LIV site was low (Table 2), but ranked family SW1 second worst among the families tested. At similar salinity concentrations (*i.e.*,  $4 \text{ g L}^{-1}$ ) under controlled conditions in ALLEN *et al.* (1994b), families SW1 and SW2 were ranked within the top four in maintenance of leaf biomass and leaf area and family SW1 ranked second in total height at harvest. Hence, results from this study do agree with ALLEN *et al.* (1994b), but only when families are compared at similar salinity concentrations and not across the range of tested concentrations. Site salinity may be higher in future years, which may lead to an even better test of intraspecific growth variation.

Intraspecific differences in absolute tissue concentrations and shifts in nutrient ratios occurred less frequently than differences among sites. ALLEN *et al.* (1997) found this same non-consistency. The combined mean for foliar Na concentrations of the three most tolerant families (*i.e.*, FA2, FA3, and CB3), two of which were used in the present study, across all salinity treatments and at the two highest treatments was significantly less than the combined mean of the remaining families. The combined mean of families FA2 and CB3 in the present study was 0.05% less than the combined mean of the other eight families across all sites, but these differences

were not significant. It is important to note that salt tolerance has been correlated negatively with foliar tissue ion concentrations of both Na and Cl (ALLEN *et al.*, 1997). Differences in grouped family mean concentrations of foliar Cl were significant in both ALLEN *et al.* (1997) and the present study at salinities lower than  $6 \text{ g L}^{-1}$ . However when sites were subjected to independent analyses, Cl concentrations were different by family on both the DEL and LIV sites (Figure 4), leading to the hypothesis that Cl exclusion may be a mechanism of family-level differentiation in baldcypress salt tolerance. Exclusion of Na, which was significantly different by family only on the higher salinity LIV site (Figure 4), may offer an additional competitive advantage for more salt-tolerant families of baldcypress under higher salinities. ALLEN *et al.* (1996) suggested that the ability to exclude both the Na and Cl ions should decrease sensitivity of baldcypress to floodwater salinity. Accordingly, TOWNSEND (1989) suggests that the ability to exclude the Cl ion may be the most important mechanism of salt tolerance in forest tree species. Ion exclusion as a mechanism of salt tolerance at higher salinities under field conditions needs further investigation, especially since this study found a direct relationship between free soil water salinity and foliar ion concentrations of Na, Cl, and Ca in baldcypress.

## CONCLUSIONS

In assessing the growth and nutrition of baldcypress under saline field conditions, this study demonstrated four things: (1) plantation sites had higher fertility (exclusive of N) than means reported for other baldcypress stands in the southeastern United States, (2) survival and growth of baldcypress seedlings varies significantly among different salinity, hydrologic, and vegetative combinations within coastal swamp forests impacted by saltwater intrusion, (3) genotypic variation among half-sib families of baldcypress under saline field conditions corresponds to experiments conducted under controlled conditions by ALLEN *et al.* (1994b) and (1997), as long as comparisons are made at similar salinity concentrations and not across a range of salinities, and (4) certain genotypes of baldcypress maintain greater height growth when outplanted in degraded coastal wetlands. Careful genotypic selection may increase growth and vigor of baldcypress plantations.

This research, like that of others, demonstrates sufficient intraspecific variation in the salt tolerance of baldcypress to warrant further studies. Within-family identification and selection of individuals with greater performance under field conditions and inclusion of these individuals in controlled breeding programs is the next suggested course of action for improving the salt tolerance of baldcypress. Once more salt-tolerant baldcypress genotypes are identified large-scale reforestation efforts can be initiated. Reclamation of these wetlands will certainly take time, but a strong restoration potential exists for degraded coastal swamp forests in Louisiana.

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