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Can We Improve the Salinity Tolerance of Genotypes of *Taxodium* by Using Varietal and Hybrid Crosses?

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Abstract. ***Taxodium distichum*** **(L.) Rich. var.** ***distichum*** **[baldcypress (BC)],** ***Taxodium distichum*** **var.** ***mexicanum*** **Gordon [Montezuma cypress (MC)], and a** ***Taxodium*** **hybrid ('Nanjing Beauty': BC × MC cross, T302) were evaluated for salt tolerance in 2006 at Nacogdoches, TX. Plants were irrigated weekly with four levels of salinity [0, 1, 3.5, and 6 ppt (0, 17, 60, and 102 mol·m^{-3})] for 13 weeks and then 0, 2, 7, and 12 ppt (0, 34, 120, and 204 mol·m^{-3}) for another 12 weeks. Salinity treatments did not have a significant effect on growth rate; however, there were significant differences in growth rate among the three genotypes. Genotype T302 produced the greatest wet weight, whereas MC had stronger apical dominance and exhibited the greatest increase in height over the course of study. As expected, sodium (Na) concentration in** ***Taxodium*** **leaves increased as sea salt concentrations increased but did not tilt Na/potassium (K) ratios to stressful disproportions. Of the three genotypes, BC exhibited the highest leaf content of Na, calcium (Ca), sulfur (S), and iron (Fe); MC had the lowest leaf content of Na, Ca, S, and Fe; and T302 was intermediate. The benefits of using a hybrid cross (T302) that maintains greater biomass than BC or MC across a range of salinities must be weighed against the potential additional pruning and training necessary for cutting-grown clones relative to BC and MC propagated from seed and flood tolerance relative to BC. Still, combining the best characteristics of different varieties of** ***T. distichum*** **should facilitate the production of favorable genotypes tolerant to a number of soil physical and chemical property fluctuations for arboricultural operations.**

Many coastal wetlands of the southeastern United States are threatened by increases in flooding and salinity as a result of both natural processes and man-induced hydrologic alterations (Allen, 1992; Conner and Toliver, 1990; Craig et al., 1979; Templet and Meyer-Arendt,

1988; Wicker et al., 1981). Of all native swamp forest tree species in the southern United States, *Taxodium distichum* has been recognized as being among the most tolerant to flooding (Hook, 1984) and salinity (Krauss et al., 2007). *Taxodium distichum* is an important wetland species of river and coastal floodplains, harboring resilience to windthrow (Conner et al., 2002) and providing a number of important forest products (Mattoon, 1915). In addition, this long-lived and generally pest-free deciduous conifer is popular in southern landscapes and is also quite tolerant of alkalinity (Arnold, 2008), which is responsible in part for its expanding distribution as a roadside and public park landscape tree in the United States and China. The combination of *Taxodium* characteristics described to date provides great opportunity for locating superior genotypes and propagating clones that fit a range of potential site requirements.

Previous literature often refers to three separate species of *Taxodium*: *Taxodium distichum* (baldcypress), *T. ascendens* (pondcypress), and *T. mucronatum* (Montezuma cypress). Although the taxonomic relationships among these three species, or varieties, of *Taxodium* remain a source of debate (Tsumura et al., 1999), the ranges of baldcypress and pond cypress overlap and these two have been recognized as possibly being two varieties of *T. distichum* (Integrated Taxonomic Information System, 2009). For the purpose of this study, we have accepted the nomenclature that combines all *Taxodium* associates into one species with three botanical varieties (Arnold and Denny, 2007), as follows: *Taxodium distichum* var. *distichum* (L.) Rich (BC); *Taxodium distichum* var. *imbricarium* (Nutt.) Croom [pondcypress (PC)]; and *Taxodium distichum* var. *mexicanum* Gordon (MC).

There has been considerable work in China that has involved controlled crosses between BC, MC, and PC, and the subsequent selection of superior genotypes that are multiplied through cutting propagation. T302 (BC × MC) was selected in China in 1988 primarily for growth rate and tolerance to alkaline and salt-rich coastal floodplains. T302 is registered at both the provincial and federal level and accepted for higher salt tolerance than BC and PC. Other attributes of T302 included 159% faster growth than BC, good form, longer foliage retention in fall and early winter, and no knees (Chen et al., 1987). Huang et al. (2006) reported that the growth of T302 had strong adaptability to a wide range of soils and climate.

Li (2006) completed a genetic analysis of 18 *Taxodium* genotypes and found considerable diversity using random amplified polymorphic DNA. According to cluster analysis, the results indicated that BC and PC are genetically nearer, whereas T302 is genetically closer to BC. Yu et al. (2009) completed the identification of *Taxodium* hybrids by sequence-related amplified polymorphism (SRAP) analysis. In this study, the authenticity of 4 reciprocal progenies from *Taxodium distichum* and *T. mucronatum* were identified by SRAP markers. Authenticity of four progenies from *T. distichum* and *T. mucronatum* was identified by 12 polymorphism primer combinations. The results indicated that four progenies were true hybrids resulting from specific bands from the male parent.

Past studies that have used only BC genotypes found evidence for modest potential gains in salt tolerance improvement in the species (Allen et al., 1994a, 1997; Krauss et al., 2000) but with almost complete mortality of all BC genotypes at salinities above 6 ppt (102 mol·m^{-3}) in as little as 30 to 90 d (Krauss et al., 2007). Those studies primarily focused on selecting plant material for coastal restoration efforts in wetland settings and therefore did not include MC, which is far less tolerant to flooding and is not native to the southeastern United States. Denny (2007) conducted a greenhouse salinity screening study to determine if there is a geographic basis for salinity tolerance in *Taxodium* and to evaluate provenances in an effort to select those that

yield individuals that are most adaptable/tolerant to these environmental stresses. The results indicated that most genotypes tolerate moderate levels of soil salts, but at high soil salinities, the tolerance appears to be highly genotype-dependent. While more salt tolerant, MC genotypes are generally more susceptible to Cercospora needle blight (McDonald et al., 2008). In this study, we evaluated growth and leaf nutrient changes in three *Taxodium* genotypes (BC, MC, and one BC × MC hybrid) exposed to acute applications of four rates of salt solution. Arboricultural operations might certainly benefit from combining the best characteristics of these disparate *Taxodium distichum* genotypes as a mechanism for improving growth and productivity on salt-impacted, or otherwise stressful, sites outside of wetland settings. Selections based on growth rate, form, salt and alkalinity tolerance, tolerance to inundation, and other characteristics are certain to have an audience with land use planners, horticulturists, and foresters seeking long-lived urban trees with those attributes.

Material and Methods

Plant material. Three genotypes representing two varieties (BC, MC) and one hybrid (T302) of *Taxodium* were evaluated. BC seed was collected from a natural source near Caddo Lake, TX, and MC seed was obtained from a nurseryman who reported to have originally collected seed from trees south of Las Cruces, NM, in a mountain canyon. Although that population provenance has yet to be verified, the trees are strongly MC in appearance, foliage, habit, growth, and seed size. Hybrid T302 (or 'Nanjing Beauty'; Creech and Yin, 2003) represents a cross between BC and MC and was propagated from cuttings of existing trees for this study. T302 has been described as having improved alkalinity and salinity tolerance (Chen et al., 1987; Zhou et al., 2000), a major reason for its use in this study. Ninety-six plants per genotype were planted in 7.6-L plastic nursery pots containing a commercial potting substrate (Woods #2; Bailey Bark Materials, Woden, TX). Nutrient content of the mix was analyzed in the SFASU Soil and Plant Tissue Testing Laboratory (Table 1). Although most of the substrate parameters are acceptable, background conductivity was considered moderately high at the initiation of the experiment but quickly stabilized. The containers were placed under full sunlight at the Pineywoods Native Plant Center nursery, Stephen F. Austin State University, Nacogdoches, TX, and grown for 60 d to a height of ≈25 cm before experimental treatments were imposed.

Experimental design. The experiment used a two-way factorial design with three *Taxodium* genotypes and four levels of salinity arranged as a completely randomized block with four blocks. Six plants per genotype were randomly assigned to each treatment for a total of 24 plants per genotype in each of the four replicate blocks. In this case, blocks served as true experimental replicates with each block serving as an independently maintained experimental unit for a total of 288 plants in the entire study.

Experimental procedures. Initial treatments included a control with no sea salt (C), a low salt concentration of 1 ppt (L: 17 mol·m^{-3}), a medium salt concentration of 3.5 ppt (M: 60 mol·m^{-3}), and a high salt concentration of 6 ppt (H: 102 mol·m^{-3}). The chemical composition of the artificial sea salt used (SaltWorks™, Woodinville, WA) mimics that of actual sea water in concentrations of major ions (Table 2).

Sea salt application was initiated on 22 May 2006 and was intended to simulate repetitive, acute exposure to roots but to allow for some flushing as well as some cumulative build-up of salinity within pots. Only substrate salinity tolerance was tested in this container study. From experimental initiation, 500 mL of each sea salt solution (i.e., C, L, M, H) was applied to the surface of each respective container every Monday afternoon for 13 weeks. After 13 weeks of salt application, no salt damage symptoms were noticed in the appearance of the trees. For this reason, the salt concentration rates were doubled beginning on 21 Aug. 2006; concentrations were increased to 0, 2, 7, 12 ppt (0, 34, 120, and 204 mol·m^{-3}) for treatments C, L, M, and H, respectively. The same application procedure was followed every Monday afternoon using these new concentrations, once per week, for another 12 weeks until 7 Nov. 2006.

Salt solutions remained in containers for at least 24 h after each salt application before irrigation with city water, which has low conductivity (less than 0.35 dS·m^{-1}) and Na below 50 ppm (data not shown). The plants were watered as needed with overhead sprinklers for ≈40 min per irrigation; plants were watered in this fashion two to three times per week to simulate horticultural irrigation. Plants were fertilized with 12.8 g of a slow-release 18N–6P–12K fertilizer (Osmocote®; Scotts Miracle-Gro Company, Marysville, OH) on 14 June 2006. Electrical conductivity (EC) of the leachate flowing out of the treatment pots was measured with a portable Myronl Agri-meter (Model ag-5; Myronl Company, Carlsbad, CA) as an indication of salt retention within sample pots.

Tissue analysis. Leaf samples were collected for foliar nutrient analysis on 27 Oct. 2006, just before the last salt application. Six leaves were taken as subsamples from each plant for a total of 36 leaves per genotype per treatment in each block. The plant samples were dried to a constant weight in a convection oven for 3 d at 60 °C. Dried subsample leaves were pooled by treatment combination to ensure adequate volume of material for analysis, generating a total of 288 samples after pooling. Samples were then ground in a cyclone grinder, homogenized, and analyzed for nutrient concentration. A nitric acid (HNO$_3$) and 30% hydrogen peroxide wet acid digestion was used to prepare the samples for phosphorus (P), K, Na, Ca, and magnesium (Mg) analysis using inductively coupled argon plasma spectroscopy (IRIS Intrepid Inductively Coupled Argon Plasma Training Manual, Thermo Electron Corporation, Franklin, MA).

Table 1. Potting substrate analysis based on saturated extract using deionized water.

pH	7.01	Magnesium	47.60
EC	2.10	Sodium	110.99
SAR	1.92	Iron	1.03
Nitrogen	1.00	Manganese	0.43
Phosphorus	10.67	Zinc	0.07
Potassium	257.27	Copper	0.04
Calcium	191.94		

EC = electrical conductivity (dS·m^{-1}); ion concentrations reported in mg·L^{-1}; SAR = sodium absorption ratio. Values represent means of three replicates.

Table 2. Chemical composition of the sea salt used in the experiment.

Components	Typical range (%)
NaCl	99.50–99.88
Calcium	0.02–0.06
Magnesium	0.01–0.05
SO$_4$	0.05–0.21

Heights and wet weights. Plant heights were measured for each plant at the beginning and conclusion of the experiment. Each plant was cut back to 5 cm above ground and the above-ground parts were weighed (grams wet weight) as a measure of the capacity for individual plant performance under the different experimental treatments.

Data analysis. The General Linear Model (GLM) procedure of SAS (SAS Institute, Inc., 2007) was used to detect significant differences in plant height, wet weight, and tissue nutrient concentrations for the different genotypes and treatments. Data were analyzed as a full-factorial using mean square error; interactions between genotype and salinity were also tested. A Tukey's studentized range test (α = 0.05) with a Bonferroni adjustment to account for sample size effects was used to identify statistical groupings if a significant effect was detected with GLM analysis. Data were normally distributed with homoscedastic variance without the need for transformation.

Results and Discussion

Electrical conductivity. EC readings identified rapid and consistent leaching of salinity from pots in as little as 2 d (Fig. 1). When sea salt application rates were doubled, essentially the ECs also doubled (data not shown), but the leaching rates after application were similar. During the 24-h exposure period each week, roots were subjected to conductivities as high as 20 dS·m^{-1} for the high salt solution. Although our study did not simulate a natural wetland setting, it is important to note how freely salinity exits substrate in container situations (Fig. 1). Salinity often remains at elevated levels for months (or even years) after hurricane overwash in coastal swamp forests (Conner et al., 2007). As simulated here in this acute exposure study, leaching rates are expected to be much greater in the less saturated substrate used; as a result, exposure to salinity occurred only 15% of growth time in our simulation. Many coastal swamp forests are

no longer freely flushed with river water, forcing an important distinction between chronic exposure in natural wetland field settings and acute simulations in roadside environments or controlled landscapes where deicing salts, fertilizer salts, or limestone applications may be present.

Growth. Wet weights of *T. distichum* genotypes did not differ significantly among the various concentrations of sea salt tested by our experiment (Table 3); however, wet weights were different among the three genotypes when analyzed across all four concentrations of sea salt (Tables 3 and 4). Although wet weights were collected at the completion of the experiment, dry weight/wet weight ratios of whole plants were developed at a later date, with BC, MC, and T302 averaging 0.32, 0.33, and 0.25, respectively. When adjusted wet weight/dry weight ratios were applied to the data set in this study, the significance among comparisons remained unchanged (Table 3). Because interactions between salinity and genotype were also not significant for either wet weight or height growth (Table 3), it is feasible to evaluate salinity effects across all genotypes.

First, although the *T. distichum* genotypes were exposed to salinities that would have certainly been detrimental to growth with chronic exposure (Conner, 1994; Krauss et al., 1999; Pezeshki, 1990; Pezeshki et al., 1986, 1987), the acute pulses of salinity at concentrations up to 6 and 12 ppt had no effect on the wet weights of plants in our study. This indicates that exposure to short pulses of salinity, as might be expected by deicing salts along roadsides, or an infrequent misapplication of a fertilizer or limestone product in the landscape, would have small effects on the genotypes if they were flushed within days of application. This result also indicates that salinity exposure in our study may not have been high enough to warrant major differences among genotypes. However, the mean wet weight of T302 was significantly greater than wet weights of both BC and MC across all four salinity treatments (Table 4). This result, the fact that genotypic rank did not change with increased salinity exposure (Table 3), indicates that T302 tended to perform better without regard to our salinity treatments and perhaps would even be expected to perform better under a range of environmental conditions beyond salinity. In support of this idea, volume growth of T302 was 331% of BC for T302 grown on an alkaline low-land area in China (Zhou et al., 2000).

Second, differences were also not detected in *T. distichum* height growth with different sea salt exposures, but similar to wet weights, significant differences in height growth were detected among genotypes (Table 4). On the other hand, MC, not T302, ranked highest in terms of height growth increment followed by BC. There were still no interactive effects between salinity treatments and genotypes (Table 3), suggesting that rankings once again transcended salinity treatment.

These data identify a potential hurdle when using hybrids in that although biomass may be high under a range of salinity exposures, apical dominance, which is a major characteristic of
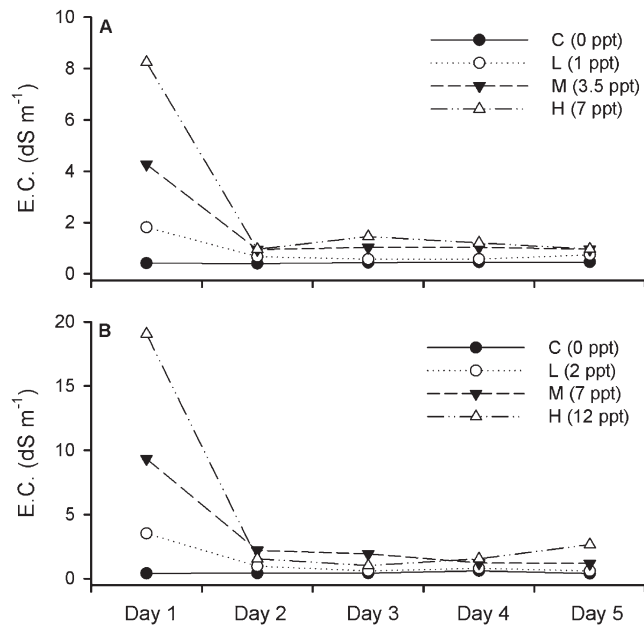
natural *T. distichum* trees propagated from seed, is compromised. T302 had the greatest wet weight, but MC had the greatest height growth during salinity exposure. This is best explained by the fact that T302 was derived by rooted cuttings, which often exhibit plagiotro-

pic growth with more branching, whereas MC, derived from seed, quickly formed a strong central leader with less branching. Because T302 is commonly propagated by cuttings, and there are many more lateral branches available for sources of cuttings than apical

Fig. 1. Electrical conductivity (EC) ($dS \cdot m^{-1}$) measurements of pot leachate over a representative 5-d cycle after application of (**A**) 500 mL of 0 ppt (C), 1 ppt (L), 3.5 ppt (M), and 6 ppt (H) sea salt solution; and (**B**) 500 mL of 0 ppt (C), 2 ppt (L), 7 ppt (M), and 12 ppt (H) sea salt solution. Day 1 reflects application day. Values represent one random sample collected per day per treatment.

Table 3. General linear model analysis of variance for (A) mean wet weight and (B) adjusted dry weight,[z] and (C) height of *Taxodium* genotypes exposed to different sea salt application rates.

| A. Wet weight | | | | | |
Source of variation	df	SS	MS	F value	Pr > F
Salinity	3	14867.26	4955.75	2.65	0.1122
Genotype	2	464224.56	232112.28	32.72	0.0006
Salinity × genotype	6	21670.38	3611.73	1.04	0.4339
B. Adjusted dry weight					
Source of variation	df	SS	MS	F value	Pr > F
Salinity	3	7479.15	2493.05	2.55	0.1214
Genotype	2	192991.27	96495.61	20.13	0.0022
Salinity × genotype	6	13119.79	2186.63	1.11	0.3930
C. Height					
Source of variation	df	SS	MS	F value	Pr > F
Salinity	3	69.15	23.05	0.69	0.5829
Genotype	2	9611.94	4805.97	51.68	0.0002
Salinity × genotype	6	281.12	46.85	0.97	0.4700

[z]Adjusted dry weight value was derived from subsequent studies with dry weight/wet weight ratios of whole plants obtained from similar size material with baldcypress, Montezuma cypress, and T302 averaging 0.32, 0.33, and 0.25, respectively.

Table 4. Mean biomass (g wet wt) and height increment (cm) of three genotypes of *Taxodium* at a sea salt application of 0 ppt (C), 1 ppt (L), 3.5 ppt (M), and 6 ppt (H) for 13 weeks, and then 0 ppt (C), 2 ppt (L), 7 ppt (M), and 12 ppt (H) for an additional 12 weeks.

| | Wet wt | | | Ht | | |
Rate	BC	T 302	MC	BC	T 302	MC
C	55.32	61.44	87.88	55.32	61.44	87.88
L	50.95	68.02	91.77	50.95	68.02	91.77
M	53.21	69.82	86.51	53.21	69.82	86.51
H	52.96	72.8	89.38	52.96	72.8	89.38
Mean	53.11 c	68.02 b	88.90 a	53.11 c	68.02 b	88.90 a

Means followed by the same letter in groups are not significantly different at the 0.05 level of probability according to Tukey's studentized range test.

BC = baldcypress; MC = Montezuma cypress.

stems, the result is often propagated trees that act like branches when planted, at least initially (Zobel and Talbert, 1984). In China, nurserymen have developed a protocol for nursery propagation and production of such clones. They typically grow cutting-propagated liners in the field for 1 year with little pruning. In the winter, the tree is cut to 6 inches above the ground and side limbs pruned away. Vigorous growth resumes in the spring, a leader quickly forms, and numerous vigorous, mostly upright cuttings are available for cutting propagation in the summer. One vigorous upright shoot is left to create the leader, which results in a tall, well-formed, and marketable tree by winter. Although plagiotrophy can be a benefit for fruit culture to reduce the time from planting to fruit production, for example, silvicultural operations have fewer uses for spindly growth patterns outside of seed orchards, with the exception perhaps of hedge rows or coastal vegetation barriers. An appropriate role for T302 or other hybrids will need to be identified, but it appears to be the most productive of the three genotypes tested under this type of salinity exposure.

Leaf tissue content. Leaf tissue elemental concentrations also differed among genotypes (Table 5). Of the three genotypes studied here, BC had a higher content of Ca, Na, S, and Fe in the foliage than MC, suggesting that BC takes up some ions associated with salinity more readily than MC. A failure to exclude Na and additional ions from leaf tissue can readily lead to increased osmotic stress, ion toxicity, or ion and hormone imbalances (Flowers et al., 1977; Greenway and Munns, 1980). By all appearances, MC had a greater capacity for excluding deleterious ions such as Na than BC; ion exclusion is likely to be an important mechanism for increasing salt tolerance in baldcypress even among individual populations of BC (Allen et al., 1996). As foliar Na concentrations increase in BC, the photosynthetic capacity of BC decreases linearly (Pezeshki et al., 1988). The hybrid (T302) registered intermediate foliar concentrations for Na but grouped with BC for K, Ca, S, and Fe (Fig. 2). Likewise, foliar K, Ca, Na, S, and Fe were significantly higher in BC and T302 than in MC with T302 having the highest foliar content of P, Mg, zinc, and copper.

We found significant differences of leaf elemental content of Na among treatments in this study (F = 18.62; P = 0.0003; Table 6). Foliar K concentrations in treatment L were significantly lower than at the sea salt concentrations for treatments M and H (F = 5.52; P = 0.0199; Table 6). Of four salinity treatments, leaf S concentration in *Taxodium* at L was significantly higher than in H (F = 4.77; P = 0.0295; Table 6). Leaf Na concentration at L, M, and H was 146%, 200%, and 269%, respectively, that of C. In addition, leaf ion Na/K ratios peaked at only 0.28 for H, offering further insight into why we observed no visible signs of stress in *T. distichum* initially. Uptake of the salts to the leaves was not proportional to sea salt concentrations applied, suggesting that differential uptake and/or exclusion of salts by plants may be occurring. Exclusion

of ions, especially chlorine, has been suggested as a primary mechanism for salt tolerance among non-halophytic trees (Allen et al., 1994b; Townsend, 1989). There was no significant difference in leaf P, Ca, and Mg content among the salinity treatments. Accordingly, no evidence of different foliar Ca concentrations was discovered for BC genotypes subjected to salinities ranging from 0 to 8 ppt in a previous study (Allen et al., 1997); however, progressive salinity increases did throw Na/Ca ratios out of balance in greenhouse and field BC studies (Allen et al., 1997; Krauss et al., 2000). It is clear that although important individual foliar ions may remain unchanged with sea salt application, imbalances of specific ions, in lieu of absolute concentrations, may be more important.

Overall concentrations of Na among leaves of all *Taxodium* genotypes increased as sea salt concentration increased (Fig. 2), but to a much different degree among genotypes. For exam-

ple, Na concentrations in T302 leaves increased from 0.1% in Treatment C to 0.37% in Treatment H. The high salt rate created leaf Na concentrations in BC up to 5500 (mg·L^{-1}), or 0.55%, which may have contributed to imbalances in Na/K ratios. For comparison, Allen et al. (1997) reported foliar Na concentrations slightly greater than 1.0% for BC seedlings exposed to 8 ppt floodwater salinity for over 3 months. Na/K ratios in *Taxodium* leaves differed significantly among sea salt treatment (Fig. 3), increasing from 0.09 in leaf tissue of plants in C to 0.22 in leaf tissue of plants at the highest salt exposure (H). Na/K ratios can freely exceed 1.0 at salinities as low as 2 ppt (Allen et al., 1997). Dilution of ions in the greater biomass of T302 might be at least a partial explanation for the elemental content of that genotype. However, because significant differences were found between BC and MC leaf elemental content, both with similar final weights, this may not be at odds with greater

Table 5. Leaf foliar nutrient concentrations for all three genotypes of *Taxodium* subjected to a range of sea salt exposure.

	Phosphorus (%)	Potassium (%)	Calcium (%)	Magnesium (%)	Sodium (%)	Sulfur (%)	Iron (mg·L^{-1})	Manganese (mg·L^{-1})	Zinc (mg·L^{-1})	Copper (mg·L^{-1})
BC	0.21^z b^y	1.35 a	1.11 a	0.14 b	0.39 a	0.21 a	65.06 a	49.87 b	23.12 c	5.12 b
T302	0.29 a	1.46 a	1.08 a	0.17 a	0.23 b	0.19 a	58.06 a	65.81 a	47.19 a	7.06 a
MC	0.26 a	0.79 b	0.79 b	0.14 b	0.09 c	0.16 b	43.37 b	66.94 a	35.37 b	5.31 ab

^{z}Values are means of 92 samples.
^{y}Means within a column followed by the same letter are not significantly different at the 0.05 level of probability according to Tukey's studentized range test.
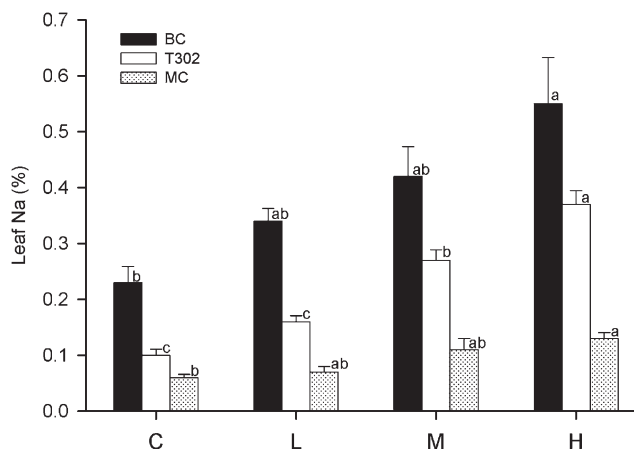BC = baldcypress; MC = Montezuma cypress.

Fig. 2. Concentrations of leaf sodium (Na) (%) for baldcypress (BC), Montezuma cypress (MC), and T302 exposed to 0 ppt (C), 1 ppt (L), 3.5 ppt (M), and 6 ppt (H) sea salt solution for 13 weeks, and then 0 ppt (C), 2 ppt (L), 7 ppt (M), and 12 ppt (H) sea salt solution for an additional 12 weeks. Values are means of 24 samples. Bars represent 1 SD of the mean. Means for a particular genotype (BC, MC, or T302) represented by the same letter among treatment (C, L, M, or H) are not significantly different at the 0.05 level of probability according to Tukey's studentized range test.

Table 6. Leaf foliar nutrient concentrations (%) of all *Taxodium* genotypes subjected to sea salt application of 0 ppt (C), 1 ppt (L), 3.5 ppt (M), and 6 ppt (H) for 13 weeks, and then 0 ppt (C), 2 ppt (L), 7 ppt (M), and 12 ppt (H) for an additional 12 weeks.

Rate	Phosphorus	Potassium	Calcium	Magnesium	Sulfur	Sodium
C	0.26 a	1.22 ab	0.97 a	0.15 a	0.18 ab	0.13 c
L	0.25 a	1.09 b	1.04 a	0.15 a	0.19 a	0.19 bc
M	0.25 a	1.23 a	1.04 a	0.15 a	0.18 ab	0.26 ab
H	0.25 a	1.25 a	0.93 a	0.14 a	0.17 b	0.35 a

Means within a column followed by the same letter are not significantly different at the 0.05 level of probability according to Tukey's studentized range test.
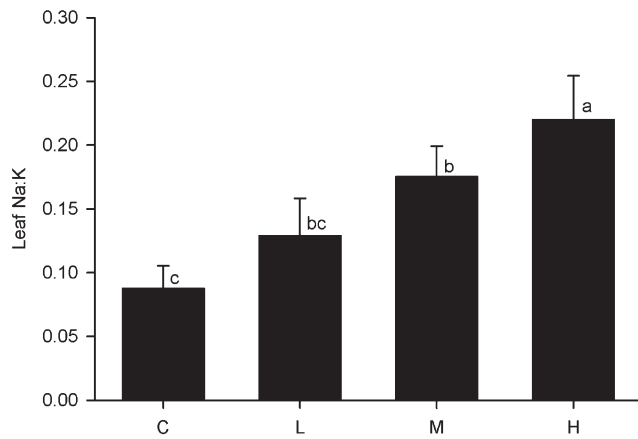
Fig. 3. Sodium/potassium (Na/K) ratios for all three *Taxodium* genotypes combined by sea salt application of 0 ppt (C), 1 ppt (L), 3.5 ppt (M), and 6 ppt (H) for 13 weeks, and then 0 ppt (C), 2 ppt (L), 7 ppt (M), and 12 ppt (H) for an additional 12 weeks. Values are means of 24 samples. Bars represent 1 SD of the mean. Means with the same letter are not significantly different at the 0.05 level of probability according to Tukey's studentized range test.

salt tolerance by way of foliar ion exclusion of Na in T302 relative to BC.

Rates of sea salt application in this study did not significantly affect the growth of *Taxodium*. Pezeshki (1990) also found that height growth, net photosynthesis, and stomatal conductance were unaffected when BC seedlings were watered with 3 ppt salinity for 60 d. Overall, it appears that *Taxodium* has fair tolerance to transient exposures of salinity as long as leaching occurs within a few days of exposure. However, similar to our results, salt treatment through watering with 3 ppt did have a significant effect on the concentrations of leaf Na, K, and S as well as Na/K ratios (Pezeshki, 1990). In our study, it was apparent that leaf Na concentration increased with increasing sea salt application rates as *Taxodium* became less adept at excluding Na. Furthermore, Pezeshki et al. (1988) reported a significant increase in Na, K, Ca, and Mg concentration of leaf tissue of BC subjected to saltwater flooding relative to freshwater flooding. Other studies have suggested that Na/K ratios provide a wonderful tool for selecting genotypes in BC; ion ratios below 1.0 represent a relatively stress-free condition for non-halophytes (Wyn Jones et al., 1979). Increases in site salinity beyond those tolerable for BC quickly vectored foliar Na/K ratios above 1.0 on field plantation sites south of New Orleans, LA (Krauss et al., 2000); ion ratios offer a tool to assist wetland scientists and arboriculturalists with selection of perspective *Taxodium* genotypes harboring greater tolerance to low salinity levels (Allen et al., 1997). Exclusion of Na from the foliage of MC and T302 is most promising and may be a primary reason why T302 demonstrated fair tolerance to salinity in past trials (Creech and Yin, 2003).

Conclusions

It appears that the salt tolerance of *Taxodium* was improved in a hybrid cross between *T. distichum* var. *distichum* (BC) and *T. distichum* var. *mexicanum* (MC) genotypes,

at least as long as salinity is delivered in a specific way such as may be the case for deicing salts along roadsides. All the plants survived the salinity treatments, and the high salt rate failed to damage plants or to inhibit plant growth over 25 weeks. The benefits of using a hybrid cross (T302) that maintains greater biomass than BC or MC across a range of salinities must be weighed against the negative effects created by plagiotropic growth form relative to BC and MC and potentially reduced flood tolerance relative to BC. The greater tolerance of BC to flooding may preclude major gains in salt tolerance improvement for use in coastal wetland restoration programs (Krauss et al., 2009); however, combining the best characteristics of different varieties of *T. distichum* may facilitate the production of favorable genotypes tolerant to a number of soil physical and chemical fluctuations for arboricultural operations.

Literature Cited

Allen, J.A. 1992. Cypress-tupelo swamp restoration in southern Louisiana. Restor. Manage. Notes 10:188–189.

Allen, J.A., J.L. Chambers, and D. McKinney. 1994a. Intraspecific variation in the response of *Taxodium distichum* seedlings to salinity. For. Ecol. Mgt. 70:203–214.

Allen, J.A., J.L. Chambers, and M. Stine. 1994b. Prospects for improving the salt tolerance of forest trees: A review. Tree Physiol. 14:843–853.

Allen, J.A., J.L. Chambers, and S.R. Pezeshki. 1997. Effects of salinity on valdcypress seedlings: Physiological responses and their relation to salinity tolerance. Wetlands 17:310–320.

Allen, J.A., S.R. Pezeshki, and J.L. Chambers. 1996. Interaction of flooding and salinity stress on baldcypress (*Taxodium distichum*). Tree Physiol. 16:307–313.

Arnold, M.A. 2008. Landscape plants for Texas and environs. Sec. Ed. Stipes Pub. LLC, Champaign, IL.

Arnold, M.A. and G.C. Denny. 2007. Taxonomy and nomenclature of baldcypress pondcypress and Montezuma cypress. One, two or three species? HortTechnology 17:125–127.

Chen, Y., M. Wang, S. Wu, L. Liu, and S. He. 1987. Interspecific hybridization and breeding of genus *Taxodium* for fast-growing and alkaline tolerance. Nanjing Zhongshan Botanical Garden Research Papers 92–98.

Conner, W.H. 1994. The effect of salinity and waterlogging on growth and survival of baldcypress and Chinese tallow seedlings. J. Coast. Res. 10:1045–1049.

Conner, W.H., K.W. Krauss, and T.W. Doyle. 2007. Ecology of tidal freshwater forests in coastal deltaic Louisiana and northeastern South Carolina, p. 223–253. In: Conner, W.H., T.W. Doyle, and K.W. Krauss (eds.). Ecology of tidal freshwater forested wetlands of the southeastern United States. Springer, New York, NY.

Conner, W.H., I. Mihalia, and J. Wolfe. 2002. Tree community structure and changes from 1987–1999 in three Louisiana and three South Carolina forested wetlands. Wetlands 22:58–70.

Conner, W.H. and J.R. Toliver. 1990. Long-term trends in the baldcypress (*Taxodium distichum*) resource in Louisiana (USA). For. Ecol. Mgt. 33/34:543–557.

Craig, N.J., R.E. Turner, and J.W. Day, Jr. 1979. Land loss in coastal Louisiana (USA). Environ. Manage. 3:133–144.

Creech, D. and Y. Yin. 2003. *Taxodium* × 'Nanjing Beauty': A new landscape plant for the south. HortScience 38:1292–1293.

Denny, G.C. 2007. Evaluation of selected provenances of *Taxodium distichum* for drought, alkalinity and salinity tolerance. PhD diss., Texas A&M University.

Flowers, T.J., P.F. Troke, and A.R. Yeo. 1977. The mechanism of salt tolerance in halophytes. Annu. Rev. Plant Physiol. 28:89–121.

Greenway, H. and R. Munns. 1980. Mechanisms of salt tolerance in nonhalophytes. Annu. Rev. Plant Physiol. 31:149–190.

Hook, D.D. 1984. Waterlogging tolerance of lowland tree species of the south. Southern J. Appl. For. 8:136–149.

Huang, L., X. Li, D. Zhang, Y. Chen, and X. Lu. 2006. Study on the growth of *Taxodium*. 'Zhongshansha 302' on hilly area. Journal of Jiangsu Forestry Science and Technology 33:6–9.

Integrated Taxonomic Information System. 2009. 3 Nov. 2010. <http:www.itis.gov/index.html>.

Krauss, K.W., J.L. Chambers, J.A. Allen, B.P. Luse, and A.S. DeBosier. 1999. Root and shoot responses of *Taxodium distichum* seedlings subjected to saline flooding. Environ. Exp. Bot. 41:15–23.

Krauss, K.W., J.L. Chambers, J.A. Allen, D.M. Soileau, Jr., and A.S. DeBosier. 2000. Growth and nutrition of baldcypress families planted under varying salinity regimes in Louisiana, USA. J. Coast. Res. 16:153–163.

Krauss, K.W., J.L. Chambers, and D. Creech. 2007. Selection for salt tolerance in tidal freshwater swamp species: Advances using baldcypress as a model for restoration, p. 385–410. In: Conner, W.H., T.W. Doyle, and K.W. Krauss (eds.). Ecology of tidal freshwater forested wetlands of the southeastern United States. Springer, New York, NY.

Krauss, K.W., R.J. Howard, and T.W. Doyle. 2009. Is there evidence of adaptation to tidal flooding in saplings of baldcypress subjected to different salinity regimes? Environ. Exp. Bot. 67:118–126.

Li, H. 2006. Study on genetic analysis on *Taxodium Rich*. using RAPD. MS thesis, Nanjing Agriculture University, Nanjing, PR China.

Mattoon, W.R. 1915. The southern cypress. Bull. 272. U.S. Department of Agriculture, Washington, DC.

McDonald, G.V., G.C. Denny, M.A. Arnold, D.L. Bryan, and L. Barnes. 2008. Comparative canopy

damage among provenances of baldcypress associated with the presence of *Cercosporidium sequoia* (Ellis and Everth.) W.A. Baker and Partridge. HortScience 43:1703–1705.

Pezeshki, S.R. 1990. A comparative study of the response of *Taxodium distichum* and *Nyssa aquatica* seedlings to soil anaerobiosis and salinity. For. Ecol. Mgt. 33/34:531–541.

Pezeshki, S.R., R.D. DeLaune, and W.H. Patrick. 1988. Effect of salinity on leaf ionic content and photosynthesis of *Taxodium distichum* L. Am. Midl. Nat. 119:185–192.

Pezeshki, S.R., R.D. DeLaune, and W.H. Patrick, Jr. 1986. Gas exchange characteristics of bald cypress (*Taxodium distichum* L.): Evaluation of responses to leaf aging, flooding, and salinity. Can. J. For. Res. 16:1394–1397.

Pezeshki, S.R., R.D. DeLaune, and W.H. Patrick, Jr. 1987. Response of baldcypress (*Taxodium distichum* L. var. *distichum*) to increases in flooding salinity in Louisiana's Mississippi River Deltaic Plain. Wetlands 7:1–10.

SAS Institute, Inc. 2007. Online Doc 9.1.3. SAS Institute, Inc., 2002–2005, Cary, NC.

Templet, P.H. and K.J. Meyer-Arendt. 1988. Louisiana wetland loss: A regional water management approach to the problem. Environ. Manage. 12:181–192.

Townsend, A.M. 1989. The search for salt tolerant trees. Arboricultural J. 13:67–73.

Tsumura, Y., N. Tomaru, Y. Suyama, and S. Bacchus. 1999. Genetic diversity and differentiation of *Taxodium* in the south-eastern United States using cleaved amplified polymorphic sequences. Heredity 83:229–238.

Wicker, K.M., D. Davis, M. DeRouten, and D. Robert. 1981. Assessment of extent and impact of saltwater intrusion into the wetlands of Tangipahoa Parish, Louisiana. Coastal Environments Inc., Baton Rouge, LA., pp. 59.

Wyn Jones, R.G., C.J. Brady, and J. Speirs. 1979. Ionic and osmotic regulation in plant cells, p. 63–103. In: Laidman, D.L. and R.G. Wyn Jones (eds.). Recent advances in biochemistry of cereals. Academic Press, London, UK.

Yu, C., Y. Yin, and J. Xu. 2009. Identification of *Taxodium* hybrids by SRAP analysis. Scientia Silvae Sinicae. 45:142–146.

Zhou, K., C. Jia, Y. Chen, Y. Yin, and Z. Sunday. 2000. Analysis on growth of *Taxodium distichum* and *T.* 'Zhongshansha' on the alkaline low-land. J. Jiangsu For. Sci. Tech. 27: 16–18.

Zobel, B. and J. Talbert. 1984. Applied forest tree improvement. Waveland Press, Inc., Prospect Heights, IL.