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Intraspecific Variation in the Response of Baldcypress (Taxodium Distichum) Seedlings to Salinity.

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INTRASPECIFIC VARIATION IN THE RESPONSE OF BALDCYPRESS (*TAXODIUM DISTICHUM*) SEEDLINGS TO SALINITY

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DEDICATION

To Kathy and our boys, Gregory, Geoffrey, and Mark.

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ABSTRACT

This study evaluated genotypic variation in responses of baldcypress (*Taxodium distichum*) seedlings to combined flooding and salinity stress. Two experiments form the core of this dissertation.

In the first experiment, seedlings of 15 open-pollinated families of baldcypress were exposed to combined salinity and flooding stress under greenhouse conditions. Ten of the families were from coastal locations that were slightly brackish. The other families were from freshwater locations. Five salinity levels were investigated - 0, 2, 4, 6, and 8 g l^{-1} artificial seawater - all with shallow flooding.

Substantial variation was found among salinity levels and families for most of the response variables assessed. In general, families from brackish sources had greater biomass, leaf area, and tolerance index values than families from freshwater sources at the highest salinities, but mean survival did not differ by source. Striking differences in seedling morphology were noted between seedlings that appeared to be salt tolerant and those that were not. More tolerant seedlings had larger mean leaf sizes and retained leaves at the top of the seedling. Less tolerant seedlings exhibited partial stem dieback and near

total defoliation, in some cases followed by partial refoliation with smaller leaves.

In the second experiment, a subset of seedlings from the greenhouse trial were periodically placed indoors under artifical light, and measurements were made of gas exchange, water potential and chlorophyll fluorescence. Also, an analysis of tissue concentrations of Cl^-, Na^+, K^+, and Ca^{2+} following harvest of the greenhouse study was included in the chapter summarizing this experiment. Significant variation was found for nearly all the physiological parameters evaluated, but only shoot concentrations of Na^+ and Cl^- were related to family-level differences in salt tolerance.

An important conclusion drawn from this study is that there appears to be adequate evidence of genotypic variation in combined flooding and salt tolerance to justify a selection and breeding program. The development of planting material with improved tolerance, combined with efforts to restore original hydrologic regimes where feasible, may be an effective strategy for restoration of coastal forests dominated by baldcypress.

INTRODUCTION

IMPORTANCE OF BALDCYPRESS

Among the most distinctive and important forested wetland tree species in the southern United States is baldcypress (Taxodium 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; Wilhite and Toliver 1990). The range of baldcypress is depicted in Figure I.1.

Together with water tupelo (Nyssa aquatica L.) and swamp tupelo (N. sylvatica var. biflora (Walt.) Sarg.), baldcypress is the major species of the baldcypress-tupelo forest type (Larsen 1980). This forest type is widely distributed in the southern United States and is of considerable ecological and economic importance. In the Coastal Plain Province of the Southcentral U.S., the area of baldcypress-tupelo swamps is estimated to be approximately 650,000 ha (McWilliams and Rosson 1990). Baldypress-tupelo swamps are quite prominent in southern Louisiana, where they cover approximately 160,000 hectares within the coastal zone (Salinas et al. 1986), and considerably more acreage just to the north of the coastal zone (Conner 1988; McWilliams and Rosson 1990).

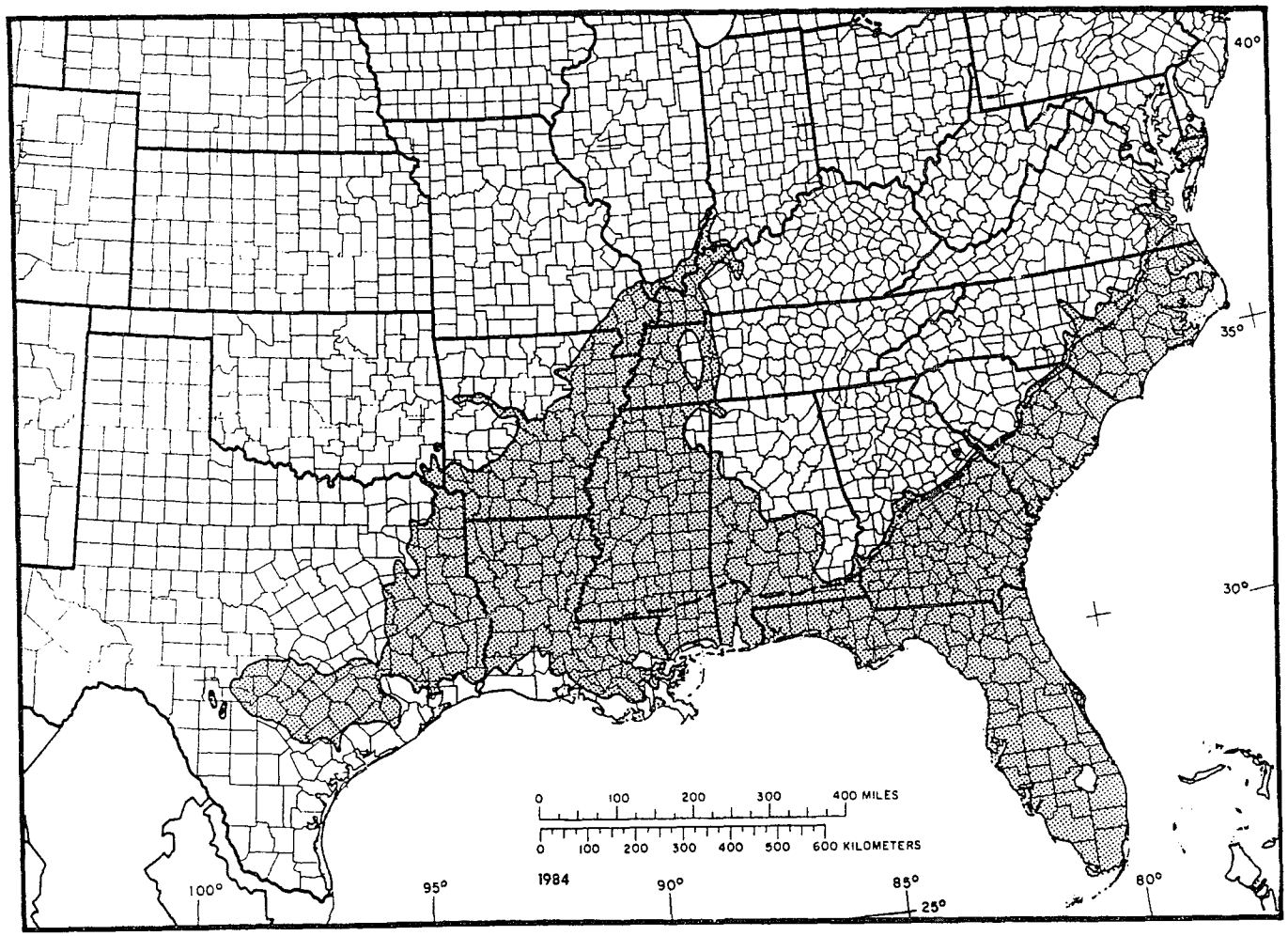

Figure I.1. The native range of baldcypress. The broken line indicates the northern limit of the variety *nutans*, pondcypress. Source: Wilhite and Toliver 1990.

Baldypress-tupelo swamps are important in part because they perform many of the same functions as terrestrial forests, such as the provision of nesting sites, feeding areas, and travel corridors for numerous species of migratory birds. In addition, because of their direct linkages to both upland and aquatic habitats, they also perform additional functions, such as provision of shelter for juvenile fish and export of organic matter to adjacent estuaries (Mitsch and Gosselink 1993; Wharton et al. 1982).

From a fish and wildlife, or biodiversity perspective, there are numerous specific values of baldcypress-tupelo swamps that could be cited. For example, in southern Louisiana, baldcypress-tupelo wetlands are frequently used as nesting sites for colonies of wading birds (Keller et al. 1984). Also, 93% of the bald eagle nests found in a survey of southern Louisiana were located in baldcypress-tupelo forests (Harris et al. 1987). Although baldcypress produces a fruit that is used by some wildlife species such as squirrels, wild turkeys and wood ducks, the tree itself is probably of greater overall value to wildlife. Trees are used by a diversity of species, ranging from black bears (for dens), to bees (for hives), to the numerous bird species that nest in its cavities or on its branches, to catfish, which spawn in hollow cypress logs (Wilhite and Toliver 1990).

In addition to their ecological importance, baldcypress-tupelo swamps have significant economic value. The wood from these swamps played an especially prominent role in the colonial-era economy of the southern U.S. Because of its durability and the relative ease with which it can be worked, baldcypress wood was particularly valuable, and was used extensively for home construction, boat-building, pilings, railroad ties, furniture, water storage tanks, boxes, crates, and caskets (Brown and Montz 1986; citations in Conner 1988). In Louisiana, baldcypress boards and timbers were the main cash crop up until the 1790's, and continued to be a mainstay of the lumber industry well into the 20th Century (Conner 1988; Conner and Toliver 1990). Although the harvesting of baldcypress dropped off considerably in the mid-1900s, harvesting is expected to increase substantially in the near future because approximately three-quarters of the current baldcypress resource consists of sawtimber size stands (Conner 1988; Rosson et al. 1991).

THREATS TO COASTAL SWAMPS

Even a casual observer, when traveling through southern Louisiana, is bound to notice that many of the region's baldcypress-tupelo swamps are severely stressed. Stands of snags and dying trees (known locally as "ghost

swamps" or "cypress cemeteries") cover hundreds of hectares in some areas (Wicker et al. 1981; Allen 1992). In other locations, where existing trees appear healthy, little or no regeneration is occurring (Conner 1988). In still other areas, tracts that were logged 30 to 100 years ago have almost entirely failed to regenerate (Mattoon 1915; Wicker et al. 1981; Conner 1988).

Numerous reasons exist for the degradation and loss of the region's swamp forests, but altered hydrology is probably the single largest factor (Craig et al. 1979; Conner 1988). In some cases, the alterations are natural. Historically, the distribution of freshwater wetlands (including swamps) closest to the coast has changed frequently because of shifts in the major river systems (*i.e.*, in the location of their channels and deltas) and corresponding changes in patterns of sediment deposition, subsidence, flooding, and saltwater intrusion (Gosselink 1984).

Human alterations are probably more prevalent currently, and include (1) levees along the main rivers; (2) large navigation canals, an extensive network of oil and gas canals, and old pullboat (logging) canals; and (3) numerous flood control and drainage projects (Craig et al. 1979; Wicker et al. 1981; Templet and Meyer-Arendt 1988). Other threats to the region's swamps include clearing for agriculture and urban development, nutria depredation on

tree seedlings (Conner 1988; Allen and Boykin 1991), increasing levels of insect defoliation of both baldcypress and water tupelo (Goyer et al. 1990; Meeker and Goyer 1993), and vine damage to planted seedlings (Platt and Brantley 1990).

Human alterations of the natural hydrologic regime have resulted in two broad types of changes in coastal swamps, both of which have the potential to produce profound impacts. The first of these is increases in flood duration. Several authors have characterized the problem of increased flood durations and/or predicted the potential impact on coastal forests (DeLaune et al. 1987; Conner and Brody 1989; Pezeshki et al. 1990).

The second major type of change, and the motivation for this study, is in the salinity regime of coastal swamps. Cypress-tupelo swamps are freshwater systems, with salinity levels generally less than 0.5 g l^{-1} (Mitsch and Gosselink 1993). In southern Louisiana swamps, however, salinity levels in excess of 2 g l^{-1} have been recorded (Wicker et al. 1981; Salinas et al. 1986). Extensive tree mortality in areas along the Mississippi River Gulf Outlet east of New Orleans, the Houma Navigation Canal south of Houma, and along Lakes Ponchartrain and Manchac is apparently due to saltwater intrusion (Wicker et al. 1981; Brown and Montz 1986).

RATIONALE FOR UNDERTAKING STUDY

The importance of the cypress-tupelo resource and the threats to this resource in the Louisiana coastal zone were addressed above. It is therefore important that scientists and land managers evaluate the probable effects of the various threats to the resource and formulate strategies to minimize or even reverse their impacts. The research undertaken in this dissertation was designed to address this need by (1) providing information that may better define the effects of saltwater intrusion and flooding on baldcypress, and (2) exploring the potential for the development of more salt-tolerant lines of baldcypress, which could be used in restoration projects.

There is currently a considerable amount of interest in restoration of coastal wetlands, including cypress-tupelo swamps (Kusler and Kentula 1990; Platt and Brantley 1990). Although reestablishment of the original hydrologic regime (*i.e.*, freshwater and seasonally to semipermanently flooded) is undoubtedly the best strategy for restoration of cypress-tupelo swamps, this may not be feasible in all cases because of the cost or because it may result in flooding of property or interference with navigation.

An alternative strategy that may be feasible in some cases is to combine partial reestablishment of hydrology with the use of planting material that is moderately salt

tolerant. This approach is analogous to that advocated by Epstein et al. (1980) and others for agriculture on saline soils. Epstein et al. (1980) believed that an "engineering approach" to the salinity problem was no longer adequate by itself and should be combined with a "genetic approach," involving the development of salt-tolerant crops.

The possibility that the genetic approach might be feasible for baldcypress is supported by Pezeshki et al. (1990). They indicated that apparently salt-resistant stands and individual baldcypresses have been reported, suggesting that intraspecific variation in salt tolerance may exist. They further proposed that the development of salt-tolerant lines of baldcypress may be possible.

SCOPE OF STUDY

Although baldcypress is widely distributed (Figure I.1), the major focus of this study is on intraspecific variation of baldcypress found in southern Louisiana. This choice is based partly on logistical considerations and partly on evidence that the problem of saltwater intrusion is particularly acute in southern Louisiana. Some trees from Mobile Bay, Alabama were also included in this study because scientists from the National Wetlands Research Center familiar with the bay suggested that they appeared to be growing on sites with particularly high salinity.

Baldcypress was chosen for this investigation rather than associated species such as water tupelo for two main reasons. First, reports (e.g., Chabreck 1972; Montz and Cherubini 1973; Wicker et al. 1981) and personal observations suggest that baldcypress is more prevalent than its common associates on sites closest to the swamp-marsh interface, where the impacts of saltwater intrusion are likely to occur first. Second, as mentioned in the previous section, there is some evidence for the existence of substantial intraspecific variation in the salt tolerance of baldcypress, but there appears to be no corresponding evidence for species such as water tupelo.

DISSERTATION OBJECTIVES

The specific objectives of this dissertation are to:

(1). Identify (*i.e.*, locate in field) individual mature baldcypress trees that appear to have a higher degree of combined salinity and flooding tolerance than the general population of baldcypress.

(2). Compare survival and growth responses of open-pollinated progeny (seedlings) obtained from the trees identified in Objective 1 to flooding with water of five salinity levels, and compare these responses to progeny of parent trees from freshwater environments.

(3). Evaluate the physiological responses of a subset of the seedlings referred to in Objective 2 to (1) better understand the overall effect of salinity on baldcypress seedlings and (2) determine whether one or more of these responses may prove useful for screening seedlings for salinity tolerance.

DISSERTATION OVERVIEW

Existing literature relevant to this study is reviewed in Chapter 1. The chapter contains two major sections. The first section is a review of the literature on the physiological and ecological impacts of flooding and salinity on baldcypress. The second section is a broad review of the literature on salt tolerance in general and, in particular, the prospects for increasing the salt tolerance of forest tree species.

Chapter 2 describes part of the results of a greenhouse experiment designed to evaluate the performance of 15 open-pollinated families of baldcypress when subjected to a range of salinity treatments. The performance of the individual families is evaluated using survival, height growth, leaf area, total biomass and two indices of tolerance as response variables. The salinity regime of the apparently salt-tolerant parent trees is summarized in this chapter.

Chapter 3 also addresses the greenhouse experiment, but the emphasis is placed on differences in biomass partitioning and seedling morphology. Specific factors examined in this chapter include differences in biomass partitioning among roots, stems and leaves, changes in mean numbers of leaves per seedling, mean size (area) of individual leaves, and changes in root density.

In Chapter 4, impacts of salinity on the physiology of baldcypress seedlings are examined. This chapter presents the results of an experiment that ran concurrently with the greenhouse study. The physiological responses were evaluated on a subset of seedlings from the larger greenhouse experiment, which were temporarily moved indoors to more controlled environmental conditions. The physiological response variables measured included net photosynthesis, stomatal conductance, transpiration rate, leaf water potential, and chlorophyll fluorescence. This chapter also includes the results of tissue analyses that were conducted at the end of the experiment. Concentrations of Na^+, K^+, Ca^{2+}, and Cl^- were measured in leaf, stem, and root tissues, and differences in concentrations are discussed in relation to salinity levels and families.

In the final chapter, research highlights are discussed and overall conclusions are drawn. In addition, suggestions for further research are presented.

Chapters 2-4 were written as stand-alone chapters intended for submission to appropriate journals. They have been reformatted for this dissertation, but otherwise have not been substantially changed. Consequently, there is some duplication of material among these chapters and also with the introduction and literature review chapters. Chapter 2 has been accepted for publication in the journal Forest Ecology and Management (Allen et al. in press). A modified (shortened) version of the second section of the literature review chapter has been published in the journal Tree Physiology (Allen et al. 1994). In addition, information from the literature review was presented at an IUFRO-sponsored workshop on the ecophysiology and genetics of trees and forests in a changing environment, held in Viterbo, Italy in May of 1993.

CHAPTER 1

LITERATURE REVIEW[1]

EFFECTS OF FLOODING AND SALINITY ON BALDCYPRESS

The baldcypress resource of greatest concern in the context of this study is that occurring in the Louisiana coastal zone. There is considerable evidence that human-induced and natural changes in the region are acting to increase both the amount of flooding in coastal swamps and, in some areas, the salinity (Wicker et al. 1981; Salinas et al. 1986; Conner 1988; Templet and Meyer-Arendt 1988). Furthermore, widely accepted scenarios for global climate change suggest that both of these problems may be greatly compounded in the future, mainly through the effects of sea level rise (Bolin et al. 1986; Titus 1988) and possibly also due to more intense (Emanuel 1987) and/or frequent hurricanes.

Effects of Flooding

Several researchers have documented recent increases in the depth and duration of flooding in coastal

[1] A substantial portion of this chapter has been published in Volume 14 of the journal Tree Physiology (Allen et al. 1994). Permission to use material from the published article has been granted by the journal (Appendix C).

baldcypress swamps (Conner et al. 1981; Wicker et al. 1981; DeLaune et al. 1987; Conner 1988). Conner (1988) and DeLaune et al. (1987), for example, showed that the number of days of flooding per year in swamp forests in the Lake Verret and/or Barataria Basins has increased dramatically since the mid-1950s, and now approaches a condition of permanent flooding. These changes in flood duration are attributed to "vertical accretion deficits," which occur when the rates of eustatic sea level rise and subsidence (*i.e.*, apparent water rise) are larger than the rate of sedimentation. Conner (1988) documented vertical accretion deficits of 2.5 mm/yr and 4.9 mm/yr in the swamps of the Barataria and Lake Verret Basins, respectively (Conner 1988). Looking at the time period of 1963-1984, DeLaune et al. (1987) documented an even larger vertical accretion deficit for a site in the Lake Verret Basin. Using ^{137}Cs dating, they determined that sedimentation averaged 0.63 cm/yr, whereas the apparent water level rise was 1.36 cm/yr, yielding a deficit of 7.3 mm/yr.

Baldcypress is consistently reported to be highly tolerant of flooding and soil saturation (McKnight et al. 1981; Hook 1984b; Brown and Montz 1986). Indeed, Keeland (1994) concluded that, once established, the optimal water table regime for baldcypress growth appears to be permanent shallow flooding. The increased flood depth and durations to which coastal swamps are being subjected, however, is

enough to threaten their long-term existence, even without the additional factor of increased salinity (DeLaune et al. 1987; Conner and Brody 1989).

One important reason for this is that baldcypress seed will generally not germinate under water (Demaree 1932), and therefore regeneration is extremely unlikely or even impossible under conditions of permanent flooding. It should be noted, however, that periodic droughts may expose the soil surface long enough to allow establishment (Conner 1988). Also, it is at least conceivable that some seedlings may become established in permanently flooded swamps either by germinating as floating seeds (Welch 1931), or by germinating on substrates such as mats of floating vegetation (Huffman and Lonard 1983). In any case, the possibilities for successful regeneration of baldcypress are likely to steadily diminish as coastal swamps become ever more deeply flooded.

Permanent, deep flooding is also likely to accelerate the decline and deaths of baldcypress trees already established. Growth is substantially reduced in permanently flooded swamps, as compared to those with intermittent flooding (Conner and Day 1976; Brown and Montz 1986), indicating that conditions are more stressful with deep permanent flooding. Mortality has been repeatedly demonstrated to increase under conditions of permanent flooding (Demaree 1932; Eggler and Moore 1961; Harms et al.

1980; Brown and Montz 1986). Regarding baldcypress trees in permanently flooded conditions, Brown and Montz (1986: p. 78) concluded that "trees in shallow water are less stressed than those in deeper water with three feet [approx. 1 m] being the depth at which the probability for death increases."

The actual mechanisms by which flooding effects trees and the adaptations by which trees cope with flooding have been reviewed several times (Gill 1970; Teskey and Hinckley 1977; Hook 1984a; Kozlowski 1984; Keeland 1994; Pezeshki 1994). When a soil is flooded, the first effect is that gas exchange between the soil and the air is drastically reduced (Armstrong 1979), which causes a series of important physical, chemical, and biological changes in the growing environment. In addition to gas exchange, Ponnamperuma (1984) described several other physical processes affected by flooding, which result in thermal effects (generally leading to lower soil surface temperatures), swelling of soil colloids, deflocculation of clays with a subsequent breakdown of soil structure, and changes in soil percolation rates (which decrease in impermeable soils and increase in permeable soils).

Shortly after flooding, microorganisms and roots usually consume the oxygen present in the soil, resulting in anaerobic, or reduced, conditions in all but a very thin layer at the soil surface (Gambrell and Patrick 1978;

Ponnamperuma 1984). If flooding persists, a well-documented sequence of chemical transformations (reductions) takes place, mediated mainly through the respiration of facultative and obligate anaerobic microbes. Gambrell and Patrick (1978) summarized the major transformations and the approximate redox value at which they occur as follows: O_2 depletion (+330 mV); NO_3^- depletion (+220 mV); appearance of Mn^{2+} (200 mV); appearance of Fe^{2+} (120 mV); depletion of SO_4^{2-} (-150 mV); and appearance of CH_4 (-250 mV).

Alterations in physical and chemical processes lead to other important changes, such as the generally observed increase in pH of acid soils, increases in specific conductance, and increases or decreases in cation exchange capacity (depending on initial pH) (Ponnamperuma 1984). The rate of decomposition of organic matter also generally decreases and the decomposer community shifts from a diverse mix of actinomycetes, bacteria and fungi to a community almost entirely composed of facultative or obligate anaerobic bacteria (Ponnamperuma 1984; Mitsch and Gosselink 1993). This community shift is critical because numerous phytotoxins are produced as the endproducts of anaerobic decomposition (Ponnamperuma 1984).

The changes in the soil environment induced by flooding affect plants in a number of ways. Aerobic metabolism of the roots is severely impaired, which in turn

reduces nearly all metabolically mediated activities such as cell extension and division and nutrient absorption (Mitsch and Gosselink 1993). If anaerobic metabolism takes place in the roots, some of the end products of fermentation can be toxic, as can the reduced forms of manganese, iron, and sulfur that occur in the soil water as a result of the transformations referred to above, if they are present in sufficient quantity (Jackson and Drew 1984). The structure of mitochondria, other organelles, and cell membranes may become irreversibly altered, leading to cell and eventually plant death (Vartapetian 1988; Jackson and Drew 1984).

Wetland plants such as baldcypress have a number of morphological and metabolic adaptations that allow them to function in an anaerobic soil environment and to complete their life cycles in situations where flooding is frequent (Hook 1984a; Drew and Stolzy 1991). Specific adaptations known for baldcypress include the ability of seeds to remain dormant under water for long periods (Wilhite and Toliver 1990); rapid juvenile growth, which helps seedlings achieve enough height to keep part of their crowns above floodwaters (Flynn 1986); the ability to develop aerenchyma in root tissue to help facilitate internal aeration (Flynn 1986; Pezeshki 1991; Yamamoto 1992; Kludze et al. 1994); development of soil water roots (Harms et al. 1980; Hook 1984a); stem hypertrophy, which appears to help facilitate

internal aeration of roots (Hook 1984a; Yamamoto 1992); ability to oxidize the rhizosphere, which may reduce the impact of toxins and improve nutrient uptake (Hook 1984a; Kludze et al. 1994), and the ability to make temporary use of anaerobic metabolic pathways (Flynn 1986; Pezeshki 1991). Whether or not baldcypress "knees" also help improve flood tolerance has not been entirely resolved, but the general consensus is their role is minor and not essential for tree survival (Hook 1984a; Brown and Montz 1986).

Much of what we know about the specific responses of baldcypress to flooding come from studies conducted on seedlings, generally under controlled conditions, although there are a number of notable studies on mature trees (Harms et al 1980; Yamamoto 1992; Keeland 1994). The focus on the seedling stage and the often short-term nature of many studies create some important limitations when attempting to assess long-term impacts to existing, mature forests. They are, however, relevant in the context of this study, because a major goal is to explore the possibility of producing seedlings capable of good initial survival and growth in situations of combined flooding and salinity stress.

Studies on baldcypress seedlings have generally found that they tolerate shallow flooding, but that flooded seedlings go through an initial period of stress and

adaptation, during which they are outperformed by unflooded, well-watered controls. For example, Shanklin and Kozlowski (1985) reported that, following 14 weeks of flooding at 2 cm above the soil surface, seedlings were 30% shorter, had 56% less leaf area, and had 51% less total dry weight than the unflooded controls. In a 126-day flooding treatment in artificial ponds, seedlings in a drained treatment had slightly higher above- and below-ground biomass, and significantly greater total biomass than seedlings flooded to a depth of 15 to 20 cm (Flynn 1986). Megonigal and Day (1992) presented a table summarizing six seedling studies with flooded versus unflooded treatments. Four showed declines in growth with flooding, one showed no effect of flooding, and one showed an increase in shoot (but not root) growth.

Seedlings generally recover from the stress imposed by continuous (but shallow) flooding and may grow as rapidly as seedlings subjected to well-watered conditions or periodic flooding. Perhaps the most interesting example of this is the three-year study of Megonigal and Day (1992), which was conducted in large outdoor rhizotrons. After one year of continuous flooding, seedlings had approximately one-third the biomass of seedlings subjected to periodic flooding. By the second year, growth of the continuously flooded seedlings had improved substantially, and by the end of the third year there were no significant differences

in total biomass between the two treatments. Improved growth in the second year coincided with morphological changes in the roots, including development of water roots and changes in root distribution.

Much of our knowledge of the physiological responses of baldcypress to flooding comes from a series of experiments first published in 1986 by Reza Pezeshki and his colleagues. In general agreement with studies of seedling growth, these experiments demonstrate that baldcypress seedlings survive and grow when flooded, but their physiological performance is initially impaired. In one 40-day experiment, Pezeshki and Chambers (1986) found that net photosynthesis (A) and stomatal conductance (g_w) of baldcypress seedlings subjected to shallow flooding declined by 21% and 41%, respectively, when compared to unflooded controls. Root elongation of flooded baldcypress seedlings was found to be depressed throughout a two-week treatment with reduced (+200 mV) soil conditions (Pezeshki 1991), and short-term declines in RUBISCO (E.C. 4.1.1.39) activity have also been found to occur following flooding (Pezeshki in press).

In at least two cases, however, recovery of A and g_w of flooded baldcypress seedlings was noted (Pezeshki et al. 1987; Pezeshki 1993). In these experiments, g_w recovered to at least 90% of pre-treatment levels and A recovered at least 80% of its pre-flooding level within a period of two

to three weeks. This recovery may be related to a resumption of root function following development of intercellular air spaces, which begin to develop in the first two weeks of flooding (Pezeshki 1991).

Effects of Salinity

In addition to increased flood durations, excess salinity is becoming a widespread factor in coastal baldcypress swamps. Although the full extent of the problem has not been defined, it is clear from reports such as those of Wicker et al. (1981) and personal observations of the author that the salinity problem is widespread. In their study of wetlands bordering Lakes Ponchartrain and Manchac, Wicker et al. (1981) concluded that the loss of 6920 hectares of baldcypress swamp between 1955/56 and 1976/78 could be attributed to saltwater intrusion. An even larger area of baldcypress swamps appear to have been lost following construction of the Mississippi River Gulf Outlet and the Houma Navigation Canal, two large canals with direct connections to the Gulf of Mexico and high salinity water (Allen 1992).

Probably the best data sets on the average level of salt tolerance of baldcypress in the Louisiana coastal zone is that of Chabreck (1972) and Wicker et al. (1981). In his study of Louisiana coastal marshes, Chabreck characterized the mean soil pore water salinity level for

five plots containing baldcypress that were near the swamp-marsh interface (i.e., the likely limit of baldcypress's mean salinity tolerance). The mean and standard deviation he reported were 1.9 and 1.4 g l^{-1}, respectively. Using data from their field surveys in Tangipohoa Parish, Wicker et al. (1981) plotted the relative rate of decrease in numbers of baldcypress trees per acre versus salinity levels, and showed that the rate of decrease began to rise sharply between approximately 1.8 and 2.1 g l^{-1}. Wicker et al. (1981) concluded from their study that baldcypress swamps are generally limited to areas where the salinity does not exceed 2 g l^{-1} for more than 50% of the time trees are exposed to inundation or soil saturation. The close agreement of these two studies is notable.

Other reports of salinity tolerance of baldcypress have been published, but are probably of less relevance or even inaccurate. Beal (1977) reported that the upper range for salinity reported for baldcypress was 0.1 g l^{-1}, which is clearly too low. Wicker et al. (1981) suggested that this value was not really meant to represent a tolerance limit, but only the range observed on the sites sampled by Beal. The highest estimate found in the literature is 8.9 g l^{-1}, reported by Penfound and Hathaway (1938). Wicker et al. (1981: p. 54) stated that "there is some question about the exact methodology used and the actual meaning of the percentage salt figure used in the Penfound and Hathaway

paper," and also indicated that this figure is generally viewed skeptically.

There is a large body of literature on the mechanisms by which salinity effects plants, which is summarized briefly in the second major section of this chapter. Relatively little information specific to baldcypress is available, especially for the effect of salinity without the additional stress of flooding.

In the few studies that subjected seedlings to salinity without flooding, baldcypress seedlings have been found to be moderately salt-tolerant. Pezeshki (1990), for example, found no significant effect on height growth, net photosynthesis, or stomatal conductance when baldcypress seedlings were watered with a 3 g l^{-1} saltwater solution for a period of 60 days. Seedlings regularly watered with a 10 g l^{-1} saltwater solution for three months also demonstrated a moderately high degree of tolerance (Conner in press). At the end of the treatment period, survival was 100% and mean height was 83% of controls watered with freshwater.

Interaction of Flooding and Salinity

Situations where baldcypress seedlings are subjected to the combination of salinity and flooding are expected to become more common in the Louisiana coastal zone. The effect of the two stresses operating concurrently should

therefore be evaluated. The possibility that there may be significant interactions appears especially likely given the conclusion of Shanklin and Kozlowski (1985) that flooding predisposes baldcypress to other types of abiotic stresses (e.g., drought and air pollution).

The combination of flooding and salinity clearly can have a dramatic impact at higher salinity levels. In contrast to seedlings watered with 10 g l^{-1} saltwater, which, as mentioned in the previous section, survived and grew reasonably well, Conner (in press) reported that seedlings continuously flooded with 10 g l^{-1} saltwater all died within two weeks. Javanshir and Ewel (1993) also reported dramatic declines in height growth and total biomass for seedlings subjected to a simulated "tidal" flooding regime with 6 and 8 g l^{-1} NaCl.

The effects of the two stresses in combination are less evident at salinity levels lower than about 4 g l^{-1}. In the same 60-day experiment cited in the previous section (Pezeshki 1990), both height growth and *A* were significantly reduced (approximately 50%) by flooding with 3 g l^{-1} saltwater when compared to well-watered controls. However, differences between the two flooding treatments (with and without saltwater), were significant only for height growth, suggesting that the addition of salt had relatively little additional impact beyond that of flooding alone. Javanshir and Ewel (1993) reported actual increases

in biomass at salinity levels of 1 and 2 g l^{-1}, and relatively little net effect on growth at 4 g l^{-1}.

A noteworthy observation of Pezeshki's (1990) study is that the combination of flooding and salinity did not significantly reduce g_w but did significantly reduce A, suggesting that non-stomatal factors are a major factor limiting photosynthesis. The predominance of non-stomatal factors in limiting photosynthesis was also evident in an earlier study (Pezeshki et al. 1988). In this study, seedlings were subjected to flooding with salinity levels of 0, 2, 4, 6, and 8 g l^{-1}, and the relationship between leaf tissue concentrations of Na^+, K^+, Ca^{2+}, and Mg^{2+} and A was examined. Relatively strong and negative correlations between leaf ionic content and A were found for all ions. This finding, along with the fact that internal leaf CO_2 concentrations were found to remain constant over a wide range of leaf ionic concentrations, suggested to the authors that excess levels of ions were disrupting photosynthesis, perhaps through inhibition of the activity of RUBISCO or other enzymes.

PROSPECTS FOR INCREASING THE SALT TOLERANCE OF FOREST TREE SPECIES

Although high concentrations of salt generally cause extensive damage and mortality in forest tree species, it has been suggested that some areas with excess salinity

also present excellent opportunities for their use (Yadav 1980; El-Lakany 1986; National Academy of Sciences 1990; Marcar et al. 1993). While the potential for commercially viable timber production on saline sites appears limited (Marcar et al. 1993), numerous other possible uses exist. Forest trees have already been used in some cases, such as combatting secondary salinization in Australia (Greenwood et al. 1992; Schofield 1992), and for fuelwood production in India and Pakistan (National Academy of Sciences 1990). There is also considerable potential for planting trees on saline sites to provide food for humans, fodder for livestock, and other products ranging from pulp and fiber to essential oils (National Academy of Sciences 1990).

In some cases, suitable planting material already exists for the applications described above. The salt tolerance of many forest tree species has been investigated in greenhouse and field trials and the results of some of these trials have been summarized. Marcar et al. (1993), for example, list 49 species of eucalypts (Eucalyptus), acacias (Acacia), melaleucas (Melaleuca), or casuarinas (Casuarina) native to Australia that are ranked as salt tolerant to highly salt tolerant. Eight of these species can tolerate average root zone salinities in the range of 15-40 dS/m (EC_es) [approximately 9-26 g l^{-1} NaCl]. El-Lakany (1986), Midgley et al. (1986), the National Academy of Sciences (1990) and Gill and Abrol (1991) also provide

information on tree and shrub species that are suitable for use on saline sites.

There are other situations where it may be desirable to improve the tolerance of a particular salt- sensitive (or at best moderately tolerant) tree species so that it can be planted on saline sites. One goal of the present research, for example, is to develop tolerant lines of the salt sensitive species baldcypress for use in restoration of swamps damaged by saltwater intrusion.

Evidence for Genotypic Variation in Salt Tolerance

To justify investments in salt-tolerance improvement programs, it must first be demonstrated that at least one of two conditions exists. Either suitable genetic variation in salt tolerance must already exist within the species of interest, or it must be feasible to introduce suitable variation, either through hybridization with related species, genetic engineering, or induced mutations. After a brief discussion of methodological considerations involved in measuring variation in salt tolerance, evidence for the existence of suitable intraspecific variation is reviewed.

Measurement of Variation in Salt Tolerance

The exact mechanisms of genetic control and the major genes controlling salt tolerance have not yet been

identified (see section on genetic control of salt tolerance). Thus, genetic variation can only be demonstrated indirectly, by measuring the response of different genotypes to various levels of salinity.

Probably the most suitable response to measure is growth or yield, especially at moderate salinities (Shannon 1985). The ability to simply survive high salt levels is also quite important and has been a widely evaluated response (Marcar et al. 1993). Maas and Hoffman (1977) proposed using a simple linear equation of the form $y = a + b(x)$, where y = yield relative to controls and x = conductivity of the saturated soil extract of the root zone (in dS/m), for comparing the range in response. Shannon (1985) described this approach as suitable for interspecific comparisons but suggested using absolute yield for intraspecific comparisons.

Other measurements of plant response to salinity that have been used or suggested include germination rates (Bangash 1977; Sands 1981; Totey et al. 1987); ion concentrations in various plant tissues (Townsend 1980; Noble and Rogers 1992); changes in water status, net photosynthesis, stomatal conductance, or chlorophyll fluorescence (Land 1974; Smillie and Nott 1982; Pezeshki and Chambers 1986); indices or symptoms of tissue damage (Land 1974; Dochinger and Townsend 1979; Francois 1982;

Treacy 1984); and recovery rates after exposure to salinity is removed (Shannon 1978).

A host of factors has been found to interact with salinity, further complicating analyses of variation in salt tolerance. Shannon (1979), citing many earlier studies, pointed out that the effect of salinity on a plant may depend on ontogeny, humidity, temperature, light, irrigation management, cultural practices, soil fertility, air pollution, and the particular growth or yield parameter measured. Others have found or suggested interactions between salinity and soil calcium levels (Cramer et al. 1990; Rengel 1992; Maas 1993), flooding (Pezeshki et al. 1990; Pezeshki 1992; van der Moezel et al. 1991), and atmospheric CO_2 levels (Ball and Munns 1992). The choice of potting media may affect results in otherwise tightly controlled greenhouse studies (Townsend 1984) and variation in conditions within a single field has been shown to be a major confounding factor in field trials (Pepper and Craig 1986; Thomson 1988).

The nature of the "salinity" imposed is also an important consideration. While most studies have used NaCl, others have used different salts, combinations of salts, seawater, or artificial seawater. Several investigators have compared the responses to different salts (e.g., NaCl vs. $NaNO_3$) and found significant differences in their effect (e.g., Banuls and Primo-Millo

1992). The rate at which the salinity of the rooting zone is increased is another important consideration, since different adaptive mechanisms may be involved in gradual acclimation to salinity versus the adjustment to a sudden increase (Thomson 1988).

Evidence of Genetic Variation

Despite frequent methodological differences between studies such as those discussed above, enough evidence exists to conclude that substantial intraspecific variation in salt tolerance exists for many species of plants. Not surprisingly, much of the best evidence for intraspecific variation comes from studies on agricultural plants, particularly annual crops. Significant intraspecific variation has been found in barley (Hordeum vulgare; Epstein et al. 1980), wheat (Triticum aestivum; Epstein et al. 1980), rice (Oryza sativa; Downton 1984) and in forage crops, such as alfalfa (Medicago sativa; Allen et al. 1985; Rumbaugh et al. 1988; Mohammed et al. 1989; Al-Niemi et al. 1992) and tall wheatgrass (Agropyron elongatum; Shannon 1978).

A significant range of salt tolerance has also been found in woody perennial species used for fruit production. In avocados, for example, it has been found that rootstocks from Guatemalan or West Indian sources are more effective in excluding Cl^- ions than rootstocks from Mexico (Kadman

and Ben-Ya'acov 1976; Downton 1978). Significant variation in response to salt of rootstocks used for stone-fruit, almond, citrus and grape production has also been demonstrated (Bernstein et al. 1956; Downton 1984; Sykes 1992; Zekri and Parsons 1992).

The wide range of salt tolerance found for some crop species has not yet been convincingly demonstrated for woody perennial fruit crops, however. Whereas some annual crops have been grown at salinity concentrations equal to seawater [approx. 35 g l^{-1}], Downton (1978) compared avocado rootstock performance over salinity levels of only 0, 0.6, and 1.2 g l^{-1} NaCl. In general, salinity concentrations used are 6 g l^{-1} NaCl or less (Ziska et al. 1991). Most woody perennial fruit crops are classified as salt sensitive (Downton 1984; Maas 1993).

Compared with annual crop and horticultural species, a much smaller body of literature exists on intraspecific variation in salt tolerance of forest trees. Also, far fewer genotypes have been evaluated for forest tree species. Studies such as that of Mohammed et al. (1989), which evaluated 229 alfalfa populations, are occasionally encountered in the literature on annual or forage crops. Studies of salt tolerance involving several thousand cultivars or accessions have been conducted for barley, wheat, and rice (Downton 1984). Published studies

evaluating more than three to four families or provenances are still rare for forest tree species.

One lesson that is clear from studies with crops is that far more extensive screening is necessary to make real progress in improving salt tolerance. An illustrative example is the study of Mendlinger and Pasternak (1992) on melons (Cucumis melo L.); of the 20 cultigens they tested with irrigation water at conductivities (EC_w) of 1.2, 7.5 and 14.0 dS/m [approximately 0.6, 4 and 8 g l^{-1} NaCl], only one line showed no decline in mean fruit weight (identified as the best selection criterion) at 14.0 dS/m.

Land (1974) investigated the response of four full-sib families each of loblolly pine (Pinus taeda) and slash pine (P. elliottii) to short-term flooding with two levels of salinity (0 and 26 g l^{-1} of an artificial seawater mix). Based on "M-score" ranks (an index based on visible injury where 1 represented a dead seedling and 4 a seedling with no visible injury), significant differences were found between families for each species. "M-scores" for each family ranged from 1.42 to 2.67 for loblolly pine and 1.75 to 3.44 for slash pine, indicating quite a substantial range in the degree of injury.

Dochinger and Townsend (1979) compared responses of one Canadian and two American provenances of red maple (Acer rubrum) to exposure to three levels of salinity (0, 2 and 4 g l^{-1} NaCl) over a 42-day period. They found a wide

range of performance in height growth relative to controls. For one provenance (from Maine), seedlings exposed to 4 g l^{-1} salinity were approximately 80% as tall as the controls, while for a less tolerant provenance from Ohio, the seedlings were approximately 40% of the height of the controls.

Treacy (1984) studied the effects of aerially applied doses of NaCl to seedlings of 11 open-pollinated families of Quercus virginiana (Live oak). Treatments of up to 0.3 g m^{-2} NaCl were applied four times each month, for a full year, to the treatment areas. Effects of higher levels of NaCl exposure were visually apparent and significant on a quantitative basis. Higher salt exposure levels also resulted in significant declines in height growth, diameter growth, leaf area, and leaf dry weight. Treacy used a salt tolerance index, based on the percent attainment of height and diameter growth relative to control treatment seedlings, to rank the salt tolerance of the open-pollinated families. Salt tolerance index for the 11 families varied from 95 to 218. The highest ranked family actually performed better under the high salt level than it did under well-watered, nonsalt exposure conditions. The highest ranked family was significantly different from the second highest ranked family. Height growth of seedlings exposed to high salt environments relative to their respective family in the control treatment was the most

sensitive variable measured. Open-pollinated families in Treacy's study were obtained from the Mississippi coastline, the Louisiana coastline, and the Baton Rouge, LA (inland) area. There were not significant differences in salt tolerance by location. Treacy's highest ranked salt-tolerant family source was located in Baton Rouge, the second ranked family was from the Mississippi coast and the lowest ranked family was from the Louisiana coast. Rankings in between the extremes varied widely within and among source locations. The lack of consistency in relation to source location of salt-tolerant families suggests that selection from areas of high-salt environments does not necessarily confer greater salt tolerance.

Sands (1981) compared germination and seedling survival and growth of three seed sources of Eucalyptus camaldulensis, which were obtained from areas of low, medium, and high soil salinities. Seed from the low salinity source had the poorest germination and subsequent seedling growth when subjected to salinity levels of 3, 6, 11 and 22 g l^{-1} NaCl. Although the 3-month treatment period was not long enough to cause mortality, Sands concluded that none of the seedlings from the lowest salinity seed source had any chance of long-term survival at 22 g l^{-1} NaCl. This was in marked contrast to the seedlings from the other two sources, which still appeared healthy,

especially those from the source with the highest soil salinity.

Significant variation in E. camaldulensis seedling survival and growth in relation to salinity was also found by Thomson (1988), who evaluated 53 seed sources from throughout the natural range of the species. The mean level of salinity causing mortality of seedlings grown in a nutrient solution varied by seed source from 21 to 37 g l^{-1} NaCl. In contrast to Sands, Thomson found that NaCl tolerance was not closely correlated with soil salinity levels from the place of origin, although he suggested that localized selection for NaCl tolerance appeared to have occurred on some of the most saline sites he investigated.

At least one other study also found significant intraspecific variation in salt tolerance in E. camaldulensis (Karschon and Zohar 1975). In addition, significant intraspecific variability has been demonstrated for numerous other Australian tree species, including other members of the genus Eucalyptus (Thomson 1988; Van der Moezel et al. 1991), Melaleuca species (Van der Moezel et al. 1991); and Casuarina species (El-Lakany and Luard 1982; Van der Moezel et al. 1989). Australian researchers have also demonstrated intraspecific variation in salt tolerance of Monterrey pine (Cromer et al. 1982).

In a study of arid zone species, Rhodes and Felker (1988) subjected 100 seedlings each of nine Prosopis

species or hybrids to a gradual increase in salinity from 0 to 33 g l^{-1}, and found that some individuals from five of the species exhibited good growth even at 33 g l^{-1} NaCl. All the Prosopis species tested had individuals capable of maintaining good growth at 18 g l^{-1} NaCl (half of seawater salinity), which would make them useful in many environments too saline for most agricultural crops.

While provenance-level variation in salt tolerance is significant in many species, the tree-to-tree, or within-population, variation also appears to be high. Thomson (1988) suggested that this has three important ramifications. First, when investigating provenance level variation, at least 10 well-spaced trees should be selected from each provenance. Second, selection within populations may produce significant gains for breeders seeking to improve salt tolerance. Third, within-population variation may hamper detection of treatment effects in physiological studies; therefore clonal plants are preferable to seedlings in physiological studies.

Mechanisms of Salt Tolerance

While not strictly necessary for a salt tolerance improvement program, it is desirable to have a detailed knowledge of both the physiological mechanisms of salt tolerance in the species of interest and the mechanisms of genetic control over salt tolerance (Shannon 1985). Such

knowledge could greatly improve the effectiveness of an improvement program in several ways, such as by providing the basis for development of rapid screening procedures or choosing breeding or propagation systems (Yeo and Flowers 1986; Waisel 1989; Noble and Rogers 1992).

Physiological Mechanisms of Salt Stress and Tolerance

Plants can be classified as halophytes (plants that thrive in moderate or high salinity) or glycophytes (nonhalophytes; salt-sensitive plants). The distinction between these two broad classes is important because they tend to have different mechanisms of coping with salt (Flowers et al. 1977; Greenway and Munns 1980; Yeo 1983). Because the tree species of concern in this paper are nonhalophytes, the remaining discussion in this section will not address halophytes.

An in-depth discussion of the large body of literature on the physiology of salt stress is beyond the scope of this chapter. In general terms, three major types of mechanisms are thought to be responsible for most of the adverse effects, each of which is briefly summarized below.

Some evidence indicates that the main effect of salinity is indirect, through its influence on plant water relations (Greenway and Munns 1980). The reduced osmotic potential of soil solutions high in salinity may make uptake of both water and nutrients more difficult for

plants unable to adjust their internal osmotic potentials sufficiently. This in turn causes drought or nutrient stress. It appears that the effects of salinity on root water status, which in turn may cause a signal resulting in reduced leaf expansion, may be the most important short-term effect of salinity on plants (Munns and Termaat 1986).

Other evidence suggests that the salt ions (primarily Na^+ or Cl^-) act upon the plant in a more direct manner, either through a specific toxicity or by disturbance of metabolic pathways due to ion imbalances. Growth or yield of some woody species such as avocado and grape have been reduced by levels of soil water Cl^- which were too low to have caused water deficits (Greenway and Munns 1980). In situations of long-term exposure to salinity, the maximum concentration of salt tolerated by fully expanded leaves is probably the most important factor affecting plant performance (Munns and Termaat 1986, Sykes 1992).

A third group of potential impacts arises from changes in the energy relations of plants (Pasternak 1987). These changes in energy may be the result of reduced ATP and reduced translocation of carbohydrates. Other changes may result from the diversion of photosynthates from growth to osmoregulation or changes in growth regulators. Pasternak indicated that still other changes in energy relations may result in increased expenditure of energy for maintenance respiration or ion transport.

The mechanisms of salt tolerance -- some use the term resistance (Levitt 1972) -- are thought to fall into two broad classes: avoidance and tissue tolerance. Avoidance refers to the ability to keep salt ions away from parts of the plant where they are harmful and may operate through passive exclusion of ions because of membrane permeability, active extrusion (via ion pumps) or dilution through the development of succulent tissue. Tissue tolerance refers to situations where salt ions accumulate in tissues, and their presence is accommodated by some means, usually by compartmentation in vacuoles and corresponding osmo-regulation in the cytoplasm (Greenway and Munns 1980; Tal 1983).

Differences in tissue tolerance have been suggested to account for intraspecific differences in salt tolerance for E. camaldulensis (Sands 1981). Considerably more evidence has accumulated, however, that demonstrates that a better ability to exclude Na^+ or especially Cl^- ions from roots or shoots is the most important mechanism operating in salt tolerant lines of woody species. Studies have demonstrated differences in the ability of individual plants, provenances, or cultivars to exclude Na^+ or Cl^- in citrus (Maas 1993), Eucalyptus spp. (Thomson 1988), Monterrey pine (Cromer et al. 1982), and numerous annual crop species (Greenway and Munns 1980). Storage of chloride ions in less sensitive areas of the plant, such as in vacuoles of

ray cells and in the lumen and cell walls of trachieds, has also been shown to occur in trees (Foster and Sands 1977).

To date, knowledge of the physiological mechanisms responsible for intraspecific differences in salt tolerance has not been used effectively for screening (Noble and Rogers 1992). It appears that the use of physiological criteria for screening is already possible, however, and may be applied on a much wider scale in the near future. For example, particular differences in lipid composition have been correlated with ability to exclude Cl^- in grapevine and citrus rootstocks (Kuiper 1968; Douglas and Walker 1984); screening for this attribute may therefore prove useful. Likewise, if the mechanism of stress is reduced intracellular water potential, and tolerant genotypes are found to possess the capability of producing large amounts of compatible solutes useful for osmotic adjustment, screening could be targeted towards locating plants with this capability (Waisel 1989).

Noble and Rogers (1992) suggested that several basic questions be answered before physiological mechanisms can be used as selection criterion for improving salt tolerance. First, they indicated that sufficiently heritable genetic variation must exist in the mechanism to allow selection and breeding to work. Second, since a combination of physiological mechanisms is almost always involved in salt tolerance, the mechanism of major

importance must be targeted. Third, rapid screening techniques must be widely available for the mechanism in question. Finally, it will be beneficial if different mechanisms can be studied separately and the results of selection later recombined for an optimum outcome. For trees this approach would require, for example, selection of families with the ability to adjust osmotically to high salinity environments, selection of other families with variation in the ability to exclude Na^+ and Cl^- ions from the foliage, and finally combination of these traits through breeding programs.

Screening of large numbers of families may require measurement of integrating physiological processes or higher level physiological response traits such as photosynthesis, stomatal conductance, pressure volume assessments of osmotic changes, changes in maintenance respiration or the appearance of certain morphological traits. Other screening measurements may include nutrient ratio changes (e.g., Ca^+/Na^+, Na^+/K^+). Changes in several of these physiological responses after exposure to salinity have been reported in trees by Pezeshki and Chambers (1986), Banuls and Primo-Millo (1992) and Golombek and Ludders (1993). Pasternak (1987) presented a model for protective physiological and morphological mechanisms for salinity tolerance that provides additional insight into

the possible areas for fruitful screening for salt tolerance based on physiological mechanisms.

Genetic Control of Salt Tolerance

A considerable amount of evidence has been amassed demonstrating that the genetic control of salinity resistance in annual crops such as soybean, wheat and rice is a complex, polygenic trait (Dvorack et al. 1992). The conclusion that a complex pattern of inheritance is also found in trees is supported by Cooper and his associates (e.g., Cooper and Gorton 1952), Furr and Ream (1969), Sykes (1992) and others working with citrus rootstocks. Both Furr and Ream (1969) and Sykes (1992), for example, demonstrated continuous variation in the pattern of Cl^- uptake in progeny of various combinations of salt tolerant, moderately tolerant, and intolerant material.

Despite the complex inheritance pattern exhibited by species investigated to date, it is apparent that genes with major effects on salt tolerance can be found and that salt tolerance is amenable to breeding. The inheritance of large differences in the capacity for Cl^- exclusion between two soybean cultivars is reportedly controlled by a single gene pair (Abel 1969). A single dominant gene has been implicated as the major factor controlling the inheritance of Cl^- exclusion in Vitis berlandieri (Newmann and Antcliff 1984). Nabors et al. (1975) and Orton (1980), based on

work with tobacco and barley, respectively, have both speculated that large gains in salt tolerance can be made with simple genetic manipulations.

Dvorack et al. (1992) cite the K^+/Na^+ discriminating locus on wheat chromosome 4D and the major effect of Lophopyrum elongatum (a wild relative of wheat) chromosome 3E as examples of progress being made in the identification of major genes. Galiba et al. (1992) also have reported progress towards the location of major genes responsible for cultivar differences in the osmo-regulation of wheat. To our knowledge, no significant progress in the identification of major genes controlling salt tolerance has been made for forest tree species, but such progress seems quite possible with sufficient effort.

Progress in Increasing Salt Tolerance

To date, little progress has been reported in increasing salt tolerance of forest tree species or in the general release of salt tolerant lines. If the results of breeding for salt tolerance in crops is a reliable indicator of what can be accomplished for forest trees, however, then the prospects appear fairly good. In the following subsections, some of the progress with crops, and what little there has been with trees, is described.

Progress Using Conventional Plant Breeding Techniques

Impressive gains in salt tolerance have been made for some crops by using conventional selection and breeding techniques. Epstein et al. (1980), for example, reported that after only a single selection cycle, they obtained strains of wheat that produced higher yields at 20, 40 and 60% of seawater salinity than an Indian variety known for its relatively high salt tolerance. Yield relative to 0% salinity controls was low even for the most tolerant strains, but repeated selection may result in much greater gains.

Some of the most impressive gains have been reported for alfalfa, at least at the level of ability to germinate in saline conditions. In one study, Allen et al. (1985) went through five cycles of mass selection, starting with seeds of the "Mesa-Sirsa" variety. During each cycle, the osmotic potential of the solution needed to produce 1% germination was calculated by subjecting a total of 10,000 seeds to five different levels of salinity and developing a regression between germination percentage and the osmotic potential of the solutions. Over the course of the five cycles, the osmotic potential required for 1% germination dropped from -1.40 MPa to -2.45 MPa [approximately 18 to 32 g l^{-1} NaCl]. Over the same five cycles, germination at a standard osmotic potential of -1.30 MPa [approximately 17 g l^{-1} NaCl] increased from 3% to 86%. The authors' estimates

of broad sense heritability averaged 49.9% over the course of the experiment, which is in the range of forest tree traits, such as wood specific gravity, that are considered amenable to improvement.

In at least one case where little intraspecific variation in salt tolerance was found within a species (tomato, Lycopersicon esculentum), it was shown that salt tolerance could be improved by hybridization. A related species (L. cheesmanii), which is found in low-lying, high-salinity areas of the Galapagos Islands, was crossed with commercial tomato cultivars. Epstein et al. (1980) reported on a series of crosses to improve salt tolerance and backcrosses to incorporate desirable fruit characteristics, which produced plants capable of growing at 70% of full-strength seawater and still producing fruit of reasonably good quality. We are not aware of any attempts made to develop salt tolerant hybrid trees, but the ease with which some species hybridize within genera with salt tolerant and sensitive species (e.g., Eucalyptus and Prosopis) suggests that this may be a viable approach.

Given that most of the reports on improvement in salt tolerance of crops are relatively recent (mid-70's or later), it is not surprising that no reports of more than an initial selection of salt tolerant varieties of forest tree species were located. Work on crops would no doubt have begun earlier due to their greater economic

importance. Also, because of the long breeding cycle of trees, studies involving multiple cycles of selection (such as Allen et al. 1985 for alfalfa) will probably not be seen for many years.

Most of the studies cited earlier to demonstrate intraspecific variability in salt tolerance of trees were not associated with tree breeding programs, and the most tolerant individuals found were not retained for breeding. A few of the papers, however, did mention that the most tolerant individuals were being retained and propagated. Rhodes and Felker (1988), for example, retained the best individual Prosopis seedlings and vegetatively propagated them. Although they have not continued their investigation of salt tolerance in Prosopis, they have kept 30 individuals for cloning and have passed on some clonal material to researchers in Pakistan (Peter Felker, Texas A&I University, pers. comm.).

Thomson (1988) and Van der Moezel et al. (1991) reported that the most tolerant individuals identified in their studies have been used for micropropagation of salt tolerant clones. Marcar et al. (1993) list 38 species for which one or more salt- tolerant clones (up to a maximum of 35 for E. camaldulensis) are being held in vitro at the CSIRO Division of Forestry and Forest Products in Canberra, Australia. A salt-tolerant line of Casuarina glauca

developed in Egypt is also reportedly available (Hosny El-Lakany, American University in Cairo, pers. comm.).

About 12 field trials using clonal material are currently underway in Australia (Nico Marcar, CSIRO, pers. comm.), a few of which are 7 years old. Field trials of salt-tolerant lines as old as 8 years are also reportedly underway in Egypt (Hosny El-Lakany, American University of Cairo, pers. comm.). Additional field trials are underway in India, Pakistan and Thailand (Beckmann 1991) and in California (National Academy of Sciences 1990).

Although there is justification for optimism regarding the prospects for improving salt tolerance of forest trees, there are also equally compelling reasons for caution in interpreting the results to date. One important reason for caution is that, to our knowledge, data from the ongoing field trials involving clonal material have not been published.

Furthermore, some general statements on the ongoing field trials are apparently contradictory. Schofield (1992: p. 7) stated that field trials in Western Australia "have demonstrated the superiority of clonal lines over unselected seedlings." In contrast, Marcar et al. (1993; p. 18), citing unpublished data, state that "preliminary trials incorporating clonal vs. seedling plants of E. camaldulensis on moderately saline sites in New South Wales

do not indicate any significant advantage of using clonal material."

It is becoming apparent that, for many applications, lines must be selected for both salt and waterlogging tolerance. This may explain the apparent contradiction in the Australian trials; clones selected for tolerance to both stresses are reportedly performing better than clones selected strictly for salt tolerance (Nico Marcar, CSIRO, pers. comm.). Some salt-tolerant clonal material of Prosopis has performed poorly in field trials in Pakistan because of low waterlogging tolerance (Felker 1992). It has been well-established that waterlogging reduces the salt tolerance of many species (Van der Moezel et al. 1991; Pezeshki and Chambers 1986; Noble and Rogers 1994; Conner in press), and clearly more attention needs to be paid to screening for both types of stress in combination.

The necessarily long-term nature of field trials also argues against too much early optimism about prospects for improving salt tolerance. In a species-level screening study in California, Donaldson et al. (1983) reported that of 55 species of Eucalyptus investigated, 6 failed within 1-2 years, 7 failed within 4-5 years and 16 more failed after 8-10 years. Only 17 species still had acceptable survival and growth after 8-10 years. Intraspecies trials may be subject to similar patterns of performance over time.

A tradeoff between yield at low salinity levels and tolerance at high salinity levels, such as mentioned earlier for wheat (Epstein et al. 1980), may also exist for forest tree species. Thomson (1988) compared the stemwood productivity of E. camaldulensis from provenance groups rated as salt tolerant, salt sensitive or of intermediate tolerance. The sensitive provenances were more productive until salinities reached about 10 dS/m [approximately 6 g l^{-1} NaCl]. This tradeoff may not be universal and may not be critical for many current applications, but is worth considering in future improvement efforts.

Progress Using Biotechnological Techniques

When low levels of genetic variation for an important trait limit traditional breeding methods, alternative approaches such as in vitro selection, somaclonal variation, mutation breeding, recombinant DNA techniques, or somatic hybridization may provide the needed variation. Efficient tissue culture systems and genetic transformation systems need to be developed for most biotechnological techniques to be successfully applied to trees. Major progress has been reported for the areas of somatic embryogenesis in conifers (Gupta et al. 1993), and stable transformation by particle bombardment and regeneration of white spruce (Picea glauca; Ellis et al. 1993) and papaya (Fitch et al. 1992). Continued progress in the

manipulation of trees by these techniques will likely follow the results of crop plants where species such as wheat (Vasil et al. 1992), which had been recalcitrant to in vitro manipulation, can now be stably transformed and whole plants regenerated.

Although many attempts have been made to increase salt tolerance of agricultural crop species by the use of cell culture techniques, little success with any plant species has been achieved with this approach to date (Dracup 1991). At least one researcher has experimented with cell culture techniques on forest tree species (Hosny El-Lakany, American University in Cairo), but we are not aware of any salt-tolerant lines of forest trees that have been developed with this approach to date. Dracup (1991) attributed the overall slow progress of cell culture techniques to the lack of a strong relation between salt tolerance at cell and whole plant levels, as well as to poor methodology in many studies. Hasegawa et al. (1990) was, however, able to select for increased NaCl tolerance (to near seawater concentrations) in cell cultures of tobacco. Regenerated plants retained the tolerance and passed the trait to their progeny. Working with Brassica juncea, Jain et al. (1991) produced two explants (out of 2620 in total) that showed increased salt tolerance, with regenerated plants retaining their salt tolerance and

producing normal seed set. Inheritance of the trait in the progeny has not been reported.

Tal (1983) cited several studies that employed tissue culture and the use of mutagens to develop lines capable of tolerating high salt concentrations. Although none of these studies involved a forest tree species, Tal cited one study of Shamouti orange (Citrus sinensis). Although Tal did not specify the increase in tolerance achieved in this study, he indicated that the increased tolerance found in the callus lines was maintained in embryos obtained from these lines. An attempt to screen for salt resistance in hybrid poplars through shoot tip and bud culture techniques reportedly met with some success (Lee et al. 1986), although we have not found any reports of subsequent field testing of the tolerant clones.

For genetic transformation to be successfully applied as a tool to increase salt tolerance, in addition to the transformation and plant regeneration systems, the genes for the trait must be available. Additionally, salt tolerance will need to be conferred by relatively few genes, as it is unlikely that polygenic traits will be manipulated by genetic engineering for the immediate future.

The presence of genes with major effects on salt tolerance suggests that genetic transformation is a viable technique that may eventually yield very substantial

results. Indeed, some progress has already been made with tobacco. Tarczynski et al. (1993) reported that they have developed transgenic tobacco plants that are able to synthesize and accumulate mannitol, an osmotically active sugar alcohol, produced by some plants and animals but not by tobacco. Transgenic plants subjected to 30 days of treatment at 15 g l^{-1} NaCl had significantly greater height and fresh weight than control plants and also had considerably better overall appearance.

In the regenerated salt-tolerant tobacco plants produced by Hasegawa et al. (1990), the mechanism for the tolerance was a modified tonoplast ATPase enzyme that allowed for greater accumulation of Na^+ and Cl^- ions in the vacuole. This ATPase has been cloned and could provide a target gene for transformation experiments.

To our knowledge, development of transgenic lines of forest trees with increased ability to synthesize and accumulate mannitol or other active osmolytes such as proline has not been attempted. We are also unaware of attempts to introduce genes for any other traits specifically for the purpose of improving salt tolerance.

Conclusions

It is apparent that there is real potential for the successful development of salt tolerant lines of some forest tree species, but little progress has been made to

date. In addition to the lack of funding put into the effort, Tal (1985) listed inadequate methods of measuring salinity, lack of information on interactions of salinity with other environmental factors, incomplete knowledge of plant responses to salinity, and the lack of reliable selection criteria as reasons for slow progress in breeding plants for salt tolerance. A greater understanding of juvenile-mature correlations of salt tolerance is also needed (Townsend 1989).

Probably the most immediate gains can be made for trees by much more intensive screening and selection and, most importantly, field progeny testing. No more than 10 to 20 provenances of most species have been evaluated for salt tolerance. Even more significant gains should be possible by individual selection (as compared to evaluation of provenances), particularly in cases where large numbers of individuals have been exposed to saline conditions.

Biotechnological approaches are also promising and should be vigorously pursued. They probably will not yield the immediate returns possible through more intensive selection and cloning, however, and should be viewed as more of a long-term strategy.

To our knowledge, no seed orchards have been developed to produce salt-tolerant seed. As the field trials established with clonal material begin to yield results, this would appear to be an important next step. The

reasonably high degree of inheritance of salt tolerance found in woody species suggests that seed orchards with several proven clones will be effective in producing salt-tolerant planting material. The idea of converting existing field trials to seed orchards is currently being considered in Australia (Nico Marcar, CSIRO, pers. comm.) and may prove to be an efficient approach.

The extensive micropropagation of salt-tolerant clones reportedly underway in Australia could also be expanded to other countries, but care should be taken to ensure that an adequate number of clones is developed to preserve overall levels of genetic variation. Large-scale micropropagation may not yet be economically feasible in all countries (Hosny El-Lakany, pers. comm.), but over time may become more widely used.

Given the increasing demands for good quality land for food production worldwide and the probability that some types of forestry may increasingly take place on lands currently considered marginal, much more emphasis should be placed on the development of salt-tolerant lines. The evidence on salt tolerance in forest trees amassed to date demonstrates that the amount of risk incurred by investing in salt tolerance breeding programs is greatly outweighed by the potential gains.

CHAPTER 2

INTRASPECIFIC VARIATION IN THE RESPONSE OF *TAXODIUM DISTICHUM* SEEDLINGS TO SALINITY[1]

INTRODUCTION

Among the most important and distinctive types of forested wetlands in the southern United States are cypress-tupelo swamps. These wetlands, dominated by baldcypress (Taxodium distichum (L.) Rich.), together with water tupelo (Nyssa aquatica L.) and swamp tupelo (N. sylvatica var. biflora (Walt.) Sarg.), occur along many of the major rivers and smaller streams in the southeastern coastal plain.

Cypress-tupelo swamps along the Gulf of Mexico and Atlantic coasts are increasingly being subjected to stress caused by saltwater intrusion (Wicker et al., 1981; Pezeshki et al., 1987, 1990). A variety of factors has contributed to the salt water intrusion problem, ranging from land subsidence to the construction of levees and canals (Templet and Meyer-Arendt, 1988). Some swamps, especially in southern Louisiana, are also being subjected to increasing levels of flooding (Salinas et al., 1986;

[1] This chapter has been accepted for publication in Volume 70 of the journal Forest Ecology and Management (Allen et al. in press). Permission to use this article here has been granted by the journal (Appendix C).

DeLaune et al., 1987). The net result of these stresses has been a substantial and ongoing loss of coastal swamp forests (Turner and Craig, 1980; Rosson et al., 1991; Allen, 1992).

There is currently a considerable amount of interest in restoration of coastal wetlands, including cypress-tupelo swamps (Kusler and Kentula, 1990; Platt and Brantley, 1990). Although reestablishment of the original hydrologic regime (i.e., freshwater and seasonally to semipermanently flooded) is undoubtedly the best strategy for restoration of cypress-tupelo swamps, this may not be feasible in all cases because of the cost or because it may result in flooding of property or interference with navigation.

An alternative strategy that may be feasible in some cases is to combine partial reestablishment of hydrology with the use of planting material that is moderately salt tolerant. This approach is analagous to that advocated by Epstein et al. (1980) and others for agriculture on saline soils. Epstein et al. (1980) believed that an "engineering approach" to the salinity problem was no longer adequate by itself and should be combined with a "genetic approach," involving the development of salt-tolerant crops.

Because salinity is such an important agricultural problem in many parts of the world, the genetic approach is being pursued most vigorously for agricultural crops (e.g.,

Downton, 1984). Research on forest tree species has focused primarily on species capable of growth in arid and semiarid areas, and the majority of work has been on species in five genera -- Eucalyptus, Casuarina, Melaleuca, Acacia, and Prosopis (El-Lakany, 1986; Thomson, 1988; van der Moezel et al., 1988, 1989; Marcar et al., 1993). The ultimate goal of much of the work on forest tree species has been either to reclaim salt-affected lands by using trees to lower water tables (Schofield 1992) or to provide fuelwood and other forest products for people living on marginal lands (El-Lakany, 1986; National Academy of Sciences, 1990).

Pezeshki et al. (1990) indicated that apparently salt-resistant stands and individual baldcypresses have been reported, suggesting that development of salt-tolerant planting material may be possible. While several studies have examined species-level responses of baldcypress to salinity (Omran et al., 1979; Pezeshki et al., 1987, 1988; Conner, in press), to my knowledge none have examined family-level variation in salt tolerance. The objective of this study was to investigate the intraspecific variability in salt tolerance found in baldcypresses growing under flooded soil conditions.

MATERIALS AND METHODS

Plant Material

First-year seedlings from 15 open-pollinated families (hereafter referred to as families) were used in this experiment. The 15 parent trees were selected to include individuals growing in a range of salinities and to emcompass a range of geographical locations and ecological conditions. Special effort was made to select trees growing in locations with high salinity levels and trees with good form and vigor. The search for trees growing in the most brackish locations was conducted using light aircraft, boats, and motor vehicles.

Ten of the parent trees were in coastal, brackish locations in southern Louisiana or Mobile Bay, Alabama. Salinity levels at the brackish sites ranged from 0.4 and 15.3 g l^{-1} at the time of collection (Table 2.1). The other five parent trees were located in areas not subjected to brackish conditions. The approximate locations of the 15 trees are shown in Figure 2.1.

Cones from the 15 parent trees were collected during November and December 1991. Following collection, the cones were air-dried, and seed was extracted and stored at 4 °C in moist sand according to the "Collection II" procedure of Faulkner (1982). The seed was germinated in a commercial potting mixture in April 1992. In mid-May

Table 2.1. Soil and surface water salinity measurements taken adjacent to parent trees from brackish locations.

Family	Time of Seed Collection[2]	Salinity (g l^{-1}) 1993 Growing Season[1] Spring	Summer	Fall
CB2	4.5	1.1 (0.1)	0.5 (0.1)	4.0 (1.7)
CB3	4.5	1.7 (0.4)	0.3 (0.1)	5.5 (1.2)
FA1	1.8	4.7 (2.6)	7.5 (1.7)	5.1 (2.0)
FA2	15.3[3]	4.5 (1.0)	3.9 (2.1)	3.7 (1.8)
FA3	3.8	2.0 (1.6)	0.9 (0.3)	1.3 (0.6)
FA4	5.9	-[4]	-	-
PB1	6.3	2.7 (0.9)	2.5 (0.9)	6.4 (2.1)
SG2	7.2	2.2 (0.3)	2.0 (0.1)	2.7 (0.9)
VE2	0.4	0.9 (0.3)	0.3 (0.2)	1.3 (0.5)
VE3	0.7	1.7 (1.0)	1.5 (1.2)	1.4 (0.7)

[1] Average and standard deviations of four interstitial water salinity measurements taken from 15 cm below the soil surface. Spring measurements were in late March, summer measurements in late July, and fall measurements in mid-October.

[2] Salinity of nearest water body to tree; in most cases the trees were standing completely or partially in the water body. Seed was collected in November and December, 1991.

[3] At the time of seed collection the base of this tree was entirely within a small puddle; this salinity measurement is from the puddle and not the larger nearby waterbody, which is the same as FA1.

[4] This tree could not be relocated in 1993 and may have been destroyed by Hurricane Andrew, which struck the region in August, 1992.

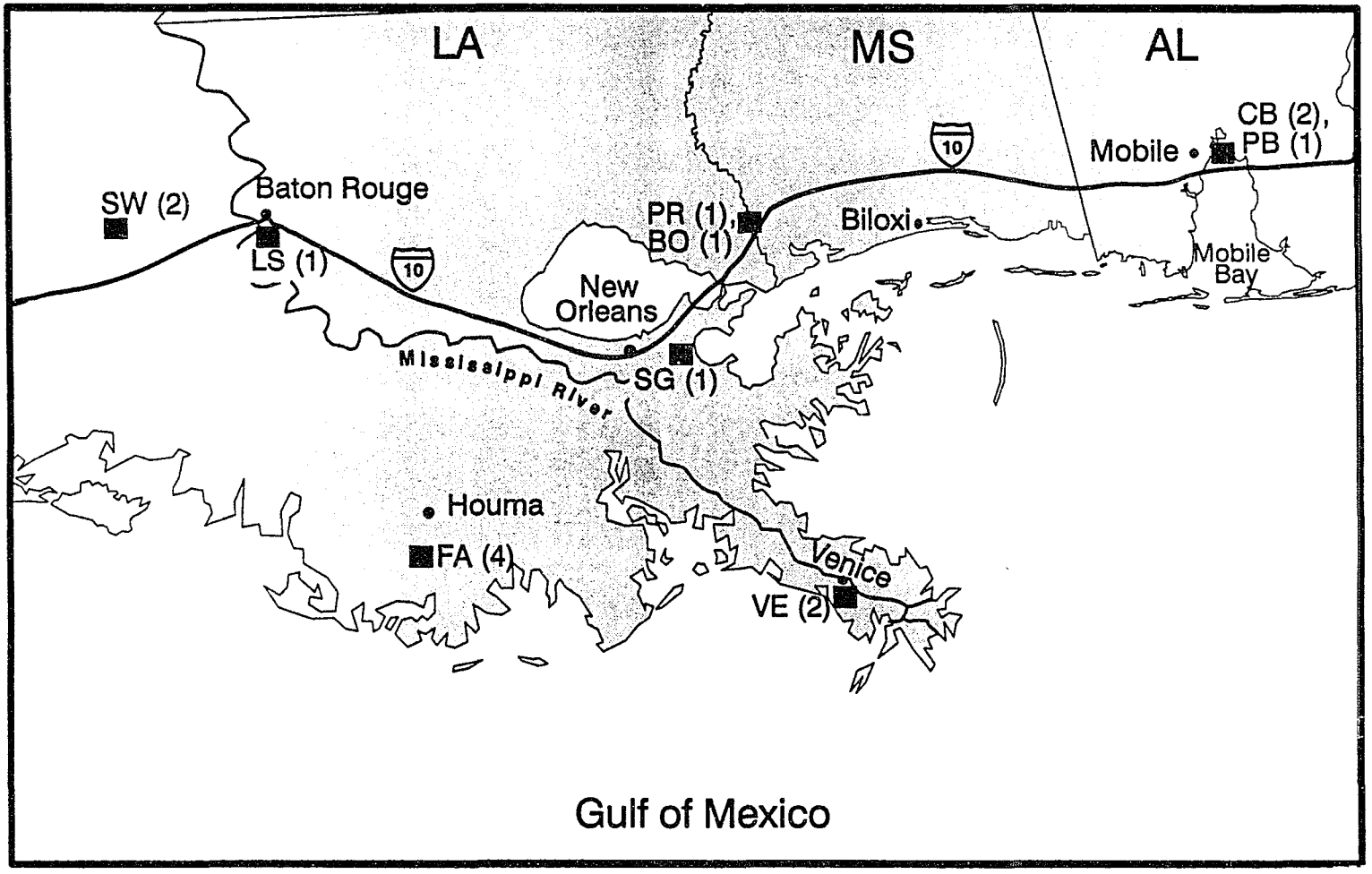

Figure 2.1. Approximate locations of parent trees. Numbers in parentheses indicate number of families from each general location.

seedlings were transplanted into 6.5 cm by 36 cm tall plastic pots ("Deepots," Stuewe and Sons, Inc., Corvallis, OR, USA) filled with equal parts sand, vermiculite, and peat.

The seedlings were kept on tables in a greenhouse until late June. They were then transferred into fiberglass tanks flooded with deionized water to approximately 5 cm above the soil surface. The tanks were located in a greenhouse under natural light conditions. The water temperature in the tanks ranged from 26 to 32 °C, with daytime temperatures generally between 28 and 30 °C. The pH of interstitial water samples taken periodically from randomly selected pots ranged from 5.9 to 6.2. Prior to flooding, the seedlings were fertilized every two weeks using a commercial 20-20-20 (N-P-K) water-soluble fertilizer (Peters Fertilizer Products, Fogelsville, PA, USA). The seedlings were fertilized with a combination of Peters 20-20-20 (2 parts) and a micronutrient fertilizer (Ferti-Lome Products, Bonham, TX, USA; 1 part) once after flooding, by injecting the fertilizer solution into the pots. After a three-week acclimation period, salt treatments were initiated in mid-July.

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 ("Forty Fathoms Marine Mix," Marine Enterprises, Inc., Baltimore, MD, USA). 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%). The seedlings were exposed gradually to their final treatment levels by raising the salinity in the tanks by 1/4 of the final treatment concentration each week for four weeks. Salinity levels were checked daily and salt or deionized water was added as necessary to maintain a nearly constant ($\pm$ 0.5 g l^{-1}) salinity level. A submersible pump was placed in the bottom of each tank to keep the water well mixed, but not aerated.

A split-plot design was used, with salinity level as the main plot treatment and family as the subplot effect. The main plots were arranged in a complete randomized block design, with three blocks. Each block consisted of five tanks (plots). Each tank contained 12 seedlings of each family, for a total of 180 seedlings per tank and 2700 seedlings in the whole experiment.

After reaching final salinity treatment levels on 6 August, the treatments were maintained through the latter part of the growing season until final harvest, which occurred over a two-week period between 26 October and 6 November.

Measurements and Data Analysis

Seedling height was monitored once a month throughout the experiment. During the harvest, height and diameter at the root collar were measured for all living seedlings. In addition, the number of leaves was counted and leaf area was measured for every third seedling. All living seedlings were separated into roots, stems, and leaves, which were dried at 70 °C to a constant weight for biomass measurement.

Because comparisons were made within one species, absolute values for height growth, leaf area, and biomass response variables were used, as suggested by Shannon (1985). To examine patterns of overall performance, two indices incorporating relative responses to salinity levels were also calculated for each family. The "Potential Survival Index" (PSI) was calculated as:

$$PSI = ((S_6+S_8)/2)/((S_0+S_2)/2)*100 * ((A_6+A_8)/2)/((A_0+A_2)/2)*100$$

where S was percent survival at the indicated salinity level (g l^{-1}) and A was mean leaf area (cm^2) at the indicated salinity level. The maximum value that could be obtained by an individual family with this index was 10,000, assuming that survival and leaf area at the 6 and 8 g l^{-1} treatments are equal to or lower than the corresponding values for the 0 and 2 g l^{-1} treatments. The

PSI was an attempt to assess future survival by combining current survival with a measure that I believed was indicative of the likelihood of future survival (remaining leaf area).

The "Potential Productivity Index" was calculated as:

$$PPI = ((S_6+S_8)/2)/((S_0+S_2)/2)*100 * ((B_6+B_8)/2)/((B_0+B_2)/2)*100$$

where B was mean biomass (g dry wt) at the indicated salinity level (g l^{-1}). The maximum value obtainable for PPI was also 10,000. This index represented an attempt to rank families both in terms of their potential survival and their potential for producing biomass (i.e., the relative productivity of surviving individuals).

Analyses of covariance were performed (using PROC GLM of the Statistical Analysis System, SAS Institute, Inc., Cary, NC, USA) to test for differences in leaf area and total biomass among salinity treatments (main plot effects), families (subplot effects) and salinity x family interactions. Because significant linear correlations were found between initial height and both leaf area and total biomass of harvested seedlings, the initial height of each seedling was used as a covariate for analyses using these variables and least square means were compared. The data on leaf area and total biomass were analyzed using the model

$$y_{ijkl}=\mu+\tau_i+\beta_j+(\tau\beta)_{ij}+\gamma_k+(\tau\gamma)_{ik}+(\tau\beta\gamma)_{ijk}+H_l$$

where y_{ijkl} = either the mean leaf area or total biomass of the kth family in the jth salinity treatment of block i, and where H_l is the covariate. Leaf area and total biomass data were log transformed to satisfy normality and homogeneity of variance assumptions.

RESULTS

Survival

Overall survival was 100% for the 0 g l^{-1} treatment (control) and only slightly lower in the 2 and 4 g l^{-1} treatments. Survival dropped to 83% and 73% in the 6 and 8 g l^{-1} treatment levels (Figure 2.2a and Table 2.2). Differences in survival among families began to become apparent at 4 g l^{-1}, with Families PB1 and PR1 showing a reduction in survival (Table 2.2). Family differences were most pronounced in the 8 g l^{-1} treatment, where survival ranged from 42% (PB1) to 97% (LS1).

While the overall range in survival at the highest salinity level was wide (55%), 11 of the families were grouped in a much narrower range between 69% and 83% survival (Table 2.2). There were no significant differences in mean survival between the 10 families from

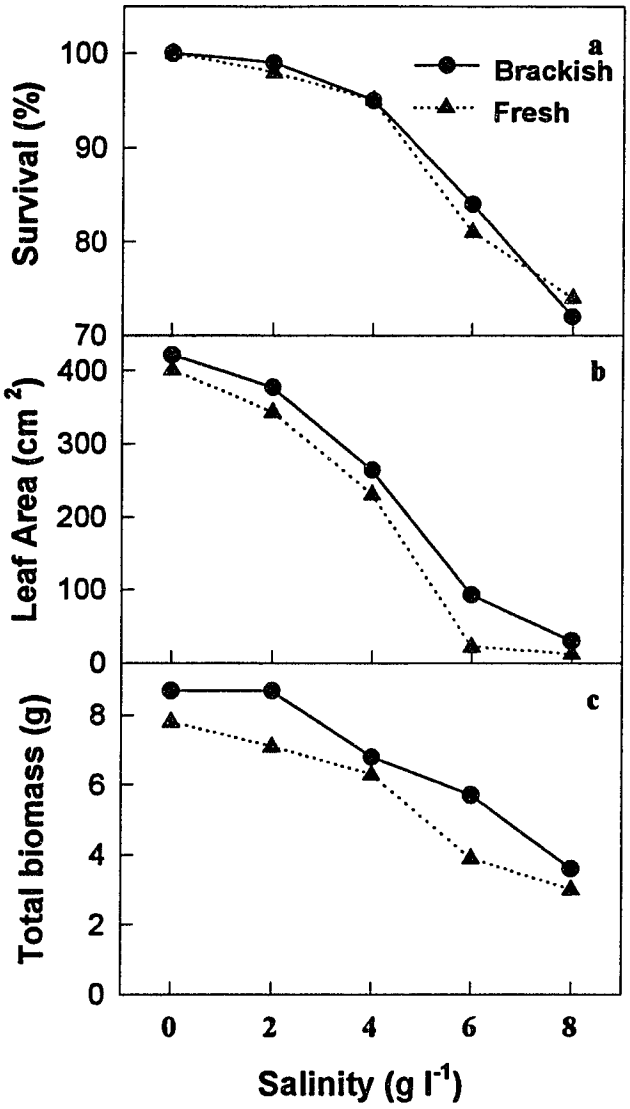

Figure 2.2. Mean values of the families from brackish and freshwater locations for (a) survival, (b) leaf area, and (c) total biomass.

Table 2.2. Percent survival by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	100	100	97	89	69
CB3	100	97	94	78	69
FA1	100	100	100	92	83
FA2	100	100	97	83	83
FA3	100	100	94	78	83
FA4	100	100	100	89	69
PB1	100	94	75	72	42
SG2	100	97	97	86	80
VE2	100	100	100	97	78
VE3	100	100	100	72	67
MEAN	100	99	95	84	72
Freshwater Sources					
BO2	100	100	100	80	72
LS1	100	97	97	97	97
PR1	100	94	86	69	58
SW1	100	100	97	86	72
SW2	100	100	94	75	72
MEAN	100	98	95	81	74
OVERALL MEAN	100	99	95	83	73

brackish and the 5 freshwater sources at any salinity level (P levels were all 0.49 or greater).

Height

Height growth was rapid during the period when salinity levels were being raised (July 17 to August 6), but declined in the following month and almost entirely stopped during the third month of the experiment (Figure 2.3). Although height growth would normally be slowing down over this portion of the growing season, the impact of salinity on height growth was evident when compared with the control (Figure 2.3). While average height for all families was greatest in the 6 and 8 g l^{-1} treatments and lowest in the 0 and 2 g l^{-1} treatments at the outset of the experiment, the pattern was almost exactly reversed by the end of the experiment.

Leaf Area

Leaf area at the time of harvest ranged from an overall mean of 415 cm^2 in the 0 g l^{-1} treatment to only 24 cm^2 in the 8 g l^{-1} treatment (Figure 2.2b and Table 2.3). Significant differences in leaf area were found among salinity levels, among families, and in salinity x family interactions (Table 2.4).

Considerable variation existed among families at each salinity level. Variation in leaf area within families was

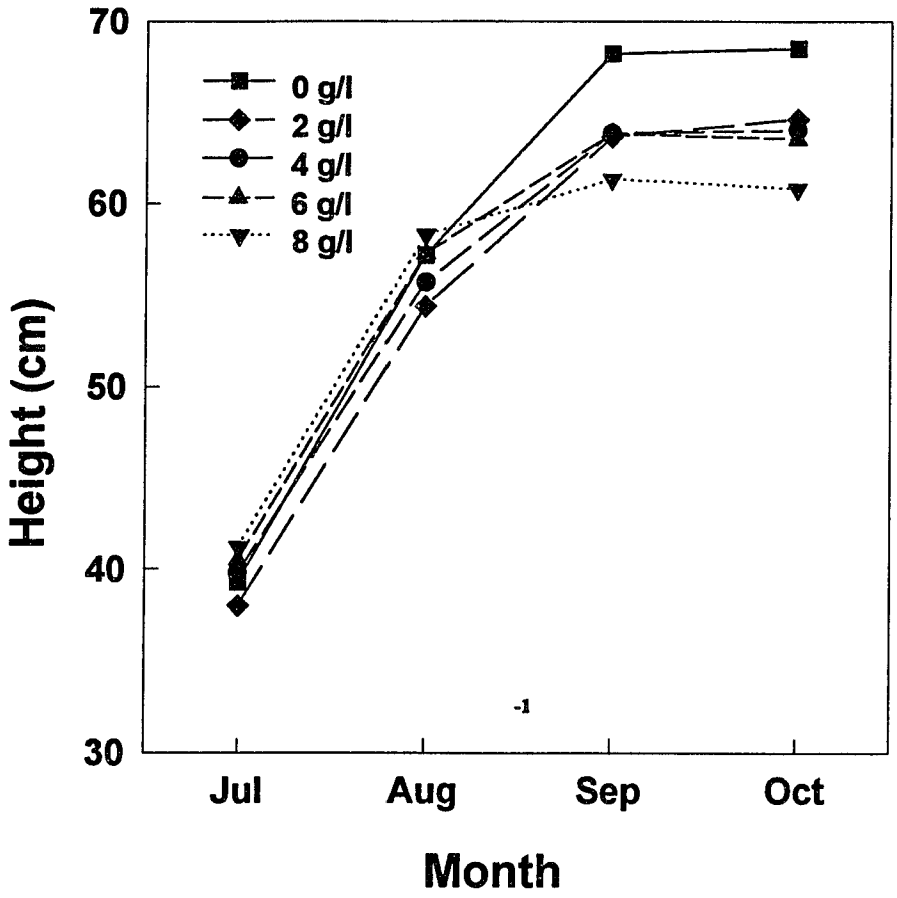

Figure 2.3. Mean height of all seedlings by salinity level.

Table 2.3. Mean leaf area and standard error (cm^2) by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	420 (85.2)	392 (43.1)	258 (48.4)	33 (18.7)	41 (34.8)
CB3	397 (81.0)	311 (46.1)	229 (77.3)	171 (51.7)	108 (47.7)
FA1	508 (60.0)	594 (90.6)	295 (59.5)	61 (25.0)	21 (9.6)
FA2	356 (52.7)	327 (48.2)	323 (33.6)	123 (71.2)	45 (29.7)
FA3	506 (91.0)	356 (64.3)	350 (65.6)	176 (67.2)	41 (19.7)
FA4	404 (72.7)	476 (54.5)	291 (53.6)	67 (30.6)	5 (4.4)
PB1	170 (34.9)	169 (57.4)	66 (37.9)	13 (7.8)	4 (3.3)
SG2	391 (29.5)	282 (55.8)	254 (43.3)	81 (30.6)	13 (6.8)
VE2	472 (45.6)	385 (65.0)	251 (42.9)	154 (108.2)	0 (0.1)
VE3	587 (83.3)	482 (52.4)	322 (54.1)	48 (16.6)	18 (11.9)
MEAN	421	377	264	93	30
Freshwater Sources					
BO2	461 (77.7)	329 (70.0)	169 (63.7)	1 (0.5)	10 (8.4)
LS1	393 (34.3)	371 (55.5)	161 (50.3)	18 (10.9)	18 (8.7)
PR1	210 (35.5)	237 (46.9)	79 (25.9)	12 (10.1)	11 (10.6)
SW1	388 (39.8)	327 (42.6)	421 (83.4)	20 (8.7)	22 (13.7)
SW2	555 (54.6)	449 (46.7)	323 (47.2)	59 (15.2)	1 (0.4)
MEAN	401	343	231	22	12
OVERALL MEAN	415	366	253	69	24

Table 2.4. Analysis of covariance table for leaf area and total biomass.

Source of Variation	DF	MSE	F Value	P Level
		Leaf Area		
Salinity	4	381.5	270.6	.0001
Family	14	7.1	5.0	.0001
Salinity x Family	56	3.5	2.5	.0001
Initial Height (Covariate)	1	56.3	39.9	.0001
		Total Biomass		
Salinity	4	51.1	210.8	.0001
Family	14	1.0	4.3	.0001
Salinity x Family	56	0.5	1.8	.0002
Initial Height (Covariate)	1	209.9	865.9	.0001

Note: Complete Analysis of Covariance tables for these variables (which include Block, Block x Salinity, and Block x Salinity x Family) can be found in Appendix B.

also high, especially at the highest salinity levels, where standard errors were often greater than 50% of the mean (Table 2.3). For one family (CB3), the maximum leaf area for an individual seedling in the 6 g l^{-1} treatment (512 cm^2) and the 8 g l^{-1} treatment (416 cm^2) both exceeded the mean leaf areas for the family in the 0 and 2 g l^{-1} treatments.

Differences in mean leaf area among families from brackish and freshwater sources were most apparent in the 6 g l^{-1} treatment where the overall mean leaf area for families from brackish sources (93 cm^2) was more than four times greater than the mean for freshwater families (22 cm^2). At the 6 and 8 g l^{-1} salinity levels, only families from brackish sources maintained mean leaf areas in excess of 60 cm^2.

At higher salinities, numerous seedlings had shed their older basal leaves, leaving only younger leaves at the growing tip of the seedlings. Many other seedlings, however, had shed all their original leaves, their growing tips had died back, and new, smaller leaves had formed (or were beginning to form) along nearly the entire living portion of the stems.

Total Biomass

Total seedling biomass declined with increasing salinity levels (Figure 2.2c). The difference between the

0 and 2 g l^{-1} treatments, however, was not significant. Seven families had higher mean biomass in the 2 g l^{-1} treatment compared to the 0 g l^{-1} treatment (Table 2.5).

Mean biomass differed significantly among families and salinity x family interactions were also significant (Table 2.4). Families from brackish areas had higher total biomass on average than families from freshwater sources at all salinity levels, but differences (on a percentage basis) were largest for the highest two salinity treatments. The mean total biomass for families from brackish locations did not decline from 0 to 2 g l^{-1}, whereas it did decline from 7.8 to 7.1 g for the freshwater source families (Table 2.4).

Tolerance Indices

Calculated values for Potential Survival Index (PSI; an index of likelihood of near term survival) ranged from 106 to 2941 (Table 2.6). The overall mean PSI for families from brackish locations (1250) is about 3 1/2 times higher than the average of families from freshwater locations (362). While families from brackish sources generally had the highest PSI values, Families PB1 and VE3 had lower PSIs than most of the families from freshwater sources.

Families from brackish locations also tended to have higher Potential Productivity Index (PPI; an index of relative productivity of surviving seedlings) values (Table

Table 2.5. Mean total biomass and standard error (g dry weight) by salinity level and family.

Family	Salinity ($g\ l^{-1}$) 0	2	4	6	8
Brackish Sources					
CB2	9.5 (0.8)	9.4 (0.6)	6.7 (0.6)	4.7 (0.5)	3.8 (0.5)
CB3	8.8 (0.7)	7.8 (0.9)	5.7 (0.6)	5.2 (0.7)	4.4 (0.6)
FA1	10.7 (0.7)	9.9 (0.8)	7.6 (0.7)	5.5 (0.7)	3.4 (0.4)
FA2	7.8 (0.5)	8.0 (0.8)	8.0 (0.6)	7.4 (1.0)	4.2 (0.3)
FA3	10.6 (1.0)	9.0 (0.9)	8.5 (0.7)	6.3 (0.8)	4.1 (0.3)
FA4	8.3 (0.6)	10.1 (0.6)	6.9 (0.6)	4.3 (0.5)	3.1 (0.3)
PB1	4.1 (0.6)	3.5 (0.5)	3.3 (0.5)	3.1 (0.5)	2.6 (0.3)
SG2	7.4 (0.4)	7.8 (0.8)	6.1 (0.6)	5.9 (0.6)	3.2 (0.3)
VE2	8.8 (0.8)	9.4 (0.8)	7.1 (0.6)	5.5 (0.7)	3.5 (0.4)
VE3	10.5 (0.8)	11.7 (0.7)	8.1 (0.6)	4.5 (0.6)	3.6 (0.4)
MEAN	8.7	8.7	6.8	5.7	3.6
Freshwater Sources					
BO2	7.6 (0.7)	5.3 (0.7)	5.4 (0.6)	3.0 (0.2)	2.5 (0.2)
LS1	7.8 (0.7)	8.6 (0.6)	5.7 (0.5)	4.2 (0.3)	3.3 (0.3)
PR1	5.5 (0.6)	5.7 (0.6)	4.8 (0.6)	3.0 (0.3)	3.1 (0.4)
SW1	8.8 (0.5)	7.0 (0.6)	7.7 (0.6)	4.3 (0.5)	3.2 (0.5)
SW2	9.1 (0.7)	9.0 (0.7)	7.7 (0.9)	4.9 (0.5)	2.9 (0.4)
MEAN	7.8	7.1	6.3	3.9	3.0
OVERALL MEAN	8.3	8.1	6.6	5.1	3.4

Table 2.6. Potential Survival Index (PSI) and Potential Productivity Index (PPI) values by family.

Family	PSI	Rank	PPI	Rank
Brackish Sources				
CB2	720	6	3553	11
CB3	2941	1	4315	6
FA1	651	7	3780	8
FA2	2042	2	6094	1
FA3	2027	3	4271	7
FA4	646	8	3177	13
PB1	295	13	4407	4
SG2	1177	5	5045	2
VE2	1572	4	4327	5
VE3	429	11	2535	15
MEAN	1250		4150	
Freshwater Sources				
BO2	106	14	3240	12
LS1	464	9	4503	3
PR1	337	12	3565	10
SW1	464	9	3750	9
SW2	439	10	3167	14
MEAN	362		3645	
OVERALL MEAN	954		3982	

2.6). The difference in means for families from brackish sources (4326) was 19% higher than the mean for families from freshwater locations (3645).

DISCUSSION

Species-Level Responses

The results of this study agree with previous studies (e.g., Omran et al., 1979 and Conner, in press), which found that baldcypress seedling survival and/or growth declined with increasing salinity levels. Omran et al. (1979) exposed first-year seedlings to seven unflooded salinity treatments ranging from 0.36 g l^{-1} to 3 g l^{-1} for 5 months and reported lower dry weights of the seedlings in high salinity treatments (0.9 g at 3 g l^{-1}) than in low salt treatments (2.2 g at 0.36 g l^{-1}). Conner (in press) found that survival and growth of one-year-old seedlings exposed to flooding with 0 and 2 g l^{-1} salinity treatments was similar, but flooding with 10 g l^{-1} water killed all seedlings within six weeks.

Both of the above studies, while showing response patterns broadly similar to those found in the present study, reported responses to salinity that were somewhat more dramatic. Variations in the magnitude of response may be attributable to differences in study methods or plant material.

Conner (in press), for example, reported much higher mortality (100%) from flooding with 10 g l^{-1} water than may be expected based on the results of the 8 g l^{-1} treatment in this study (27%). One possible explanation for this difference is that a threshold of tolerance was crossed between 8 and 10 g l^{-1}. Possible support for this explanation is provided by Penfound and Hathaway (1938), who reported a maximum tolerance of 8.9 g l^{-1} for mature baldcypress occurring naturally in southern Louisiana swamps. I believe a more probable explanation, however, is that the seedlings in this study were first acclimated to flooding and then gradually exposed to increasing salinity, whereas no acclimation to flooding or salt was reported by Conner (in press). Although I believe the gradual exposure to flooding and salt is more typical of natural settings during most years, baldcypress is also occasionally exposed to major pulses of flooding with salt water (Hook et al., 1991). Knowledge of both types of responses is therefore important.

Similarly, Omran et al. (1979) reported a more substantial decline in total biomass at low levels of salinity than was observed in this study. One possible explanation for this is that the plant material those researchers used was smaller than what was used in this study. Although the age of the seedlings does not seem to be very different than those used in this study, the much

lower biomass of seedlings in their 0.36 g l^{-1} treatment (2.2 g) compared to my 0 g l^{-1} treatment (8.3 g) suggests a smaller average seedling size at the beginning of the experiment. Differences in tolerance of seedlings at slightly different ages or sizes may be an important factor affecting natural regeneration on saline sites, but may be less critical where artificial regeneration with relatively large seedlings is used.

Intraspecific Variation

Three families - CB3, FA2 and FA3 - seemed to be the best overall performers at the higher salinity levels in this study. In particular, these families tended to retain the most leaf area and to have the greatest total biomass at the highest salinity levels. Although these families also had high PSI or PPI values, only FA2 ranked in the top three families for both indices.

A notable feature of the family-level responses was the complexity in their pattern (i.e., the significant interactions between salinity level and family). Family CB3, for example, had a steadily lower mean leaf area with increasing salinity levels, whereas Family VE2 showed a similar pattern up to 6 g l^{-1}, followed by an essentially complete loss of leaves at 8 g l^{-1} (Table 2.3). The survival of Family VE2, on the other hand, was higher at 8 g l^{-1} than it was for Family CB3, although there was also a

considerable drop from the survival of Family VE2 from 6 to 8 g l^{-1}. Family VE2 may have crossed a threshold between 6 and 8 g l^{-1}, at which point survival and leaf area, both of which were relatively high up to and including the 6 g l^{-1} treatment, began to decline rapidly. A longer experiment may have yielded much additional information of value about the various patterns of response.

Individual seedlings exhibited a broad range of responses to salinity, some of which are characteristic of more salt-tolerant species. The seedlings with the best overall appearance at the higher salinity treatments, for example, lost older basal leaves but retained younger leaves. This characteristic was reported of the more salt-tolerant species in a screening trial of seven Australian tree species (van der Moezel et al., 1988). On the other hand, many seedlings in this experiment exhibited dieback of the growing tip, a characteristic van der Moezel et al. (1988) found to be associated with least tolerant species in their study.

In an interspecific comparison of salt tolerance in the genus Casuarina, it was noted that the species with the lowest overall tolerances tended to have the highest intraspecific variation (van der Moezel et al., 1989). This suggests that, by employing a sufficiently intense selection, substantial gains may be made in improving the tolerance of some relatively intolerant species.

Baldcypress may be another example of this pattern of variation.

The degree of among-family variation found in this study suggests that substantial gains in salt tolerance may be possible in the short term by simply using seed from individual parent trees from brackish locations to produce seedlings. Seedlings from Families CB3, FA2 and FA3, for example, had 5% greater mean first-year survival, 2.7 times as much mean leaf area, and 25% greater mean total biomass than the overall average of the 15 families. The generally poor results obtained from Family PB1, however, show the need for first conducting progeny tests.

The use of full-sib seedlings or clonal material potentially could increase the differences in tolerance between freshwater and brackish sources. There was no evidence of barriers to gene flow between populations or individual trees in brackish sites and those in nearby freshwater sites, so half-sib progeny might be expected to be highly variable in salt tolerance. For example, the parent tree SG2 appeared to be growing vigorously in a swamp where almost every other tree was killed by saltwater intrusion. The performance of Family SG2 at high salinity levels, however, was not exceptional. One explanation may be the location of the tree, which is not far from a healthy swamp with numerous mature trees. The healthy swamp was separated from the dying swamp by a levee, which

prevented the intrusion of saltwater into the healthy swamp but not the movement of pollen from the (possibly) less tolerant baldcypress in the freshwater site to SG2. Many of the resulting progeny may therefore be less tolerant than the parent tree SG2.

The greatest gains in improving salt tolerance of baldcypress can probably be made through clonal propogation of either seedlings selected in screening trials or mature trees growing on saline sites. Selection of seedlings and subsequent micropropogation is being used effectively in the development of salt-tolerant lines of Eucalyptus species and species in other genera in Australia (Marcar et al., 1993) but to my knowledge has not been attempted with baldcypress. The increased variability at 6 g l^{-1} suggests that this may be an appropriate salinity level for screening of baldcypress.

I believe the results of this study demonstrate that sufficient intraspecific variability exists within the species baldcypress to justify a salt-tolerance improvement program. Such a program could provide useful plant material for wetland restoration projects in the United States and for applications in other parts of the world that require a tree species with combined waterlogging and salt tolerance.

CHAPTER 3

VARIATION IN BIOMASS PARTITIONING AND MORPHOLOGICAL TRAITS OF *TAXODIUM DISTICHUM* IN RESPONSE TO SALINITY

INTRODUCTION

Among the most distinctive forested wetland tree species in the southern United States is baldcypress (Taxodium 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 seedling production, commercial forestry, or horticultural perspectives, such as seed size, number of seeds per cone, first-year growth, and crown shape (Faulkner 1982; Dirr 1983; Faulkner 1985). There is also some evidence of genetic variation in tolerance to various biotic and abiotic stresses. Variation in leaf morphology, for example, appears to be an important factor affecting susceptibility to insect herbivory (Meeker and Goyer 1993) and, possibly, tolerance to different soil moisture regimes (Sharma and Madsen 1978). Genetic variation along a

latitudinal gradient has also been found, such as in photoperiod response and in cold acclimation (Flint 1974).

One abiotic stress of particular concern to managers of baldcypress in coastal locations 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). Pezeshki et al. (1990) stated that stands or individuals of baldcypress have been reported to occur on sites exposed to salinity stress, suggesting that substantial genetic variation in salinity tolerance may occur in baldcypress. The possibility that significant variation in salt tolerance may exist within the species also was suggested by Javanshir and Ewel (1993). Allen et al. (in press) recently demonstrated that significant variation exists in salinity tolerance among seedlings from open-pollinated families of baldcypress. In this paper, further evidence of intraspecific variation is presented and possible explanations for the observed variation in tolerance are explored.

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. Salinity levels at the brackish sites were between 0.4 and 15.3 g l^{-1} at the time of collection (Allen et al. in press). The other five parent trees were from areas not subjected to brackish conditions. The approximate locations of the 15 trees are shown in Allen et al. (in press). Details of seed collection, seed processing and storage, and the production of seedlings are also provided in Allen et al. (in press).

Salinity Treatments

Five salinity treatments (0, 2, 4, 6, and 8 g l^{-1}) were prepared by using a commercial seawater mix (Marine Enterprises, Inc., Baltimore, MD, USA). 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%). The seedlings were exposed gradually to their final treatment levels by raising the salinity in the tanks by 1/4 of the final treatment concentration each week for 4 weeks. Salinity levels in the tank water were

checked daily and salt or deionized water was added as necessary to maintain a nearly constant ($\pm$ 0.5 g l^{-1}) salinity level. A submersible pump was placed in the bottom of each tank to keep the water well-mixed, but not aerated.

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

After reaching final salinity treatment levels on 6 August, the treatments were maintained through the latter part of the growing season until final harvest, which occurred over a 2-week period between 26 October and 6 November.

Measurements and Data Analysis

During the seedling harvest, height, diameter at the root collar, and root volume were measured for all living seedlings. Root volume measurements were based on Archimede's principle, and were done by submerging whole root systems into a cylinder of water on a scale and measuring the change in weight (volume displacement). In addition, the number of leaves and leaf area was measured

for every third seedling. Leaf area was measured by using a leaf area meter (Li-Cor, Model LI-3000A meter with Model LI-3050A conveyer, Lincoln, NE, USA). All living seedlings were separated into roots, stems, and leaves, which were dried at 70 °C to a constant weight for biomass measurement.

Analyses of covariance were performed (using the PROC GLM procedure of the Statistical Analysis System, SAS Institute, Inc., Cary, NC, USA) to test for differences among salinity treatments (main plot effects), families (subplot effects), and salinity x family interactions. A 0.05 level of significance was used to test whether the differences among the salinity treatments, families, and their interactions were significant. Because significant linear correlations were found between initial height and all response variables evaluated, the initial height of each seedling (in cm) was used as a covariate and least-square means were compared. To satisfy normality and homogeneity of variance assumptions, natural log transformations were carried out on all response variables except root weight ratio and specific leaf area.

RESULTS

Biomass

Baldcypress seedlings from all families tolerated low level (2 g l^{-1}) salinity. Differences between mean leaf and stem biomass were not significant between 0 and 2 g l^{-1}, and mean root biomass actually increased slightly (significant at $P < 0.01$ level). Salinity levels of 4 g l^{-1} and above, however, clearly inhibited growth of leaves, stems, and roots (Table 3.1). Differences among all salinity treatments above 2 g l^{-1} were significant for mean leaf, stem and root biomass.

There were significant differences among families for leaf, stem, and root biomass means (Table 3.2). In general, families from brackish locations had higher biomass than families from inland locations at the highest salinity levels (Table 3.3). Differences were most pronounced 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.

There were also significant interactions between salinity and family for leaf, stem and root biomass (Table 3.2), indicating that families responded to salinity treatments in different ways. An example of the differences in response of four families is depicted in

Table 3.1. Mean biomass, leaf and root characteristics by salinity level.

Response Variable	Salinity 0	2	4	6	8
Leaf Biomass (g dry wt)	2.14a (0.05)	1.99a (0.05)	1.44b (0.05)	0.58c (0.05)	0.16d (0.02)
Stem Biomass (g dry wt)	3.66a (0.09)	3.60a (0.09)	2.91b (0.07)	2.60c (0.06)	2.17d (0.04)
Root Biomass (g dry wt)	2.39b (0.06)	2.56a (0.07)	2.31c (0.06)	1.54d (0.06)	1.04e (0.04)
Root Weight Ratio (Root/Total Biomass)	0.29c (0.003)	0.30b (0.003)	0.34a (0.004)	0.31b (0.004)	0.30c (0.006)
Leaf Size (cm^2)	8.15a (0.25)	8.11a (0.23)	7.88a (0.27)	4.03b (0.36)	1.64c (0.25)
Leaf Number	51.5a (2.1)	44.3a (1.7)	29.8b (1.5)	11.7c (1.1)	9.2c (0.9)
Specific Leaf Area ($m^2\ g^{-1}$)	0.0197a (.0006)	0.020a (.0003)	0.0181a (.0004)	0.0193a (.0010)	0.0183a (.0011)
Root Density Index ($g\ cm^{-3}$)	0.108d (0.003)	0.101c (0.006)	0.101c (0.003)	0.082b (0.002)	0.069a (0.002)

Note: Values are actual (unadjusted) means and standard errors for the 15 families combined. Means within a row followed by the same letter are not significantly different ($P > 0.05$); means separation is based on comparison of least square means.

Table 3.2. Analysis of covariance table for response variables.

Response Variable	F Value			
	Salinity d.f.=4	Family d.f.=14	Salinity x 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	35.83***	4.86***	1.80***	50.78***
Leaf Size (cm^2)	195.76***	3.32***	2.36***	14.94***
Leaf Number	178.02***	5.30***	2.13***	45.68***
Specific Leaf Area ($m^2\ g^{-1}$)	2.22n.s.	1.18n.s.	0.95n.s.	14.13n.s.
Root Density Index ($g\ cm^{-3}$)	146.21***	5.12***	2.94***	91.96***

n.s. Not significant at .05 level.
*** Significant at .001 level.

Note: Complete Analysis of Covariance Tables are provided in Appendix C.

Table 3.3 Mean leaf (L), stem (S) and root (R) biomass (g dry wt) by salinity level and family.

	Salinity ($g\ l^{-1}$)														
Family	0			2			4			6			8		
Brackish Sources	L	S	R	L	S	R	L	S	R	L	S	R	L	S	R
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

Figure 3.1 for leaf biomass. Two of the families (CB3 and SG2) exhibited similar and essentially linear declines in biomass with increasing salinity. Another family (FA2) maintained relatively high leaf biomass up through 6 g l^{-1} 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). The 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 (Table 3.1). Within the shoot, leaf biomass was much more affected than stem biomass. Stem biomass at 8 g l^{-1} was 59% of the 0 g l^{-1} mean, but leaf biomass at 8 g l^{-1} 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.

Leaf Characteristics

The mean area of individual leaves was not significantly different among the 0, 2, and 4 g l^{-1} treatments (Table 3.1). Mean leaf area dropped by nearly 50% between 4 and 6 g l^{-1} and by nearly 60% between 6 and 8 g l^{-1}.

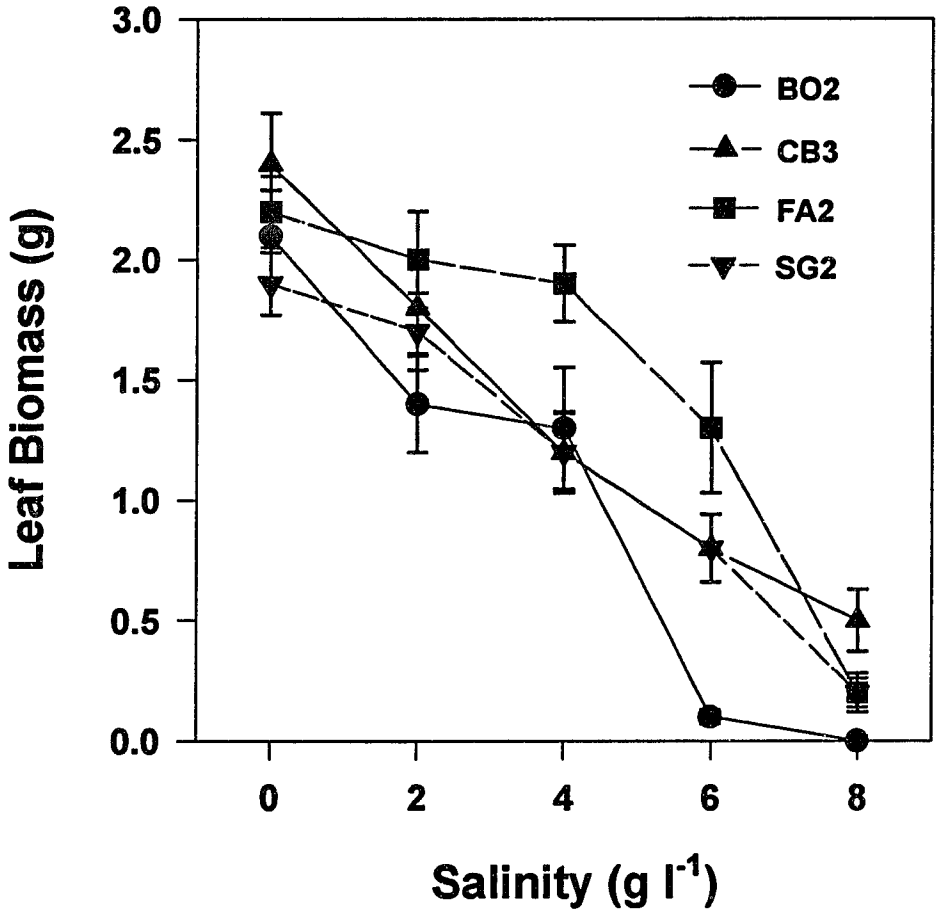

Figure 3.1. Mean leaf biomass by salinity level for selected families.

Significant differences in leaf area were found among families at 4, 6, and 8 g l^{-1}. As was the case with biomass, families from brackish locations tended to have greater mean leaf area, with the differences being most pronounced at 6 g l^{-1} (Table 3.4). In the highest salinity treatment, the two "CB" families stood out in their ability to maintain relatively large leaves, followed by two of the "FA" families (2 and 3). The correlation coefficient between mean leaf area and total biomass consistently increased with increasing salinity, ranging from 0.33 at 0 g l^{-1} ($P < 0.0001$) to 0.69 at 8 g l^{-1} ($P < 0.0001$). This appears to be further evidence that the most tolerant seedlings were those that were able to maintain large leaves.

The average number of leaves per seedling was 51.5 for the 0 g l^{-1} treatment, but declined to only 9.2 for the 8 g l^{-1} treatment (Table 3.1). Two general patterns were evident for seedlings subjected to 6 and 8 g l^{-1} salinity levels. The seedlings that apparently were the most salt tolerant gradually lost their older leaves, while always maintaining younger leaves near the top portion of the stem. Most surviving seedlings, however, lost all or nearly all their leaves and also exhibited partial stem dieback. Many surviving seedlings produced new leaves, which were dark green and apparently healthy at the harvest

Table 3.4. Mean leaf area (of single leaves) and standard error (cm^2) by salinity and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	6.6 (1.0)	9.5 (1.0)	8.2 (0.6)	3.1 (1.5)	4.0 (0.7)
CB3	6.9 (0.7)	6.8 (0.5)	7.3 (1.3)	6.9 (0.9)	3.7 (1.1)
FA1	8.5 (0.7)	9.5 (0.8)	11.5 (1.0)	4.3 (1.3)	1.3 (0.6)
FA2	9.0 (1.7)	7.3 (0.7)	9.1 (0.8)	4.0 (1.7)	2.7 (1.1)
FA3	8.2 (0.8)	8.4 (0.8)	8.8 (0.7)	10.1 (1.4)	1.7 (0.7)
FA4	8.7 (0.7)	8.4 (0.6)	8.5 (0.9)	4.6 (1.5)	0.6 (0.4)
PB1	6.8 (1.1)	5.5 (1.0)	3.9 (1.1)	2.3 (0.8)	0.8 (0.5)
SG2	9.6 (0.7)	7.7 (0.8)	8.3 (0.9)	5.3 (1.4)	1.1 (0.5)
VE2	10.1 (0.7)	7.7 (0.5)	8.5 (0.6)	4.7 (1.5)	0.2 (0.0)
VE3	10.2 (1.5)	9.9 (1.6)	8.3 (1.0)	2.9 (0.6)	1.1 (0.6)
MEAN	8.5	8.1	8.2	4.8	1.7
Freshwater Sources					
BO2	8.3 (1.1)	7.9 (1.3)	5.3 (1.0)	1.7 (0.7)	1.3 (0.5)
LS1	8.2 (0.6)	9.2 (0.6)	5.8 (1.1)	1.2 (0.6)	1.6 (0.5)
PR1	6.2 (0.7)	7.6 (1.3)	5.4 (1.0)	1.4 (0.9)	1.1 (0.9)
SW1	7.1 (0.7)	7.4 (0.5)	8.4 (1.0)	2.9 (1.2)	1.2 (0.7)
SW2	7.6 (0.6)	8.4 (0.7)	8.8 (0.9)	3.6 (1.0)	0.2 (0.0)
MEAN	7.5	8.1	6.7	2.2	1.1

period, but the new leaves were smaller than those of seedlings that retained leaves throughout the experiment.

No trends were apparent in the data on specific leaf area. Differences among salinity treatments, families, and in salinity x family interactions were not significant (Table 3.2). Mean specific leaf area ranged from 0.0181 m^2 g^{-1} for the 4 g l^{-1} treatment to 0.0197 m^2 g^{-1} for the 0 g l^{-1} treatment. Families regarded as the most salt tolerant (e.g., CB3, FA2 and FA3) exhibited no differences in specific leaf area that might help explain their higher tolerance (Appendix A).

Root Density Index

There was an overall trend of decreasing root density index (root biomass/root volume) with increasing salinity (Table 3.1). Decreases were especially notable between the 4 and 6 g l^{-1} and the 6 and 8 g l^{-1} treatments. On average, root density index values at 8 g l^{-1} were only 63% as large as at 0 g l^{-1}. Differences between all salinity levels were significant with the exception of 2 and 4 g l^{-1}. Mean root density index by family and salinity level is shown in Table 3.5; significant differences were found among both families and salinity treatments (Table 3.1).

A possible tendency for more productive seedlings to have denser roots is suggested by the significant correlation ($P < 0.0001$, $r = 0.27$) between root density

Table 3.5. Mean root density index and standard error (cm^3/g dry wt) by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	0.106 (0.003)	0.187 (0.087)	0.097 (0.004)	0.068 (0.004)	0.067 (0.004)
CB3	0.097 (0.003)	0.091 (0.003)	0.088 (0.005)	0.083 (0.003)	0.066 (0.005)
FA1	0.099 (0.003)	0.098 (0.007)	0.091 (0.005)	0.089 (0.004)	0.060 (0.003)
FA2	0.096 (0.003)	0.085 (0.003)	0.101 (0.004)	0.089 (0.005)	0.085 (0.006)
FA3	0.121 (0.009)	0.096 (0.003)	0.107 (0.004)	0.097 (0.007)	0.084 (0.011)
FA4	0.103 (0.003)	0.101 (0.002)	0.100 (0.004)	0.071 (0.005)	0.062 (0.004)
PB1	0.085 (0.004)	0.074 (0.007)	0.100 (0.018)	0.101 (0.030)	0.063 (0.006)
SG2	0.109 (0.002)	0.101 (0.004)	0.106 (0.004)	0.091 (0.006)	0.067 (0.003)
VE2	0.104 (0.004)	0.093 (0.003)	0.098 (0.006)	0.086 (0.009)	0.064 (0.004)
VE3	0.107 (0.004)	0.100 (0.002)	0.096 (0.004)	0.087 (0.014)	0.068 (0.006)
MEAN	0.103	0.103	0.098	0.086	0.069
Freshwater Sources					
BO2	0.108 (0.003)	0.108 (0.018)	0.088 (0.005)	0.075 (0.004)	0.066 (0.005)
LS1	0.102 (0.004)	0.104 (0.006)	0.093 (0.011)	0.082 (0.007)	0.056 (0.004)
PR1	0.121 (0.013)	0.094 (0.007)	0.156 (0.036)	0.067 (0.005)	0.117 (0.025)
SW1	0.148 (0.004)	0.091 (0.004)	0.100 (0.004)	0.070 (0.003)	0.063 (0.005)
SW2	0.109 (0.003)	0.090 (0.004)	0.097 (0.005)	0.070 (0.003)	0.052 (0.004)
MEAN	0.118	0.097	0.107	0.073	0.071

index and total seedling biomass across all salinity levels. Also, the correlation coefficient tended to increase with increasing salinity, suggesting a possible relationship between root density and salt tolerance, but the trend was not as consistent as it was for mean leaf size. The correlation was also weaker than it was for mean leaf size--correlation coefficients for individual salinity treatment levels were between 0.15 and 0.40.

DISCUSSION

General Responses to Salinity

Based on the overall performance of the surviving seedlings, in terms of total biomass production at 4, 6, and 8 g l^{-1} compared with the 0 g l^{-1} control, baldcypress would be classified as "moderately tolerant" using the system of Maas and Hoffman (1977). If the level of tolerance exhibited by seedlings during this short-term experiment were to persist to maturity, baldcypress would be ranked as more salt tolerant than many common fruit and ornamental tree species (Maas 1990). This degree of tolerance, combined with its well-documented tolerance of saturated or flooded soil conditions, may mean that baldcypress is suitable for some applications that require a tree species where both forms of stress are encountered.

A substantial degree of intraspecific variation in

salt tolerance was found in this study, with families from brackish locations generally exhibiting greater tolerance than families from freshwater locations. At 6 g l^{-1}, Family FA2 clearly stood out, with the highest mean total biomass (7.1 g dry wt) and the highest percent 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 highest biomass-producing families at 8 g l^{-1} were CB3, FA2, FA3, and CB2 -- again all from brackish locations.

At 6 g l^{-1}, the family with the highest biomass production (FA2) also had the highest relative biomass production. At 8 g l^{-1}, the situation was considerably different. Families PB1 and PR1, which were amongst the least productive families at every salinity level, were the two best performers in terms of relative biomass production. These two families had a relative biomass production (8 versus 0 g l^{-1}) of 71% and 60%, respectively. It is conceivable that these families develop in the way that Chapin (1991) suggested is typical of species from low-resource or otherwise stressful environments (*i.e.*, with a low growth rate and a low capacity to respond to less stressful conditions). Such a possibility appears

unlikely in this case, however, since at 8 g l^{-1} these families had the poorest survival (Allen et al. in press) and maintained very little leaf biomass (Table 3.3).

Biomass Partitioning

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.

Several reasons why an increased proportion of biomass is partitioned to roots in response to low to moderate levels of salinity can be proposed. 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 several split-root studies. Zekri and Parsons (1990), for example, demonstrated that sour orange seedlings could maintain near-normal growth when half the root system was kept in a low salinity environment while the other half was exposed to osmotic potentials ranging from -0.10 to -0.35 MPa. 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.

The root weight ratio declined in the 6 and 8 g l^{-1} treatments to a value similar to that of 0 g l^{-1} controls, indicating that root growth was affected more than shoot growth above salinity levels of 4 g l^{-1}. The proportion of biomass within the shoot components (leaves and stems) was very different at high versus low salinities, however, and it was clear that leaves were the organs most affected at the highest salinity levels.

Above 4 g l^{-1}, most seedlings were not able to maintain a large number of healthy leaves, and premature leaf abscission occurred on virtually every seedling. At 8 g l^{-1}, the vast majority of seedlings had what might be regarded as an unhealthy balance between leaf, stem, and root biomass, with leaves accounting for only about 5% of the total seedling biomass, compared with 26% for the controls. Because most of the seedlings were still alive in the 8 g l^{-1} treatment at the time of harvest (Allen et al. in press) and many had developed a new set of leaves, a longer-term experiment would have been valuable for

assessing the ability of the seedlings to restore a "healthier" pattern of biomass partitioning.

Morphological Variation

The most striking differences in morphology observed in this study were in mean leaf size and distribution. The individual seedlings and families that appeared most tolerant based on characteristics such as biomass and tolerance indices (Allen et al. in press) tended to have the largest mean leaf size and also maintained leaves near the top of the seedling (new growth). In contrast, apparently less tolerant seedlings exhibited partial stem dieback and refoliation along the lower (i.e., living) portion of the stem. This latter response was also noted by Conner and Askew (1992), who used seedlings from freshwater sources.

The overall tendency for the root density index to decrease with increasing salinity was also noteworthy. One possible explanation for this trend is that roots that developed in the presence of salinity had a different internal structure, possibly with greater development of aerenchyma. Another possibility is that the proportion of different types of roots, which may differ in structure and density, changed as salinity increased. Waisel and Breckle (1987), found that initiation of new laterals of young radish plants (Raphanus sativus cv. Rex) was less affected

than extension of either tap roots or first lateral roots. It is possible a change of this nature occurred in baldcypress, thus affecting the overall root density index. A third possibility is that the higher salinity levels caused a significant amount of cell death and collapse, resulting in deteriorated roots with more internal space (but not organized, functional air space as in the first case). The significant positive correlation between the root density index and total biomass suggests that the latter possibility may be most important, since seedlings with significant root deterioration could be expected to be less productive. A more detailed examination of the response of roots to salinity may provide useful insights into reasons for some of the variation in salt tolerance observed in this study.

CHAPTER 4

PHYSIOLOGICAL RESPONSES OF 15 OPEN-POLLINATED FAMILIES OF BALDCYPRESS (*TAXODIUM DISTICHUM*) TO SALINITY

INTRODUCTION

Coastal swamps in parts of the southern United States are being subjected to increasing levels of stress caused by soil salinity. Natural events, such as land subsidence and eustatic sea-level rise, as well as man-made hydrologic alterations, such as levees and canals, act to allow saltwater intrusion into formerly freshwater swamps (Salinas et al. 1986; Templet and Meyer-Arendt 1988). The problem is particularly acute in southern Louisiana, where in some swamps salinity levels have increased from less than 0.5 to greater than 3 g l^{-1} (Wicker et al. 1981; Salinas et al. 1986).

Baldcypress (Taxodium distichum (L.) Rich.), one of the most prominent species in coastal swamps, is salt-sensitive (Brown and Montz 1986; Pezeshki et al. 1986, 1987). Healthy baldcypress swamps generally do not occur in areas where the interstitial soil water salinity exceeds 2 to 3 g l^{-1} for more than 50% of the time that the soil is saturated or flooded (Chabreck 1972; Wicker et al. 1981; Brown and Montz 1986). There is evidence, however, that significant intraspecific variation in salt tolerance

exists within the species. Pezeshki et al. (1990) reported that apparently salt-tolerant stands or individual baldcypress trees occur in coastal Louisiana, and individual trees or small stands have been observed in brackish areas in other southern states (personal observation). The possibility that significant variation in salt tolerance within the species may exist also was suggested by Javanshir and Ewel (1993). Recently, significant intraspecific variation in survival and growth of seedlings was found among 15 open-pollinated families of baldcypress from Louisiana and Alabama exposed to flooding with water of different salinity levels was observed (Allen et al. in press).

The existence of significant intraspecific variation in salt tolerance at the seedling stage opens up the possibility of developing salt tolerant lines of baldcypress for use in coastal forest restoration projects. The task of screening very large numbers of seedlings for salinity tolerance is time-consuming and expensive, however. A number of researchers have suggested that measurements of physiological responses such as gas exchange, chlorophyll fluorescence, plant water status, or tissue nutrient concentrations may prove to be effective as tools for screening large numbers of plants (Noble and Rogers 1992; Krishnaraj et al. 1993; Belkhodja et al. 1994).

The present study was therefore designed primarily to evaluate the potential of a range of physiological responses for use as tools for screening for salinity tolerance. An important secondary goal was to characterize more broadly the species-level physiological responses of baldcypress to salinity, since most previous studies have been limited to salinity effects on gas exchange and leaf ion concentrations.

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, brackish locations in southern Louisiana and Mobile Bay, Alabama. Salinity levels at the brackish sites were between 0.4 and 15.3 g l^{-1} at the time of collection. The other five parent trees were located in areas of southern Louisiana not subjected to brackish conditions. Details on the location of the parent trees, the salinity levels to which the parent trees from brackish locations were exposed, and the procedures used to produce the seedlings are provided in Allen et al. (in press).

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 ("Forty Fathoms Marine Mix," Marine Enterprises, Inc., Baltimore, MD, USA). 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%). The treatments were initiated in mid-July, 1992. The seedlings were exposed gradually to their final treatment levels by raising the salinity in the tanks by 1/4 of the final treatment concentration each week for four weeks. Salinity levels were checked daily and salt or deionized water was added as necessary to maintain a nearly constant ($\pm$ 0.5 g l^{-1}) salinity level. A submersible pump was placed in the bottom of each tank to keep the water well mixed, but not aerated.

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

Gas Exchange, Chlorophyll Fluorescence and Leaf Water Potential Measurements

In mid-August and again in mid-September, 225 seedlings (1 seedling/family/salinity level/block) were randomly selected, removed from the greenhouse, and placed

under controlled conditions in a laboratory. The seedlings were placed in tanks flooded to the same depth with water of the same salinity level as they were in the greenhouse. A combination of fluorescent and incandescent lighting yielded approximately 400-450 μmol m^{-2} s^{-1} PPFD at the top of the plants (measured with a Model LI-189 light meter, Li-Cor, Lincoln, NE, USA). The photoperiod was 14 hours. 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 hours prior to initiation of measurements. All measurements were made between 10:00 and 16:00 h, and were typically completed over a three-day period.

Net photosynthesis (A), stomatal conductance (g_w), and transpiration (E) 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 μmol 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 (n = 6-10 per salinity treatment) during each of the two sample periods.

Chlorophyll fluorescence was measured on the seventh fully expanded leaf or an adjacent leaf. Measurements were made with a Model CF-1000 chlorophyll fluorescence measurement system (P.K. Morgan Instruments, Inc., Andover, MA, USA). Leaves were dark-adapted in small cuvettes (placed approximately half-way along the mid-rib) for a minimum of 15 min, after which they were irradiated with 500 μmol m^{-2} s^{-1} PPFD actinic light for a 30 s sample period.

Tissue Analyses

Cl^-, Na^+, K^+ and Ca^{2+} concentrations in leaf, root and stem tissue were sampled on a subset of seedlings randomly selected at the time of the harvest (late October-early November). One seedling/family/salinity level/block (n=225) was selected. For analysis of Na^+, K^+, and Ca^{2+} concentrations, oven-dried leaf, root and stem tissues were ground in a Wiley Mill sufficiently to pass through a 20 mesh screen, digested in HNO_3, and filtered. Na^+ and K^+ concentrations were analyzed by flame emission spectrophotometry and Ca^{2+} and Mg^{2+} concentrations were analyzed by flame absorption spectrophotometry (both using a Model 5100 atomic absorption spectrophotometer, Perkin-

Elmer Corp., Norwalk, CT, USA). Cl^- concentrations were measured using a digital chloridometer (LABCONCO, Kansas City, MO, USA), following extraction in distilled water.

Data Analysis

Analyses of Variance (using PROC GLM of the Statistical Analysis System, SAS Institute Inc., Cary, NC, USA) were used to test for differences in the gas exchange, water potential, chlorophyll fluorescence parameters, tissue concentrations of Cl^-, Na^+, K^+ and the Na^+/K^+, and Na^+/Ca^{2+} ratios among salinity treatments, families, and salinity x family interactions. Means for the August and September time periods were used for all analyses except those related to tissue ion concentrations. 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 several indicators of salt tolerance.

RESULTS

Gas Exchange

The means of A, g_w and E for the 15 families combined each declined substantially with increasing salinity (Table 4.1). The means for A, g_w and E at 8 g l^{-1} were less than

Table 4.1. Means and standard errors for gas exchange and leaf water potential by salinity level.

Response Variable	Salinity 0	2	4	6	8
Gas Exchange					
A (μmol (CO2) m^{-2} s^{-1})	3.88a[1]	3.18b	3.30ab	2.17c	1.11d
	0.30	0.16	0.18	0.23	0.12
g_w (mmol m^{-2} s^{-1})	91.8a	74.0b	70.2b	38.1c	21.4d
	5.7	2.9	4.9	2.0	1.3
E (mmol (H_2O) m^{-2} s^{-1})	1.76a	1.36b	1.46b	0.88c	0.48d
	0.07	0.07	0.08	0.05	0.03
Water Relations					
Midday Leaf Xylem Pressure Potential (MPa)	-0.91a	-1.02ab	-1.13b	-1.03ab	-1.53c
	0.023	0.030	0.024	0.035	0.115
Predawn Leaf Xylem Pressure Potential (MPa)	-0.22a	-0.33b	-0.46c	-0.53c	-0.68d
	0.008	0.010	0.013	0.019	0.029

[1] Means within a row followed by the same letter are not significantly different at the 0.05 level.

30% of the corresponding values for the freshwater controls. A similar pattern of decline was observed for each of the gas exchange measures. There was an initial and significant ($P \leq 0.05$) drop in all three variables 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 (Table 4.1).

Substantial variation among the 15 families was found for A, g_w, and E. Differences in overall family means (i.e., across salinities) were significant for all three variables, but salinity x family interactions were not (Table 4.2). An example of the variation observed among families is depicted in Table 4.3 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. Within-family variation was also high, and 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 (Table 4.3, Appendix A) and differences between the two sources were not significant for any of the gas exchange variables (data not shown). There were large differences between the two sources (and

Table 4.2. Analysis of variance table for gas exchange, water relations and chlorophyll fluorescence variables.

Variable	Salinity (d.f.=4)[1] MSE	F	P	Family (d.f.=14) MSE	F	P	Salinity x Family (d.f.=56) MSE	F	P
Gas Exchange									
A	53.59	76.93	.001	4.68	2.33	.028	1.47	0.84	.763
g_w	0.036	80.36	.001	0.001	2.63	.014	0.0006	1.07	.384
E	11.22	129.36	.001	0.38	2.86	.009	0.20	1.36	.089
Water Relations									
Midday Leaf	251.95	33.75	.001	14.03	0.80	.657	14.57	0.93	.607
Predawn	19.95	210.55	.001	0.79	8.31	.002	0.27	2.85	.035
Chlorophyll Fluorescence									
Fo	10237.03	1.53	.283	12434.24	4.03	.001	6034.73	2.28	.001
Fm	139484.04	2.45	.130	113138.13	3.29	.003	37182.85	1.18	.236
Fv/Fm	0.010	3.44	.065	0.005	2.16	.041	0.004	1.96	.002
Fq	46814.36	1.15	.399	46688.21	3.28	.004	16904.33	1.01	.471

[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 x family.

Table 4.3 Net photosynthesis (μmol (CO_2) m^{-2} s^{-1}) $\pm$ 1 s.e. by salinity and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	3.6 ±0.42	3.0 ±0.67	3.4 ±0.20	3.5 ±0.42	0.3 ±0.27
CB3	4.5 ±1.30	1.6 ±0.12	2.9 ±0.97	1.9 ±0.86	1.4 ±0.22
FA1	4.3 ±0.64	3.7 ±0.43	4.2 ±0.29	3.0 ±0.54	0.8 ±0.16
FA2	3.5 ±0.47	3.4 ±0.36	3.9 ±0.05	1.0 ±0.47	1.2 ±0.22
FA3	3.9 ±0.56	3.4 ±0.24	3.3 ±0.42	2.7 ±0.25	1.5 ±0.27
FA4	4.4 ±1.92	3.5 ±0.21	3.1 ±0.14	2.3 ±0.40	1.7 ±0.03
PB1	2.4 ±0.17	2.2 ±0.82	2.9 ±0.14	1.3 ±0.12	0.6 ±0.06
SG2	3.1 ±0.41	3.2 ±0.09	3.5 ±0.48	2.2 ±0.65	0.7 ±0.22
VE2	3.9 ±0.44	3.0 ±0.70	3.3 ±0.86	0.7 ±2.52	1.2 ±0.62
VE3	7.1 ±3.53	4.3 ±0.66	3.2 ±0.18	2.6 ±0.64	0.8 ±0.94
MEAN	4.1	3.1	3.4	2.1	1.0
Freshwater Sources					
BO2	3.6 ±0.18	2.1 ±0.76	1.0 ±0.38	1.1 ±0.21	1.0 ±0.05
LS1	4.1 ±0.07	3.7 ±0.36	4.6 ±0.53	2.9 ±0.02	2.3 ±1.03
PR1	2.6 ±0.88	2.8 ±1.10	1.9 ±0.27	1.6 ±0.46	0.9 ±0.35
SW1	4.0 ±0.81	4.4 ±0.57	4.6 ±1.29	3.2 ±0.29	1.8 ±0.21
SW2	3.4 ±0.75	3.6 ±0.11	3.1 ±0.29	1.9 ±0.72	0.5 ±0.14
MEAN	3.5	3.3	3.0	2.1	1.3
OVERALL MEAN	3.9	3.2	3.3	2.1	1.1

among individual families) in total photosynthesis on a per seedling basis, however, due to the differences in total leaf area (Allen et al. in press). The mean rate of CO_2 uptake per seedling for brackish sources at 6 and 8 g l^{-1} were 180 and 33 μmol s^{-1}, respectively, compared to 50 and 20 μmol s^{-1} for seedlings from freshwater sources.

Leaf Water Relations

Mean predawn leaf water potentials ranged from -0.22 MPa for the 0 g l^{-1} treatment to -0.68 MPa for the 8 g l^{-1} treatment (Table 4.1). 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 x family interaction were significant for the predawn sample (Table 4.2). The differential response to salinity among families was only apparent at 8 g l^{-1}, however (Figure 4.1).

A less consistent trend was apparent 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 (Table 4.1). 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

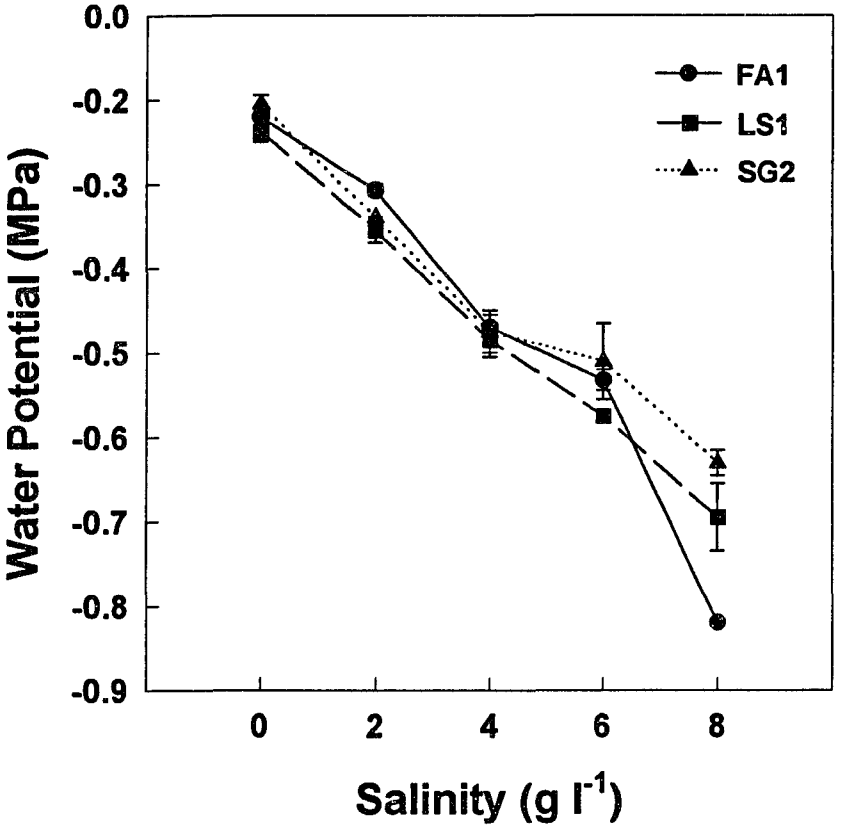

Figure 4.1. Mean predawn leaf water potential for three selected families.

large standard error, which is more than three times that of any other salinity treatment. In contrast to the predawn sample, family and salinity x family interactions were not significant for midday leaf water potential (Table 4.2).

Chlorophyll Fluorescence

Mean non-variable fluorescence (Fo) for the 15 families combined remained relatively stable as salinity increased (Figure 4.2). There was some indication of a progressive reduction in overall means for measures of both fast (Fm and Fv/Fm) and slow (Fq) fluorescence kinetics with increasing salinity, but no salinity treatment effects were found to be statistically significant (Table 4.2).

There were overall family differences for all chlorophyll fluorescence parameters measured and significant salinity x family interactions for Fo and Fv/Fm (Table 4.2). The patterns of change in the chlorophyll fluorescence measures with salinity were not consistent and not readily interpretable. For example, while 12 families had lower means for Fv/Fm at 8 g l^{-1} than at 0 g l^{-1}, 6 of the 12 had higher means at some intermediate salinity level (Appendix A). Families that exhibited relatively high salt tolerance (e.g., CB3, FA2, and FA3; Allen et al. in press), did not stand out as having above or below average values for any of the chlorophyll fluorescence parameters

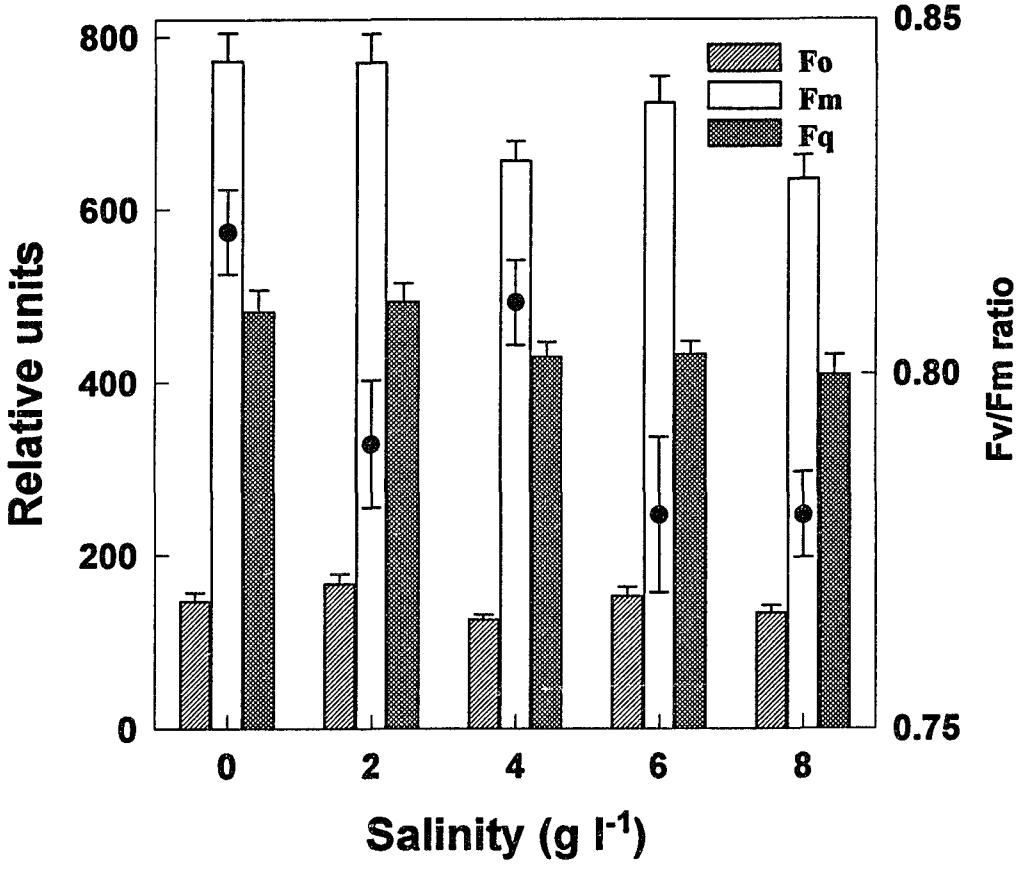

Figure 4.2. Means for chlorophyll fluorescence measures by salinity level. The variable Fv/Fm is indicated by (•).

(Appendix A). The overall means for the 10 families from brackish locations did not differ significantly from the five families from freshwater locations for any of the chlorophyll fluorescence parameters (data not shown).

Tissue Ion Concentrations

Concentrations of Na^+ and Cl^- in leaf, stem and root tissue increased significantly with the addition of salinity (Figures 4.3a and 4.3d). Cl^- accumulated to the highest concentrations in leaf tissue, whereas Na^+ concentrations were nearly equal in leaf and root tissue (Figures 4.3a and 4.3d). 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 4.3b). The differential pattern of K^+ concentrations in the three organs is reflected strongly in the Na^+/K^+ ratio. 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 4.3f). Ca^{2+} concentrations changed less than the other ions

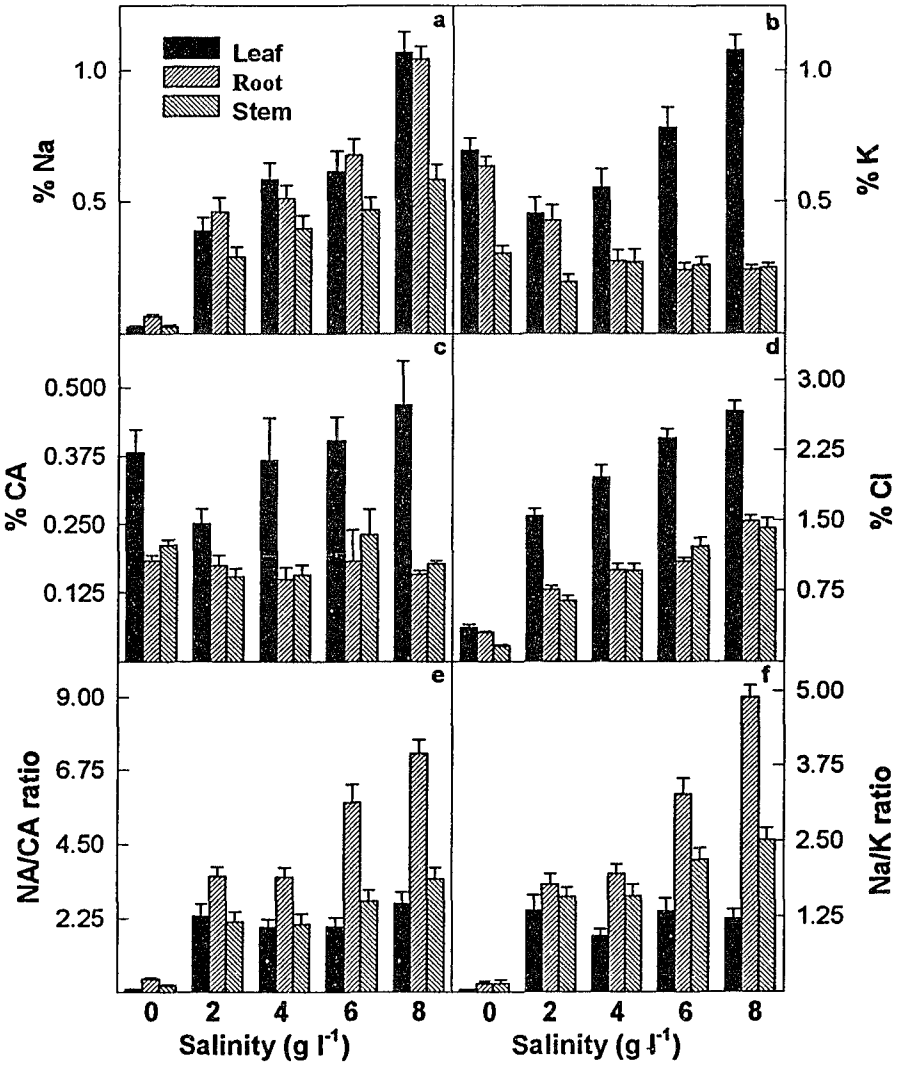

Figure 4.3. Means and standard errors by salinity level and tissue type for concentrations of (a) Na^+, (b) K^+, (c) Ca^{2+}, (d) Cl^-, and for the (e) Na^+/Ca^{2+}, (f) Na^+/K^+ ratios.

(Figure 4.3c). The most notable change was in the root Na^+/Ca^{2+} ratio, which increased significantly at higher salinities (Figure 4.3e).

Family differences were less frequently significant than differences among salinity treatments (Table 4.4). The most important differences among families are in Na^+ and Cl^- concentrations. In Figures 4.4 and 4.5, 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 4.4), 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 (Fig. 4.4). 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.

Table 4.4. Analysis of variance table for leaf, root and stem ion concentrations.

Variable	Salinity (d.f.=4) MSE	F	P	Family (d.f.=14) MSE	F	P	Salinity x Family (d.f.=56) MSE	F	P
Cl^- - Leaf	16.62	147.34	.001	0.31	1.95	.064	0.14	1.06	.435
Cl^- - Root	7.91	32.06	.001	0.08	1.10	.508	0.08	1.10	.333
Cl^- - Stem	10.46	13.34	.001	0.35	2.32	.028	0.27	1.49	.042
Na^+ - Leaf	4.89	28.71	.001	0.31	3.08	.005	0.12	1.40	.091
Na^+ - Root	5.44	15.57	.001	0.07	0.75	.714	0.07	0.85	.747
Na^+ - Stem	1.95	11.66	.002	0.13	2.94	.007	0.08	1.38	.086
K^+ - Leaf	1.85	2.18	.162	0.18	2.07	.049	0.11	0.78	.835
K^+ - Root	1.27	7.04	.010	0.06	0.87	.598	0.06	1.06	.399
K^+ - Stem	0.07	0.60	.673	0.03	1.14	.367	0.03	0.99	.509
Ca^{2+} - L	0.27	1.01	.455	0.12	1.07	.419	0.13	0.90	.666
Ca^{2+} - R	0.01	0.16	.954	0.07	1.19	.335	0.03	1.00	.487
Ca^{2+} - S	0.05	0.76	.580	0.02	0.79	.673	0.02	0.85	.746
Na^+/K^+ - L	12.90	3.01	.086	2.20	2.28	.031	1.13	1.04	.425
Na^+/K^+ - R	138.70	36.57	.001	1.58	1.66	.123	1.15	0.70	.934
Na^+/K^+ - S	36.85	12.73	.001	1.20	2.00	.057	1.06	0.92	.635
Na^+/Ca^{2+} - L	40.22	5.88	.017	4.55	1.07	.426	2.75	0.87	.716
Na^+/Ca^{2+} - R	297.48	18.58	.001	5.94	0.99	.488	4.44	1.08	.365
Na^+/Ca^{2+} - S	68.74	7.29	.009	6.36	1.81	.088	4.21	1.50	.037

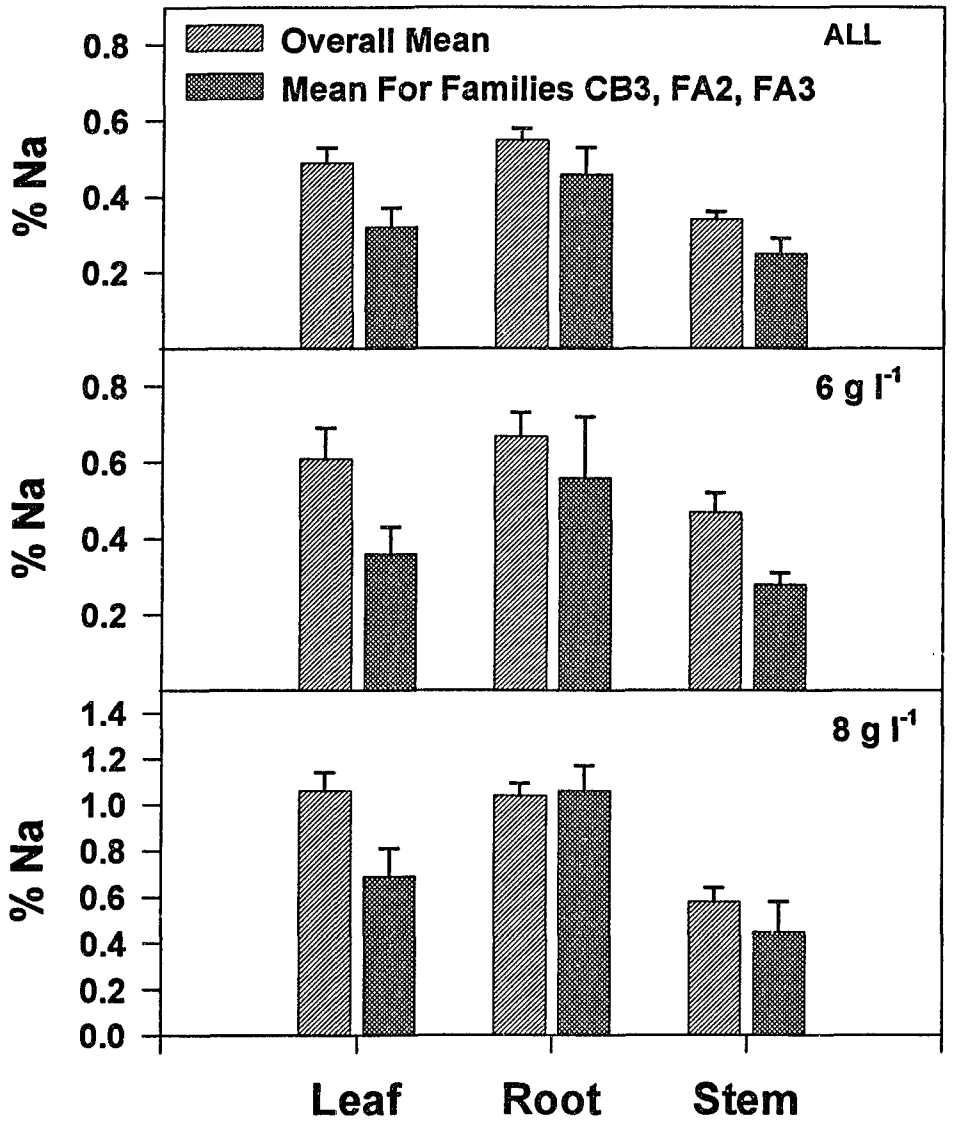

Figure 4.4. Means by tissue type and salinity level for Na^+ concentrations for all 15 families and for Families CB3, FA2, and FA3.

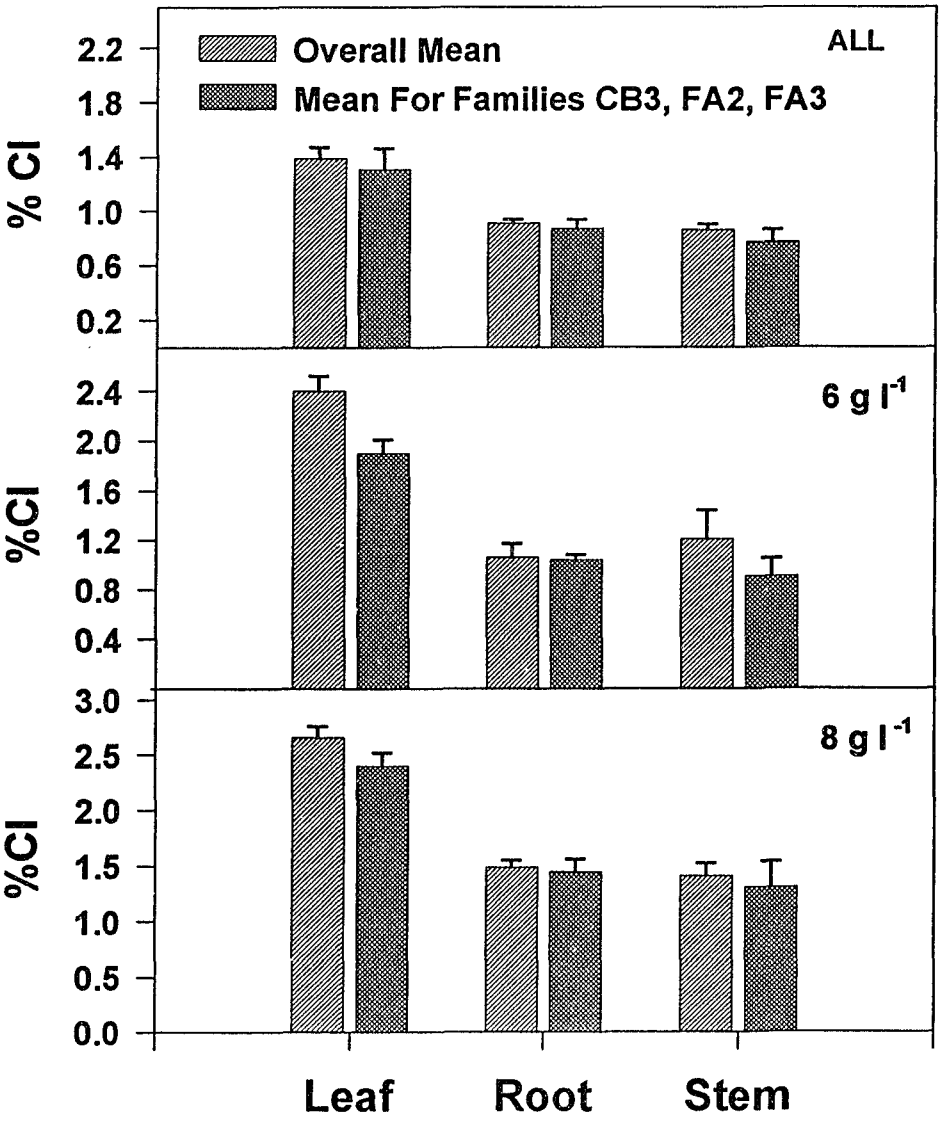

Figure 4.5. Means by tissue type and salinity level for Cl^- concentrations for all 15 families and for Families CB3, FA2, and FA3.

Relationships between Physiological Measures and Indices of Salt Tolerance

Linear correlations between gas exchange, water potential, and chlorophyll fluorescence measures and the derived indices of salt tolerance (Potential Survival Index and Potential Productivity Index; Allen et al. in press) were not significant (Table 4.5). There were several significant linear correlations between tissue concentrations of ions in leaf tissue and PSI and PPI, most notably for Na^+ and Cl^-. All significant correlations were negative, indicating that high ion concentrations were associated with low salt tolerance.

DISCUSSION

Species-level Responses

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%. Likewise, Pezeshki et al. (1986) reported a 90%

Table 4.5 Linear correlation coefficients (r) and P values for relationships between selected physiological measures and indices of salt tolerance.

	Potential Survival Index		Potential Productivity Index	
Response Variable	r	P	r	P
Gas Exchange				
A (0)	0.06	0.81	-0.44	0.10
A (2)	-0.32	0.25	-0.19	0.51
A (4)	0.15	0.59	0.36	0.19
A (6)	-0.19	0.50	-0.31	0.25
A (8)	0.20	0.47	0.19	0.49
Chlorophyll Fluorescence				
Fv/Fm (0)	-0.07	0.81	0.04	0.88
Fv/Fm (2)	-0.04	0.88	-0.20	0.47
Fv/Fm (4)	0.14	0.61	0.03	0.92
Fv/Fm (6)	-0.11	0.69	-0.33	0.23
Fv/Fm (8)	0.32	0.25	0.13	0.65
Tissue Ion Concentrations				
Na^+ - L (all)	-0.82	0.00	-0.58	0.02
Cl^- - L (all)	0.10	0.72	0.13	0.66
Na^+/K^+ - L (all)	-0.40	0.13	-0.25	0.37
Na^+/Ca^{2+} - L (all)	-0.44	0.10	-0.30	0.27
Na^+ - L (6)	-0.55	0.03	-0.52	0.04
Cl^- - L (6)	-0.88	0.00	-0.54	0.09
Na^+/K^+ - L (6)	-0.36	0.19	-0.30	0.28
Na^+/Ca^{2+} - L (6)	-0.25	0.36	-0.19	0.49

reduction in A of young leaves when seedlings were flooded with 7 to 8 g l^{-1} artificial seawater, compared to a 72% reduction (for the 8 g $^{-1}$ treatment) in this study.

One reason why observed declines in A and g_w may have been less 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. The lower light may be a major reason for the lower levels of A and g_w observed in the control seedlings compared to those of earlier studies. Control levels for A in earlier studies range from approximately 4.5 to 10 μmol m^2 s^{-1} (Pezeshki et al. 1986, 1987), compared to only 3.9 in this study. It is unlikely that lower light levels account for all the differences with previous reports, however, because the light saturation level for baldcypress is reportedly around 500 μmol m^{-2} s^{-1} (S.R. Pezeshki, pers. comm.).

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 appear 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 (Appendix A), 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 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 higher 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*.

On the other hand, there was only weak evidence of a direct effect of salinity on the photosynthetic apparatus, as assessed by chlorophyll fluorescence. The fluorescence parameter Fv/Fm, which has often been correlated with the photochemical efficiency and electron transport capacity of PSII (Bjorkman and Deming 1987; Krause and Weis 1991), exhibited only a slight (and non-significant) decline with increasing salinity. The variable Fq, which is reported to be indicative of the efficiency of fluorescence quenching and energy dissipation (Bolhar-Nordenkampf and Oquist 1993), declined substantially with salinity, but again the differences among treatments were not significant.

In contrast to this study, significant salinity-related differences in chlorophyll fluorescence patterns have been reported for some other species (Smillie and Nott 1982, Downton and Miller 1985; Belkhodja et al. 1994). One possible reason why significant differences were not detected in the current study (assuming they did occur) is the choice of chlorophyll fluorescence parameters for evaluation. Smillie and Nott (1982) and Belkhodja et al. (1994), for example, reported differences in chlorophyll fluorescence parameters that took into consideration the initial rise (to "I") on the Kautsky fluorescence induction curve (Krause and Weis 1991). Because the fluorescence system (the P.K. Morgan Model CF-1000) used in this study

does not record data on F_I, parameters comparable to those earlier studies could not be assessed.

It is also possible that had older leaves been selected for measurement, differences in chlorophyll fluorescence may have been more pronounced. An increasing gradient of response to salt with leaf age was reported for sunflower (*Helianthus annuus* L.; Smillie and Nott 1982). The relatively young leaves sampled in this study may not have reached a stage where sufficient damage to the photosynthetic apparatus had occurred. Other possible reasons why significant differences might not have been detected (again, assuming such differences did occur) include inherent problems in measuring baldcypress leaves (which consist of numerous small leaflets, making it difficult to sample exactly the same amount of leaf area on each measurement) and the relatively short measurement period (30 s), which may not have been long enough to fully capture differences in fluorescence quenching (*i*.e., Fq).

It was shown previously (Chapter 3) that biomass partitioning to roots increased at low salinities, but that at salinity levels above 4 g l^{-1} root biomass was reduced more than shoot biomass. 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 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.

Family-Level Variation

Significant family-level variation was found for all measures of gas exchange, water potential, and chlorophyll fluorescence with the exception of midday water potential. There was no clear indication, however, that the variation observed was related to the salt tolerance of the 15 families. Linear correlations between these variables and indicators of salt tolerance (the PSI and PPI tolerance indices) 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 is 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

(Bernstein et al. 1969; Thomson 1988; Maas 1993), and exclusion of both Na^+ and Cl^- appears 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 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; p. 104), 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 appear to be an important research priority and one with high potential for producing gains in salt tolerance of baldcypress.

OVERALL CONCLUSIONS

RESEARCH HIGHLIGHTS

A major goal of this dissertation research project was to assess the potential for employing a genetic improvement approach to the restoration of coastal forests dominated by baldcypress. The success of such an approach is dependent on the ability to identify (or create) and propagate genotypes of baldcypress that are more salt-tolerant than planting material currently available. The most important overall conclusion that can be drawn from this portion of the dissertation is that there does appear to be some potential for the use of a genetic approach. In support of this conclusion are two lines of evidence.

First, mature trees were located in the field that appeared to be growing successfully in salinity regimes much higher than those of most healthy baldcypress swamps. As reported in Chapter 2, several individual trees were found on sites where the salinity measured in the soil or surface water exceeded 2 g l^{-1} throughout the growing season and occasionally reached levels as high as 4 to 7.5 g l^{-1}. While the possibility of some type of "escape" mechanism, such as a portion of the root system growing in a zone of low salinity, cannot be ruled out for any of these trees, there is clearly at least the potential that salt-tolerant mature trees exist.

Second, as reported in Chapters 2 and 3, substantial variation in the response to flooding with saline water was found among the 15 open-pollinated families investigated. Some families, and individual seedlings within families, performed much better than the overall average under elevated levels of salinity. Differences among families in performance, as assessed by variables such as total biomass and leaf area, were not only statistically significant, but were substantial enough to justify some hope that they may translate into real, long-term differences in field performance. The conclusion that there will be differences in field performance, of course, cannot be drawn from the present work, which was a relatively short-term study conducted under controlled (greenhouse) conditions.

The second major goal of this research was to investigate the general responses of seedlings to salinity for the purposes of (1) better understanding the reasons for differences in response of baldcypress seedlings to salinity and (2) assessing the potential for the use of physiological measures to screen seedlings for salt tolerance.

Based on the results presented in Chapter 4, salinity clearly imposes a significant degree of stress upon baldcypress seedlings. Even at the lowest salinity treatment (2 g l^{-1}), significant declines in the physiological function (e.g., gas exchange) of seedlings

were evident. At higher salinity levels, numerous signs of salinity stress were apparent. The water status of the leaves declined substantially, tissue concentrations of Cl^- and Na^+ increased dramatically, and Na^+/K^+ and Na^+/Ca^{2+} ratios rose in roots and stems. Also, not only was net photosynthesis on a leaf area basis reduced, but the average number and size of leaves, and thus seedling leaf area, was also reduced. This in turn greatly reduced the total capacity of the seedlings for carbon assimilation. At the same time, salinity appeared to be imposing additional metabolic costs upon the seedlings, such as that needed to maintain uniform Na^+/K^+ ratios in the leaves against an increasing Na^+ activity gradient. The net effect was first a decrease in leaf biomass, and then decreases in both root biomass and seedling survival with increasing salinity.

Different patterns of response to salinity were evident at the family and particularly at the individual seedling level. The differences appear to be related to salt tolerance and may therefore serve as useful mechanisms for screening. As noted in Chapters 2 and 3, the most striking differences between apparently tolerant and apparently intolerant seedlings are morphological. The more tolerant seedlings had larger leaves and did not exhibit any dieback at the top of seedlings. Less tolerant seedlings exhibited partial stem dieback and near total

defoliation followed by partial refoliation with smaller leaves.

While there were significant differences in family means for gas exchange, leaf water potential, and chlorophyll fluorescence, no clear relationship existed between these variables and salt tolerance (as assessed by two tolerance indices). Their potential value as tools for screening, therefore, appears to be limited. Their possible utility cannot be entirely ruled out, however. Several factors that may have resulted in less than optimal differentiation of these response variables (e.g., light levels, particular chlorophyll fluorescence variables measured), are discussed in Chapter 4.

The clearest relationships with salt tolerance were found for concentrations of Na^+ and Cl^- in tissues, especially leaves. Correlations with the two tolerance indices were consistently negative, indicating that the salt tolerant families were more effective at excluding Na^+ and Cl^- from their shoots.

RECOMMENDATIONS FOR FURTHER RESEARCH

The long-term goal addressed in part by this dissertation is the restoration of baldcypress swamps affected by saltwater intrusion. With that in mind, a number of suggestions for further research can be made

based either directly or indirectly on this work. These suggestions fall into three broad categories, each of which is addressed below in a separate subsection.

Better Data on the Extent of the Problem

One very important need is for better data on the current status of the saltwater intrusion problem and the likelihood of an expansion of the problem in the future. Existing reports on the saltwater intrusion problem (e.g., Wicker et al. 1981) are sufficient to conclude that current losses of baldcypress swamps due to saltwater intrusion are on the scale of several thousands of hectares. Personal observations of this author made in the course of searching for mature, apparently salt-tolerant trees further support this conclusion. Areas of dead baldcypress swamp (that apparently are due to saltwater intrusion) on the scale of that reported by Wicker et al. (1981) were located in at least two other areas -- along the Mississippi River Gulf Outlet and along the Houma Navigation Canal. Numerous smaller areas of mortality that appeared to be caused by saltwater intrusion were also located, such as along the southern and western shores of Lake Ponchartrain.

A formal assessment of the areas currently affected by saltwater intrusion may help to provide guidance for planning restoration projects and should certainly provide ample justification for their implementation. Specific

research suggestions for provision of better data on the extent of the problem include: (1) determination of the area of dead and dying baldcypress forests using conventional techniques (delineation using aerial photography and ground-truthing); (2) a review of the data on subsidence rates, sea level rise and salinity trends to identify potentially threatened swamps; (3) development of techniques for assessing the level and cause of stress in living trees--perhaps based on leaf nutrient and salt ion content; and (4) development of a technique for identifying sublethal stress in baldcypress swamps based on remotely sensed data.

Opportunities and Techniques for Restoring Hydrology

The primary reason for salinity-related stress and mortality in baldcypress swamps is altered hydrology. While the genetic approach explored in this dissertation is advocated as one part of an overall solution, it is important to acknowledge that reestablishment of the original hydrologic regime (i.e., freshwater and seasonally to semipermanently flooded) is undoubtedly the best strategy for restoration. Other types of forests have been shown to recover quickly once salt stress was reduced (e.g., Walters and Auchmoody 1989). There is no reason to believe that baldcypress swamps would not also recover if soil salinity was reduced by inputs of fresh water,

assuming that other factors such as nutria (Conner 1988; Allen and Boykin 1991) are not limiting the capacity for regeneration.

Restoring hydrology is unlikely to be feasible in many areas since it would result in flooding of property or have a negative impact on navigation. Still, many projects designed to improve hydrologic conditions for coastal wetland restoration have been proposed (Wetland Conservation and Restoration Task Force 1990), and at least two of them are designed in part to help restore baldcypress swamps (Manchac and Falgout Canal). By using the results of the research proposed in the previous subsection, it should be possible to go through on a case-by-case basis and evaluate the potential for restoring hydrology in each of the areas found to be killed or stressed due to saltwater intrusion.

It may be possible to develop guidance by studying cases where, whether or not by design, hydrologic modifications have helped protect swamps. An interesting example is the Mereaux Pumping Station in Chalmette. The fresh water (and possibly sediments) pumped by this station have kept a small semi-circle of baldcypress swamp alive in an area where an otherwise vast acreage of forest has been killed by saltwater intruding inland via the Mississippi River Gulf Outlet (personal observation).

Another example is the Falgout Canal project south of Houma (Wetland Conservation and Restoration Task Force 1990). A system of levees and water control structures has been constructed to limit saltwater intrusion into a large complex of marsh and swamp. Based on the presence of old snags, it appears that virtually all of the enclosed area was baldcypress swamp prior to construction of the Houma Navigation Canal. It would be instructive to monitor the soil salinity within this enclosed area to determine how rapidly salinity declines. It would also be interesting to monitor the site to determine whether baldcypress is able to reestablish on the site naturally.

Improving the Salt Tolerance of Baldypress

Although it is concluded in this dissertation that the possibility for developing salt tolerant lines of baldcypress appears promising, much research remains to be conducted before this can be determined for certain. As stated in Chapter 1, probably the most immediate gains from research can be made from more intensive screening, followed by field progeny testing. The bottom line, of course, is performance in the field, and the importance of moving into the field trial stage cannot be overemphasized. Sites such as the one mentioned in the last paragraph of the previous section would make ideal locations for field trials.

Ideally, field trials would address a number of research questions in addition to differences in performance amongst genotypes. It may be particularly critical to evaluate (1) the feasibility of various site preparation techniques (e.g., bedding) and their effects on initial survival and growth, (2) the effects of acclimating seedlings to salinity prior to planting, and (3) the effects of different types of planting stock (e.g., bare-root vs. containerized).

Important questions also need to be addressed regarding propagation techniques, especially if clonal material is to be used. Although baldcypress is reportedly more difficult to propagate vegetatively than many tree species, some success in producing rooted cuttings has been reported (Lee et al. 1979; Dirr 1983; Copes and Randall 1993). Especially promising are the results of Copes and Randall (1993) who reported that they were able to root up to 58% of cuttings taken from clones of 20-year-old trees, using techniques normally applied for Douglas-fir. It would be highly desirable to determine if their technique could be used to propagate seedlings from older trees that have apparently withstood long-term exposure to salinity. Testing current techniques for rooting cuttings is one logical approach, but techniques such as tissue culture may also prove effective.

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APPENDIX A

MEANS AND STANDARD ERRORS BY SALINITY LEVEL AND FAMILY FOR RESPONSE VARIABLES NOT REPORTED IN THE MAIN TEXT

Table A.1. Initial height (cm) ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	40.1 ± 1.0	39.7 ± 1.2	40.2 ± 1.1	42.3 ± 1.0	42.5 ± 1.2
CB3	42.9 ± 1.1	39.2 ± 0.9	37.9 ± 0.8	39.3 ± 1.0	41.4 ± 1.5
FA1	42.5 ± 1.0	39.1 ± 1.1	41.0 ± 0.6	41.6 ± 1.5	43.0 ± 1.0
FA2	39.2 ± 0.7	38.2 ± 0.8	38.7 ± 1.0	39.9 ± 1.2	42.0 ± 0.9
FA3	42.6 ± 1.1	39.8 ± 1.3	41.8 ± 1.1	40.4 ± 1.3	42.9 ± 1.0
FA4	38.1 ± 1.1	40.3 ± 0.9	38.8 ± 0.9	39.9 ± 1.2	39.9 ± 1.2
PB1	32.5 ± 1.1	31.5 ± 1.0	33.6 ± 1.2	37.6 ± 0.8	39.6 ± 1.5
SG2	38.8 ± 0.9	38.0 ± 1.0	41.6 ± 0.7	42.2 ± 0.9	38.7 ± 0.9
VE2	41.5 ± 1.1	39.8 ± 1.0	40.5 ± 0.9	42.6 ± 1.0	42.1 ± 1.0
VE3	42.9 ± 1.1	43.3 ± 0.7	43.1 ± 1.0	41.3 ± 1.0	41.1 ± 1.0
MEAN	40.1	38.9	39.7	40.7	41.3
Freshwater Sources					
BO2	37.8 ± 1.0	34.4 ± 1.3	37.4 ± 0.8	40.7 ± 0.9	39.7 ± 1.0
LS1	39.0 ± 1.1	39.3 ± 0.7	41.2 ± 0.8	40.8 ± 0.9	42.4 ± 0.9
PR1	34.3 ± 1.3	32.7 ± 1.1	36.5 ± 1.0	37.3 ± 0.9	39.3 ± 0.8
SW1	38.8 ± 1.0	36.8 ± 0.8	40.9 ± 0.9	40.8 ± 0.9	40.6 ± 0.9
SW2	38.5 ± 1.3	37.3 ± 0.9	42.0 ± 1.2	39.4 ± 0.8	41.1 ± 0.8
MEAN	37.7	36.1	39.6	39.8	40.6
OVERALL MEAN	39.3	38.0	39.7	40.5	41.2

Table A.2. Height at harvest (cm) ± 1 s.e. by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	65.7 ± 2.2	59.9 ± 1.9	59.7 ± 2.1	61.7 ± 1.3	58.8 ± 1.9
CB3	70.0 ± 2.3	63.7 ± 2.5	60.3 ± 2.1	56.0 ± 2.0	58.7 ± 1.7
FA1	86.2 ± 2.6	78.7 ± 2.3	75.0 ± 2.2	73.9 ± 1.6	69.1 ± 1.7
FA2	69.8 ± 2.2	65.3 ± 2.3	68.4 ± 1.9	65.2 ± 2.3	60.1 ± 1.2
FA3	74.9 ± 3.0	66.2 ± 2.9	68.5 ± 2.2	60.2 ± 1.6	62.7 ± 1.3
FA4	60.5 ± 2.5	65.5 ± 2.3	59.1 ± 1.9	59.4 ± 1.7	55.9 ± 1.3
PB1	50.0 ± 2.3	47.9 ± 1.8	51.2 ± 2.7	58.1 ± 1.5	54.9 ± 2.5
SG2	64.2 ± 2.3	59.9 ± 2.4	64.9 ± 1.7	66.0 ± 1.4	58.6 ± 1.5
VE2	72.5 ± 2.3	72.7 ± 2.3	70.1 ± 2.1	64.0 ± 1.6	61.2 ± 1.4
VE3	78.3 ± 2.4	73.9 ± 2.3	67.4 ± 2.0	65.3 ± 1.9	61.0 ± 1.9
MEAN	69.2	65.4	64.5	63.0	60.1
Freshwater Sources					
BO2	59.7 ± 2.3	50.3 ± 2.7	54.4 ± 1.8	53.5 ± 1.7	54.0 ± 1.5
LS1	74.9 ± 2.5	70.7 ± 2.3	67.4 ± 2.1	72.6 ± 1.6	66.4 ± 1.4
PR1	56.8 ± 2.4	54.0 ± 2.3	56.0 ± 2.0	56.1 ± 1.9	56.9 ± 1.9
SW1	71.5 ± 2.5	68.0 ± 2.3	71.6 ± 2.3	66.2 ± 1.4	65.8 ± 1.6
SW2	70.8 ± 2.3	68.1 ± 2.1	63.5 ± 2.2	66.9 ± 2.3	61.0 ± 1.5
MEAN	66.7	62.2	62.6	63.1	60.8
OVERALL MEAN	68.4	64.4	64.1	63.3	60.8

Table A.3. Root weight ratio ± 1 s.e. by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	0.303 ±0.008	0.325 ±0.010	0.340 ±0.008	0.299 ±0.019	0.310 ±0.025
CB3	0.275 ±0.009	0.301 ±0.010	0.322 ±0.015	0.333 ±0.010	0.303 ±0.022
FA1	0.280 ±0.011	0.280 ±0.014	0.312 ±0.013	0.319 ±0.010	0.280 ±0.021
FA2	0.256 ±0.011	0.267 ±0.010	0.335 ±0.009	0.347 ±0.022	0.337 ±0.019
FA3	0.285 ±0.014	0.293 ±0.008	0.343 ±0.010	0.337 ±0.017	0.310 ±0.011
FA4	0.286 ±0.017	0.315 ±0.008	0.325 ±0.012	0.297 ±0.016	0.323 ±0.020
PB1	0.301 ±0.015	0.279 ±0.020	0.332 ±0.026	0.309 ±0.018	0.279 ±0.029
SG2	0.305 ±0.013	0.319 ±0.012	0.344 ±0.011	0.350 ±0.015	0.309 ±0.013
VE2	0.314 ±0.010	0.314 ±0.010	0.365 ±0.017	0.343 ±0.018	0.307 ±0.017
VE3	0.298 ±0.010	0.333 ±0.007	0.354 ±0.009	0.320 ±0.017	0.289 ±0.025
MEAN	0.290	0.303	0.337	0.325	0.305
Freshwater Sources					
BO2	0.290 ±0.011	0.330 ±0.020	0.329 ±0.015	0.302 ±0.011	0.323 ±0.022
LS1	0.307 ±0.014	0.346 ±0.011	0.364 ±0.014	0.307 ±0.016	0.281 ±0.020
PR1	0.293 ±0.019	0.307 ±0.018	0.364 ±0.024	0.274 ±0.017	0.287 ±0.023
SW1	0.267 ±0.022	0.264 ±0.010	0.317 ±0.015	0.265 ±0.017	0.328 ±0.035
SW2	0.271 ±0.009	0.282 ±0.010	0.327 ±0.013	0.296 ±0.010	0.239 ±0.027
MEAN	0.286	0.306	0.340	0.289	0.292
OVERALL MEAN	0.288	0.304	0.338	0.315	0.302

Table A.4. Leaf number ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	54.1 ± 8.7	42.3 ± 4.7	31.7 ± 5.8	7.3 ± 3.2	6.3 ± 2.6
CB3	56.5 ±10.5	44.3 ± 5.7	27.5 ± 8.3	21.8 ± 4.7	21.9 ± 5.0
FA1	60.3 ± 6.0	61.0 ± 7.1	27.0 ± 5.7	12.7 ± 2.0	13.6 ± 3.4
FA2	44.7 ± 4.7	43.3 ± 4.0	37.2 ± 4.1	18.0 ± 5.8	10.1 ± 4.0
FA3	59.0 ±10.3	41.3 ± 6.9	38.0 ± 6.0	15.7 ± 4.6	16.9 ± 4.2
FA4	48.8 ± 8.5	61.7 ± 9.7	31.4 ± 4.4	11.0 ± 4.4	6.2 ± 1.6
PB1	23.7 ± 2.6	27.3 ± 9.0	11.1 ± 4.1	4.2 ± 1.9	6.5 ± 4.6
SG2	42.3 ± 3.7	35.8 ± 6.7	28.4 ± 4.1	12.8 ± 3.4	10.6 ± 2.4
VE2	47.1 ± 3.9	49.3 ± 7.8	29.7 ± 5.0	18.7 ± 7.5	0.6 ± 0.5
VE3	67.2 ±15.1	51.9 ± 4.7	35.9 ± 5.4	13.8 ± 2.8	8.3 ± 3.2
MEAN	50.4	45.8	29.8	13.6	10.1
Freshwater Sources					
BO2	55.3 ± 7.3	38.3 ± 5.4	25.3 ± 6.5	0.7 ± 0.3	4.1 ± 2.6
LS1	49.1 ± 4.8	39.8 ± 4.1	20.9 ± 4.9	9.1 ± 2.9	8.8 ± 2.9
PR1	32.1 ± 3.4	28.4 ± 2.3	13.0 ± 3.8	6.3 ± 2.5	7.0 ± 5.3
SW1	58.1 ± 5.3	43.3 ± 4.1	46.3 ± 7.9	6.2 ± 1.3	9.1 ± 3.5
SW2	74.5 ± 8.6	54.8 ± 5.5	37.7 ± 5.1	17.3 ± 4.5	4.9 ± 1.6
MEAN	53.8	40.9	28.6	7.9	6.8
OVERALL MEAN	51.5	44.3	29.8	11.7	9.2

Table A.5. Specific leaf area (m^2 g^{-1}) ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	.0190 ±.0011	.0181 ±.0007	.0168 ±.0005	.0208 ±.0081	.0158 ±.0043
CB3	.0171 ±.0016	.0184 ±.0005	.0175 ±.0008	.0172 ±.0011	.0188 ±.0026
FA1	.0200 ±.0037	.0207 ±.0012	.0195 ±.0017	.0185 ±.0022	.0187 ±.0054
FA2	.0170 ±.0018	.0198 ±.0013	.0163 ±.0008	.0206 ±.0030	.0172 ±.0012
FA3	.0194 ±.0011	.0201 ±.0019	.0189 ±.0012	.0174 ±.0008	.0206 ±.0031
FA4	.0202 ±.0047	.0167 ±.0006	.0189 ±.0014	.0158 ±.0041	.0109 ±.0033
PB1	.0109 ±.0010	.0213 ±.0017	.0181 ±.0014	.0169 ±.0059	.0183 ±.0042
SG2	.0189 ±.0008	.0196 ±.0015	.0181 ±.0022	.0180 ±.0019	.0211 ±.0042
VE2	.0188 ±.0014	.0197 ±.0013	.0187 ±.0007	.0196 ±.0020	.0265 ± -
VE3	.0208 ±.0024	.0195 ±.0017	.0187 ±.0010	.0265 ±.0072	.0160 ±.0013
MEAN	.0182	.0194	.0181	.0191	.0184
Freshwater Sources					
BO2	.0215 ±.0017	.0206 ±.0010	.0145 ±.0026	.0119 ±.0083	.0188 ±.0013
LS1	.0223 ±.0034	.0208 ±.0022	.0172 ±.0006	.0217 ±.0025	.0202 ±.0053
PR1	.0203 ±.0014	.0199 ±.0016	.0207 ±.0030	.0237 ±.0027	.0206 ± -
SW1	.0179 ±.0017	.0199 ±.0009	.0188 ±.0013	.0185 ±.0042	.0133 ±.0084
SW2	.0237 ±.0037	.0177 ±.0009	.0187 ±.0012	.0194 ±.0019	- ± -
MEAN	.0211	.0198	.0180	.0190	.0183
OVERALL MEAN	.0197	.0195	.0181	.0193	.0183

Table A.6. Stomatal conductance (mmol m^{-2} s^{-1}) ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	121.9 ±31.5	71.2 ± 1.5	76.8 ±19.6	34.7 ± 3.5	19.1 ± 2.4
CB3	93.9 ±24.4	45.0 ± 9.9	70.2 ±12.1	31.9 ± 9.3	25.9 ± 3.4
FA1	82.6 ±10.3	63.6 ± 7.2	98.8 ±18.7	56.6 ± 9.2	16.6 ± 1.5
FA2	72.8 ± 9.2	83.5 ±15.2	68.4 ± 1.8	25.0 ± 4.7	21.2 ± 1.9
FA3	87.0 ±19.3	80.2 ± 2.9	55.6 ± 8.7	46.8 ± 6.0	22.6 ± 6.7
FA4	89.1 ±39.1	84.8 ±10.3	57.5 ± 4.3	36.0 ± 1.5	29.8 ± 5.0
PB1	73.5 ± 9.1	73.1 ± 9.8	78.8 ± 2.3	30.8 ± 0.6	12.1 ± 0.5
SG2	66.0 ± 3.4	67.1 ± 2.5	78.8 ±15.6	30.3 ± 2.5	17.6 ± 3.4
VE2	93.2 ± 6.1	69.4 ± 2.9	58.2 ± 9.2	43.8 ± 9.0	22.6 ±11.8
VE3	134.8 ±57.3	81.6 ± 1.8	65.1 ± 2.3	35.3 ± 2.5	17.4 ± 8.9
MEAN	91.5	72.0	70.8	37.1	20.5
Freshwater Sources					
BO2	102.2 ±12.6	66.3 ±14.6	30.0 ± 5.4	26.4 ± 2.1	14.6 ± 2.3
LS1	104.5 ±15.0	82.7 ±10.3	77.2 ±14.1	48.8 ± 4.5	31.5 ± 6.7
PR1	78.1 ±16.0	63.6 ±19.5	37.2 ± 1.0	36.1 ± 5.2	18.4 ± 3.4
SW1	98.7 ±21.4	99.4 ±15.4	142.2 ±33.9	57.2 ± 6.3	29.1 ± 1.9
SW2	78.7 ±10.4	78.9 ±10.8	58.3 ± 5.3	32.1 ± 6.4	22.1 ± 4.7
MEAN	92.4	78.2	69.0	40.1	23.1
OVERALL MEAN	91.8	74.0	70.2	38.1	21.4

Table A.7. Transpiration (mmol (H_2O) m^{-2} s^{-1}) ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	2.2 ±0.22	1.3 ±0.16	1.5 ±0.18	1.0 ±0.13	0.3 ±0.03
CB3	1.4 ±0.40	0.8 ±0.20	1.4 ±0.45	0.7 ±0.18	0.6 ±0.07
FA1	2.0 ±0.22	1.5 ±0.08	1.9 ±0.48	1.1 ±0.31	0.5 ±0.03
FA2	1.7 ±0.07	1.5 ±0.29	1.5 ±0.17	0.5 ±0.14	0.5 ±0.06
FA3	1.6 ±0.39	1.5 ±0.13	1.3 ±0.14	1.2 ±0.10	0.5 ±0.10
FA4	1.3 ±0.20	1.5 ±0.22	1.1 ±0.04	1.0 ±0.00	0.7 ±0.11
PB1	1.8 ±0.20	0.9 ±0.26	1.9 ±0.13	0.7 ±0.10	0.2 ±0.02
SG2	1.5 ±0.03	1.5 ±0.16	1.7 ±0.40	0.9 ±0.07	0.5 ±0.18
VE2	1.7 ±0.21	1.1 ±0.26	1.3 ±0.16	1.0 ±0.19	0.4 ±0.10
VE3	2.0 ±0.25	1.6 ±0.12	1.7 ±0.27	0.7 ±0.06	0.5 ±1.05
MEAN	1.7	1.3	1.5	0.9	0.5
Freshwater Sources					
BO2	2.4 ±0.27	1.0 ±0.35	0.7 ±0.27	0.7 ±0.05	0.3 ±0.03
LS1	2.2 ±0.27	1.8 ±0.14	1.5 ±0.18	1.1 ±0.10	0.7 ±0.12
PR1	1.4 ±0.41	1.1 ±0.29	1.0 ±0.27	0.7 ±0.03	0.4 ±0.06
SW1	1.8 ±0.37	1.7 ±0.25	2.1 ±0.25	1.2 ±0.21	0.7 ±0.10
SW2	1.6 ±0.10	1.6 ±0.27	1.4 ±0.10	0.7 ±0.27	0.4 ±0.08
MEAN	1.9	1.4	1.3	0.9	0.5
OVERALL MEAN	1.8	1.4	1.5	0.9	0.5

Table A.8. Leaf internal CO_2 conc. (p.p.m.) ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	241 ±17.2	261 ± 4.5	238 ± 9.7	221 ±44.7	314 ±11.5
CB3	260 ±10.3	287 ± 2.2	255 ±18.8	285 ±28.3	266 ±13.9
FA1	245 ± 6.9	238 ±15.3	236 ± 2.3	251 ± 4.4	277 ±12.4
FA2	257 ± 4.2	264 ±12.8	212 ± 4.2	295 ±14.2	260 ±11.6
FA3	255 ± 1.6	259 ± 8.7	220 ±15.8	245 ± 7.1	254 ±18.9
FA4	250 ± 0.4	257 ± 6.5	233 ± 8.3	230 ±13.1	278 ± 8.0
PB1	264 ±10.6	292 ±15.7	242 ± 1.1	256 ±10.8	291 ±13.5
SG2	211 ± 6.4	256 ±11.0	225 ± 9.3	267 ±32.3	282 ±14.5
VE2	225 ±19.7	262 ±14.3	230 ±14.6	231 ±18.3	273 ± 8.3
VE3	252 ± 3.5	234 ±13.5	238 ± 1.9	217 ±12.9	338 ± .
MEAN	246	261	233	250	279
Freshwater Sources					
BO2	246 ± 6.3	285 ±11.9	287 ± 8.9	281 ± 9.8	247 ± 2.6
LS1	245 ± 9.6	243 ± 8.1	216 ± 6.0	234 ±16.9	285 ±24.1
PR1	264 ±16.6	253 ±10.3	262 ± 1.7	270 ±10.2	278 ±19.8
SW1	246 ± 5.4	253 ± 4.1	233 ±13.2	237 ±13.2	264 ± 6.8
SW2	247 ± 6.5	251 ± 5.7	226 ±11.2	280 ±17.6	302 ± 3.1
MEAN	250	257	244	259	274
OVERALL MEAN	247	260	236	253	278

Table A.9. Midday leaf water potential (MPa) ± 1 s.e. by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	-0.96 ±0.04	-0.92 ±0.14	-1.22 ±0.10	-1.03 ±0.11	-0.87 ±0.07
CB3	-0.88 ±0.03	-0.80 ±0.11	-1.13 ±0.09	-1.01 ±0.21	-1.19 ±0.10
FA1	-0.93 ±0.03	-0.85 ±0.02	-1.19 ±0.08	-1.23 ±0.05	-1.43 ±0.23
FA2	-0.70 ±0.05	-1.06 ±0.06	-1.27 ±0.06	-0.78 ±0.07	-1.22 ±0.07
FA3	-0.92 ±0.05	-0.98 ±0.03	-1.21 ±0.08	-1.25 ±0.08	-1.47 ±0.29
FA4	-0.77 ±0.08	-0.95 ±0.06	-1.08 ±0.08	-1.19 ±0.39	-1.66 ±0.45
PB1	-0.73 ±0.07	-0.89 ±0.13	-1.09 ±0.13	-0.85 ±0.03	-2.20 ±0.76
SG2	-0.84 ±0.09	-0.84 ±0.11	-1.03 ±0.03	-1.05 ±0.09	-1.71 ±0.86
VE2	-1.03 ±0.05	-1.00 ±0.06	-1.08 ±0.12	-1.08 ±0.19	-2.46 ±0.65
VE3	-1.11 ±0.01	-1.22 ±0.07	-1.29 ±0.03	-0.80 ±0.08	-1.68 ±0.71
MEAN	-0.89	-0.95	-1.16	-1.03	-1.59
Freshwater Sources					
BO2	-1.07 ±0.06	-0.98 ±0.11	-0.81 ±0.08	-1.09 ±0.09	-1.67 ±0.39
LS1	-1.02 ±0.04	-1.23 ±0.11	-1.15 ±0.04	-1.09 ±0.10	-1.57 ±0.46
PR1	-0.79 ±0.06	-1.03 ±0.06	-0.95 ±0.05	-0.99 ±0.06	-1.22 ±0.31
SW1	-0.94 ±0.10	-1.32 ±0.10	-1.18 ±0.04	-1.11 ±0.08	-1.21 ±0.13
SW2	-0.98 ±0.153	-1.20 ±0.07	-1.21 ±0.04	-0.86 ±0.13	-1.35 ±0.35
MEAN	-0.96	-1.15	-1.07	-1.03	-1.40
OVERALL MEAN	-0.91	-1.01	-1.13	-1.03	-1.53

Table A.10. Fo (relative units) ± 1 s.e. by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	104.0 ±33.3	234.8 ±42.2	132.8 ±13.8	164.2 ± 9.6	78.8 ±18.1
CB3	141.2 ±44.7	158.8 ±46.6	123.5 ±29.8	113.5 ±36.0	106.3 ±14.1
FA1	98.2 ±24.3	116.5 ±12.9	106.5 ±13.0	117.8 ± 6.4	127.7 ±11.9
FA2	165.0 ±48.3	188.0 ±55.1	105.7 ±12.1	239.2 ±36.8	118.0 ± 3.5
FA3	191.3 ±74.8	169.0 ±21.1	117.2 ±15.1	142.0 ±23.3	155.8 ±30.4
FA4	177.5 ±30.9	105.2 ± 7.1	121.3 ± 8.6	267.3 ±16.3	105.0 ±18.1
PB1	94.0 ± 7.6	244.5 ±71.6	129.3 ±14.7	138.5 ±15.0	213.2 ±48.0
SG2	172.8 ±17.9	208.3 ±60.3	140.7 ± 6.9	167.7 ±26.3	154.7 ±38.0
VE2	117.2 ±16.2	160.2 ±14.6	130.2 ±19.5	72.0 ±13.0	109.7 ± 7.3
VE3	92.5 ± 9.3	115.2 ±15.7	89.3 ±23.9	87.5 ±10.9	185.7 ±76.7
MEAN	135.4	170.1	119.7	151.0	135.5
Freshwater Sources					
BO2	186.0 ±11.5	345.3 ±52.4	233.3 ±56.1	150.3 ±17.6	140.3 ±41.7
LS1	91.3 ±17.3	106.3 ±15.4	93.8 ±15.1	132.5 ±23.1	110.3 ±18.5
PR1	264.7 ±41.6	110.7 ±14.8	130.0 ±16.4	109.7 ± 8.5	112.3 ±15.7
SW1	143.8 ±28.6	98.7 ± 5.7	94.3 ±15.2	125.8 ± 6.4	120.3 ± 6.3
SW2	154.5 ±20.9	126.5 ±23.1	121.3 ±10.9	249.8 ±88.6	126.0 ± 5.5
MEAN	168.1	157.5	134.5	153.6	121.8
OVERALL MEAN	146.3	165.9	124.6	151.9	130.9

Table A.11. Fm (relative units) ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	613.2 ±139.0	919.5 ± 92.2	693.7 ± 59.9	796.0 ± 29.2	411.2 ±101.3
CB3	788.7 ±185.9	740.7 ± 65.7	626.3 ± 44.5	687.5 ±166.0	586.8 ± 81.2
FA1	630.3 ±118.2	653.0 ± 89.3	601.7 ± 71.9	589.8 ± 33.5	559.3 ± 62.3
FA2	811.0 ±145.8	777.7 ±191.1	515.7 ± 32.6	781.5 ±219.1	612.5 ± 96.0
FA3	897.8 ±220.3	975.7 ±137.2	690.0 ±119.2	715.2 ± 70.8	798.0 ± 97.7
FA4	799.7 ± 73.6	634.0 ± 20.1	725.0 ± 51.0	960.0 ±122.0	541.2 ± 75.4
PB1	588.3 ± 27.7	887.3 ±133.6	678.5 ± 70.5	784.0 ± 42.0	826.0 ± 71.3
SG2	172.8 ± 17.9	964.8 ±241.3	799.0 ± 32.0	826.7 ± 76.7	712.3 ±103.7
VE2	704.0 ± 84.2	694.8 ±103.2	652.5 ± 74.6	416.3 ± 40.7	562.0 ± 42.5
VE3	605.5 ± 32.6	639.7 ± 96.7	590.7 ±123.7	490.0 ± 35.7	723.2 ±190.6
MEAN	661.1	788.7	657.3	704.7	633.3
Freshwater Sources					
BO2	977.7 ± 12.9	1073.7 ± 79.2	832.5 ±212.8	775.5 ± 75.6	733.3 ±238.7
LS1	580.7 ± 90.7	662.0 ± 98.6	592.7 ± 47.6	718.7 ± 99.9	501.8 ± 43.0
PR1	1089.5 ±142.5	669.3 ± 53.9	625.0 ± 57.4	678.7 ± 52.3	634.5 ± 90.5
SW1	799.8 ±123.2	596.7 ± 47.8	507.7 ± 76.9	683.0 ± 37.6	716.5 ± 42.0
SW2	766.5 ± 44.3	659.2 ± 39.9	710.5 ± 58.5	955.5 ±183.9	618.5 ± 56.0
MEAN	842.8	732.2	653.7	762.3	640.9
OVERALL MEAN	721.7	769.9	656.1	723.9	635.8

Table A.12. Fv/Fm ± 1 s.e. by salinity level and family.

	Salinity (g l^{-1})				
Family	0	2	4	6	8
Brackish Sources					
CB2	0.834 ±0.019	0.767 ±0.013	0.805 ±0.011	0.782 ±0.024	0.809 ±0.011
CB3	0.826 ±0.012	0.793 ±0.052	0.813 ±0.028	0.838 ±0.014	0.811 ±0.010
FA1	0.848 ±0.013	0.811 ±0.017	0.827 ±0.001	0.799 ±0.005	0.760 ±0.034
FA2	0.801 ±0.020	0.745 ±0.012	0.801 ±0.015	0.637 ±0.090	0.808 ±0.011
FA3	0.791 ±0.032	0.827 ±0.006	0.821 ±0.014	0.792 ±0.023	0.786 ±0.029
FA4	0.767 ±0.030	0.836 ±0.007	0.833 ±0.003	0.721 ±0.047	0.797 ±0.016
PB1	0.855 ±0.011	0.751 ±0.046	0.810 ±0.002	0.823 ±0.011	0.741 ±0.014
SG2	0.808 ±0.026	0.783 ±0.041	0.824 ±0.005	0.799 ±0.007	0.770 ±0.025
VE2	0.833 ±0.005	0.743 ±0.065	0.803 ±0.011	0.832 ±0.018	0.794 ±0.008
VE3	0.845 ±0.024	0.795 ±0.037	0.848 ±0.011	0.809 ±0.022	0.749 ±0.028
MEAN	0.821	0.785	0.819	0.783	0.783
Freshwater Sources					
BO2	0.809 ±0.011	0.695 ±0.035	0.721 ±0.011	0.799 ±0.032	0.800 ±0.001
LS1	0.845 ±0.007	0.834 ±0.011	0.843 ±0.011	0.811 ±0.011	0.768 ±0.025
PR1	0.757 ±0.023	0.833 ±0.016	0.777 ±0.039	0.825 ±0.020	0.817 ±0.009
SW1	0.824 ±0.006	0.834 ±0.004	0.806 ±0.016	0.791 ±0.038	0.823 ±0.023
SW2	0.803 ±0.016	0.801 ±0.027	0.823 ±0.008	0.741 ±0.050	0.761 ±0.043
MEAN	0.808	0.799	0.794	0.793	0.794
OVERALL MEAN	0.816	0.790	0.810	0.787	0.786

Table A.13. Fq (relative units) ± 1 s.e. by salinity level and family.

	Salinity ($g\ l^{-1}$)				
Family	0	2	4	6	8
Brackish Sources					
CB2	371.5 ± 91.1	627.2 ±112.1	439.5 ± 33.0	488.3 ± 26.0	249.2 ± 59.1
CB3	522.0 ±108.4	477.5 ± 69.9	411.2 ± 54.3	365.0 ± 91.5	343.5 ± 63.8
FA1	378.8 ± 78.7	380.0 ± 32.0	369.5 ± 50.2	386.8 ± 34.5	341.3 ± 48.6
FA2	568.5 ±157.6	486.3 ±163.0	349.3 ± 27.3	480.5 ±103.6	449.7 ± 77.3
FA3	505.7 ±141.8	612.3 ± 52.8	435.8 ± 89.3	439.7 ± 47.9	585.5 ± 86.3
FA4	476.8 ± 83.7	415.0 ± 16.9	485.5 ± 43.1	554.3 ± 54.7	359.5 ± 74.0
PB1	303.8 ± 15.1	460.5 ± 56.3	404.5 ± 54.0	435.5 ± 10.5	368.3 ± 49.2
SG2	549.7 ± 73.0	600.5 ±126.5	579.8 ± 20.0	516.7 ± 58.7	478.5 ± 91.3
VE2	414.7 ± 28.3	477.8 ± 85.3	431.2 ± 87.1	283.5 ± 11.0	360.0 ± 13.0
VE3	409.8 ± 61.6	455.3 ± 75.8	391.8 ± 64.5	330.0 ± 25.9	490.5 ±158.7
MEAN	450.1	499.2	429.8	428.0	402.6
Freshwater Sources					
BO2	558.8 ± 6.9	649.3 ± 40.0	538.7 ±154.3	437.7 ± 40.8	499.5 ±199.5
LS1	362.8 ± 55.3	472.7 ± 82.9	385.0 ± 34.3	401.3 ± 54.1	293.8 ± 33.4
PR1	730.7 ±159.5	482.5 ± 25.0	419.8 ± 72.2	421.8 ± 21.8	453.5 ± 67.5
SW1	586.3 ±115.3	396.0 ± 31.0	335.8 ± 50.3	406.8 ± 34.9	509.7 ± 13.7
SW2	481.2 ± 12.7	398.8 ± 23.3	451.7 ± 39.2	530.8 ± 83.3	429.0 ± 57.0
MEAN	544.0	479.9	426.2	439.7	437.1
OVERALL MEAN	481.4	492.8	428.6	431.9	414.1

APPENDIX B

ANALYSIS OF COVARIANCE TABLES

FOR RESPONSE VARIABLES DESCRIBED IN CHAPTERS 2 AND 3

Table B.1. Analysis of covariance tables for mean leaf area, mean total biomass and mean leaf biomass.

Mean Leaf Area			
Sources	DF	F Value	Pr>F
Block	2	2.44	.0881
Salinity	4	270.56	.0001
Block x Salinity	8	4.01	.0001
Family	14	5.02	.0001
Salinity x Family	56	2.49	.0001
B x S x F	133	1.27	.0380
Initial Height	1	39.91	.0001
Mean Total Biomass			
Sources	DF	F Value	Pr>F
Block	2	3.08	.0462
Salinity	4	210.78	.0001
Block x Salinity	8	4.31	.0001
Family	14	5.02	.0001
Salinity x Family	56	2.49	.0001
B x S x F	133	1.59	.0001
Initial Height	1	865.93	.0001
Mean Leaf Biomass			
Sources	DF	F Value	Pr>F
Block	2	5.12	.0060
Salinity	4	398.24	.0001
Block x Salinity	8	8.71	.0001
Family	14	11.15	.0001
Salinity x Family	56	3.61	.0001
B x S x F	136	1.93	.0001
Initial Height	1	222.80	.0001

Table B.2. Analysis of covariance tables for mean stem biomass, mean root biomass and mean root weight ratio.

Mean Stem Biomass			
Sources	DF	F Value	Pr>F
Block	2	9.69	.0001
Salinity	4	107.46	.0001
Block x Salinity	8	4.06	.0001
Family	14	7.71	.0001
Salinity x Family	56	1.66	.0017
B x S x F	139	1.62	.0001
Initial Height	1	1128.67	.0001
Mean Root Biomass			
Sources	DF	F Value	Pr>F
Block	2	1.48	.2280
Salinity	4	213.38	.0001
Block x Salinity	8	8.41	.0001
Family	14	3.68	.0001
Salinity x Family	56	2.15	.0001
B x S x F	139	1.42	.0014
Initial Height	1	798.35	.0001
Mean Root Weight Ratio			
Sources	DF	F Value	Pr>F
Block	2	0.55	.5763
Salinity	4	35.83	.0001
Block x Salinity	8	20.37	.0001
Family	14	4.86	.0001
Salinity x Family	56	1.80	.0003
B x S x F	138	1.48	.0004
Initial Height	1	50.78	.0001

Table B.3. Analysis of covariance tables for mean leaf size, mean leaf number and specific leaf area.

Mean Leaf Size			
Sources	DF	F Value	Pr>F
Block	2	3.12	.0452
Salinity	4	195.76	.0001
Block x Salinity	8	3.48	.0006
Family	14	3.32	.0001
Salinity x Family	56	2.36	.0001
B x S x F	133	1.15	.1494
Initial Height	1	14.94	.0001
Mean Leaf Number			
Sources	DF	F Value	Pr>F
Block	2	0.47	.6245
Salinity	4	178.02	.0001
Block x Salinity	8	2.04	.0401
Family	14	5.30	.0001
Salinity x Family	56	2.13	.0001
B x S x F	133	1.19	.0991
Initial Height	1	45.68	.0001
Specific Leaf Area			
Sources	DF	F Value	Pr>F
Block	2	9.16	.0001
Salinity	4	2.22	.0656
Block x Salinity	8	3.35	.0010
Family	14	1.18	.2854
Salinity x Family	56	0.95	.5713
B x S x F	119	1.17	.1353
Initial Height	1	14.13	.0002

Table B.4. Analysis of covariance table for root density index.

Root Density Index			
Sources	DF	F Value	Pr>F
Block	2	3.72	.0244
Salinity	4	146.21	.0001
Block x Salinity	8	25.28	.0001
Family	14	5.12	.0001
Salinity x Family	56	2.94	.0001
B x S x F	139	1.96	.0001
Initial Height	1	91.96	.0001

APPENDIX C

LETTERS OF PERMISSION

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VITA

James Andrew Allen was born on November 12, 1958 in Washington, D.C. He spent his childhood in various towns in New York, Tennessee and New Jersey, and graduated from Shawnee High School in Medford, New Jersey. After high school, he enrolled first in the Pre-Professional Forestry program at Paul Smith's College, where he obtained an Associate of Arts and Sciences degree, and later in the Forestry and Wildlife program at Virginia Polytechnic Institute and State University, where he obtained a Bachelor of Science degree in 1980. Following completion of his Bachelor's degree, he joined the Peace Corps and served as a forester in Swaziland for three years. Upon his return to the U.S., he completed a Master's degree in Resource Policy and Planning from Cornell University. He returned to Swaziland to conduct his Master's thesis research on fuelwood production and consumption in two rural communities. Since 1986, he has been employed as an ecologist first by the U.S. Fish and Wildlife Service and then the newly created National Biological Survey. He is based at the Southern Science Center in Lafayette, Louisiana. He is married to Katherine Lewis Allen, whom he met while they were both Peace Corps Volunteers in Swaziland. They have three children, Gregory (6), Geoffrey (3), and Mark (1).

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: James Andrew Allen

Major Field: Forestry

Title of Dissertation: Intraspecific Variation in the Response of Baldcypress (Taxodium distichum) Seedlings to Salinity

Approved:

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

Date of Examination:

October 20, 1994