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Submergence Impacts on Selected Wetland/Bottomland Tree Species.

Jian Sun
Louisiana State University and Agricultural & Mechanical College

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SUBMERGENCE IMPACTS ON SELECTED WETLAND/
BOTTOMLAND TREE SPECIES

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in
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by
Jian Sun
B.S., Beijing Forestry Institute, 1982
M.S., Beijing Forestry University, 1985
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ABSTRACT

Flooding is a common natural stress occurring in wetland/bottomland forests. Submergence, total immersion, is a special case of flooding, which has received limited attention in the literature. This study provides information on the impacts of three submergence treatments on three bottomland tree species. The results indicated that submergence would inhibit shoot and root growth for the three tested species during the submergence period. However, the survival of these species under submergence conditions were different. *Taxodium distichum* (L.) Rich survived even after 30 days of water coverage and survival continued to be high during the recovery period. *Quercus nuttallii* Palmer was a moderately submergence tolerant species with most seedlings able to survive 20 days of submergence treatment. *Quercus michauxii* Nutt. was the least submergence tolerant species with high mortality occurring after submergence for only 20 days. During the recovery stage, the rapid resumption in root growth, and shoot growth of baldcypress was indicative of its tolerance to submergence impacts. However, the two oak species responded with inhibited growth of both shoots and roots. Physiological responses measured after de-submergence such as photosynthetic rates did not yield significant or consistent differences related to apparent submergence tolerance of these species. Two stress tolerance indices were developed to provide a quantitative means of describing the submergence tolerance for the three tested species. These indices appear to provide information consistent with cluster analysis. They also provide a quantitative ranking of stress tolerance, potentially useful in models of species change related to stress levels the environment.
INTRODUCTION

The approximately 12.5 million hectares of bottomland forests are a major component of the forest ecosystems in the southeastern United States (McKnight et al. 1981). These forests form a unique landscape, and have great commercial value. The importance of these forests as habitats for many wildlife and fish species can not be overstated (Allen and Kennedy 1989). The sound management of these bottomland forests is greatly dependent on an understanding of the structure and functions of these ecosystems.

Periodic flooding is one of the most important characteristics of bottomland forests in the southeastern U.S. (Putnam et al. 1960). The resulting anaerobic conditions greatly change the soil physical and chemical properties, which include gas diffusion through soils, change in redox status, and accumulation of toxic organic or inorganic compounds (Drew 1990). The diversified responses of plants to flooding have been extensively summarized in the literature (Teskey and Hinckley 1977, Whitlow and Harris 1979, Kozlowski 1984).

Baldcypress (*Taxodium distichum* (L.) Rich) is one of the most important wetland tree species in the southeastern U.S. (Dicke and Toliver 1990). There are regeneration problems in baldcypress, which result from flooding, salt concentration increases in flood waters, and animal damage to young seedlings (Conner and Toliver 1990). There are a variety of hardwood tree species occurring on wetland soils, which are also important components in the succession of bottomland forests. An understanding of flood and submergence impacts on baldcypress and bottomland...
hardwood tree species will be valuable to our understanding of the structural and functional dynamics of these forests.

Submergence is the complete immersion of plants in water and is common in bottomland forests (Putnam et al. 1960). Submergence is especially common for young seedlings. The effects of submergence on bottomland tree species have received little attention in the literature, although some of the early studies on submergence were done by foresters (Demaree 1932, Hosner 1960, Loucks and Keen 1973). The lack of systematic and well designed experiments are the main reason for the limited understanding of submergence impacts on tree species.

Three bottomland tree species have been selected for this study. Baldcypress is generally considered a flood tolerant species. Nuttall oak (*Quercus nuttallii* Palmer) is considered to have intermediate flood tolerance and swamp chestnut oak (*Q. michauxii* Nutt.) is considered flood intolerant (Teskey and Hinckley 1977). The objectives of this study were 1) to examine the effects of submergence on survival, shoot growth and root growth of the three bottomland tree species (Chapter Two); 2) to evaluate the impacts of submergence on biomass, leaf number, root volume, and specific weight of root systems for the three tested species (Chapter Two). 3) to monitor the physiological performance of baldcypress and Nuttall oak seedlings following the release from submergence (Chapter Three); 4) to develop quantitative indices of stress tolerance for the three wetland/bottomland tree species (Chapter Four).

Chapter Two examines the null hypothesis that the 10 days, 20 days, 30 days submergence have no effects on the survival, shoot growth, and root growth for the three tested bottomland tree species. The submergence treatments also have no effects on the final harvest results of biomass, and root volume. Chapter Three tests the null hypothesis that the physiological parameters examined are not affected by submergence
treatments for the selected bottomland tree species. Chapter Four is aimed at providing a quantitative description of submergence tolerance for the three tested species. Chapter Five summarizes the overall results, conclusions, and suggests further research needs related to submergence stress in forests.
CHAPTER ONE

LITERATURE REVIEW

INTRODUCTION

Flooding is common in the natural environment, although its study may not be as popular as that of water stress. About six percent of the earth's land surface can be classified as wetlands (Maltby 1991). At least seasonal or short term flooding are routinely observed in these natural habitats. The dramatic impacts of excess water on plants have been reported many times in the literature. Decline in crop yield or damage to forest health caused by flooding are of the most concern to agronomists and to foresters. The tremendous effects of flooding on natural vegetation are also important, because wetland communities constitute critical wildlife and fisheries habitats. In addition, agricultural development, and human activities, such as, construction of dams, canals, and reservoirs are creating problems for bottomland forests as well (Wilén and Tiner 1993).

The concern about flooding has been elevated by the projected impacts of global change. An associated response to global temperature rise is sea level rise. Recent literature indicates that the relative sea level rise will increase at a rate of one meter per century along the coast of Louisiana (Hicks et al. 1983, Salinas et al. 1986). Both coastal marshland and coastal wetland forests in Louisiana may be substantially affected by sea level rise (Salinas et al. 1986, Conner and Toliver 1990).

Species distribution in bottomland forests along the Gulf Coast of the United States are well matched with the abilities of the species to deal with flooding. The
species with greatest flooding tolerance are found in bottomlands or swamps, while the species with greatest drought tolerance are found on upland exposed sites (Teskey and Hinckley 1977). The composition, succession, and regeneration of bottomland forests and the vulnerability of these forests are also greatly dependent on the flooding situation (Hosner and Minckler 1963, McWilliams and Rosson 1990). For example, in lowlands and swamps, baldcypress and water tupelo often occur in pure, dense, even-aged stands. The regeneration success of the two species often depends on good seedfall and free time from prolonged inundation during growing season (Putman et al. 1960, Kennedy 1992). So, an understanding of flood tolerance mechanisms is critical to successful management of the bottomland forests. The effects of a global change in sea level for woody vegetation are yet to be studied. But the greater chance and greater duration of submergence on bottomland tree species are to be expected.

Excellent reviews and books on flooding effects on plants can be found in the literature (Teskey and Hinckley 1977, Whitlow and Harris 1979, Wharton 1982, Kozlowski 1984, Crawford 1989, Drew 1990). Volumes of research papers in the recent decade do show the increased concern about flooding. Studies from ecological, ecophysiological, and especially molecular biology perspectives have made great progress in understanding flood tolerance mechanism and responses. This chapter will discuss some general aspects of flooding effects and provide an overview of the flooding problem in woody plants. Finally, it will discuss current knowledge on submergence impacts on plants.

SOIL PHYSICAL AND CHEMICAL PROPERTIES

Flooding causes dramatic changes in the soil physical and chemical environment. The most direct alteration is the low oxygen concentration or lack of
molecular oxygen in root environment. The dissolved oxygen in flood waters can be consumed by plants and microorganism in very short time (Drew 1990). The slow diffusion rate of oxygen in solution rapidly creates anoxic conditions in the soils. A sequence of reductions will take place that curtail oxygen supply. Fitter and Hay (1987) summarized the series of reduction common to flooded soils. So, a much lower redox potential is observed in waterlogged soils (McKee 1970, Dionigi et al. 1985, Pezeshki and Chambers 1985). Several species of the reduced products are toxic to plants (Janiesch 1991). Hydrogen sulfide can inhibit cytochrome oxidase and block aerobic respiration (Drew 1990). The soluble Fe\(^{++}\) and Mn\(^{++}\) will injure enzyme structure in cytosol (Drew 1990). Another important compound accumulated in waterlogged soil is ethylene. The sources of ethylene in the soil can be partially attributed to the entrapment of ethylene from plant metabolic products. The slow diffusion of ethylene to the external environment may be one of the reasons for ethylene accumulation (Jackson 1985). Jackson (1985) also supplied some evidence to show that soil microorganisms might also contribute to the high ethylene concentration in waterlogged soils.

Nutrient supply in waterlogged soils is also affected by the anaerobic conditions (Mendelssohn and Burdick 1988). Nitrogen is a limiting factor for productivity in some natural wetland habitats and coastal marshes even though the total nitrogen level is high in these soils (Patrick and DeLaune 1976). Mineralization of organic nitrogen to inorganic forms is inhibited by the lack of oxygen (Ponnampерuma 1984). Further, organic nitrogen may be lost in a denitrification process. All of these activities will contribute to the limitation of nitrogen supply in flooded soils (Mengel and Kirkby 1982). Phosphorus may also be limited in reduced soils (Gambrell et al. 1991).
GENERAL PLANT RESPONSES TO FLOODING

The profound impacts of flooding have been addressed in the literature. Generally recognized responses of plants include the negative or positive effects on shoot growth (Hunt 1951, Dickson et al. 1965, Gomes and Kozlowski 1980), inhibition of new root initiation and inhibition of root elongation (Hosner 1959, Kennedy 1970, DeBell et al. 1984). In severe situations, flooding will lead to plant mortality (Hook and Brown 1973). The effects of flooding are greatly dependent on the species and the environment (Kozlowski 1984). Based on extensive field observations and experiments, several authors have ranked flooding tolerance for a number of bottomland tree species (Hosner and Boyce 1962, Broadfoot and Williston 1973, Teskey and Hinckley 1977, Whitlow and Harris 1979, McKnight et al. 1981). Baldcypress (Taxodium distichum (L.) Rich), water tupelo (Nyssa aquatica L.), green ash (Fraxinus pennsylvanica Marsh.), and black willow (Salix nigra Marsh.) are some of the very flood tolerant species. American elm (Ulmus americana L.), water oak (Quercus nigra L.), Nuttall oak (Q. nuttallii Palmer), and sycamore (Platanus occidentalis L.) are often ranked as flood tolerant. Moderately flood tolerant species include loblolly pine (Pinus taeda L.), pecan (Carya illinoensis K. Koch), and southern red oak (Q. falcata Michx). Swamp chestnut oak (Q. michauxii Nutt), white oak (Q. alba L.), and yellow-poplar (Liriodendron tulipifera L.) are some of the most intolerant species. The flooding tolerance of trees is affected by age. Older trees are generally more flood tolerant (Broadfoot and Williston 1973). Among environmental conditions, many researchers believe that flood timing, flood duration, flood frequency, nature of flood waters, and depth of flood waters play the most important roles in plant responses (Broadfoot and Williston 1973, Hook and Schottens 1978, Kozlowski 1984). Flooding occurring in the dormant season seems to have limited harmful effects on tree growth and mortality.
(Hall and Smith 1955, McAlpine 1961, Hook et al 1970). Flooding during the growing season often has more severe impacts on tree growth and survival (McAlpine 1961, Hosner and Leaf 1962). However, not all studies show a negative growth response to flooding. Broadfoot (1967) observed cottonwood, green ash, and sweetgum had a 90% increment in radial growth when plants were exposed to temporary flooding during the growing season. The same phenomenon was also observed in alder (Alnus rugosa Spreng) by McDermott (1954). An improved water supply in growing season is attributed to growth improvement (Broadfoot and Williston 1973). Prolonged flooding always has a more negative effect than short time flooding on tree growth and survival (Hall and Smith 1955). Only a few species have been reported to survive multiple years of flooding (Dicke and Toliver 1990). Frequent flooding also seems to be more harmful to tree health. The state of flood waters is also crucial to tree growth. Moving flood water often produces less harm to tree than stagnant water. Harms (1973) observed that swamp and water tupelo grow poorly in stagnant water. The higher CO₂ concentration and a lower oxygen level observed in stagnant water by Hook and Schottens (1978) is postulated to be the cause of higher mortality and greater growth impacts.

PLANT RESPONSES TO FLOODING AND INTERNAL AERATION

Plants develop either avoidance, tolerance or both mechanisms to deal with the anaerobic soil environment (Crawford 1982). One of the most studied avoidance mechanisms in the literature is the development of internal aeration. Stomata of leaves, hypertrophied lenticels on the stems, and adventitious roots are considered as the main entrance point for oxygen during flooding. Oxygen from the photosynthetic process has also been postulated to be one of the major source of oxygen supply (Gleason and
Zieman 1981, Sand-Jensen et al. 1982). It has been suggested that photosynthetically derived oxygen can be transported to root by internal channels (Laan and Blom 1990).

Several researchers have studied internal aeration channels. Dye methods, pressure methods, and trace methods have been used to explore the possibility of internal aeration channels (Armstrong 1968, Fisher and Stone 1990, Smits et al. 1990). Philipson and Coutts (1978) measured oxygen transport by indigo-carmine dye. Their results did show oxygen transport existed in waterlogged lodgepole pine and Sitka spruce seedlings. In completely submerged seedlings no oxygen movement was measured. Armstrong and Read (1972) tested five conifer species. They found a very large increase in the oxygen flux from the roots of the seedlings when air was supplied to flooded seedlings of pine. Spruce had much lower oxygen flux in the same situation. The internal aeration channel was proved convincingly with trace gases. Dacey and Klug (1982) studied gas circulation with $^{18}O_2$ and $^{14}CO_2$. The results showed that oxygen transported from the shoot is the major source for plant respiration in the rhizome of yellow waterlily ($Nuphar luteum$). A similar approach was elegantly used by Yoshida and Eguchi (1994). When $^{18}O_2$ was applied to aerial parts of Cucumis sativus, the oxygen was then transported to the roots and converted to $H_2^{18}O$ in the respiration process. The experiment did show an increased ratio of $H_2^{18}O$ in the root environment. Wolffang et al. (1992) found Taxodium distichum (L.) Rich, Betula pubescens, and Populus tremula L. improved oxygen supply by an internal conduction channel but no such channels was found in Acer pseudoplatanus or Ilex aquifolium.

During the last two decades, many investigations have been conducted to find the mechanism of aerenchyma formation. Early studies showed that waterlogging could induce aerenchyma tissue formation. The early interpretation was that the insufficient supply of energy and carbohydrates caused the death of cells (Sifton 1945). The hypothesis was challenged by a experiment conducted by Kawase (1974). He found
application of ethephon (an ethylene releasing material) to unflooded sunflower seedlings would also induce the aerenchyma tissues. Since then, intensive work focused on the action of ethylene has been conducted. Three hypotheses have been extensively tested by researchers. First, does flooding cause an ethylene increase in plants? Although there were numerous papers purporting that flooding causes the ethylene concentration increase in plants, there were no clear interpretations of how this ethylene was produced until Bradford and Yang (1980) proposed the synthesis pathway of ethylene. They found flooding causes the rapid synthesis of aminocyclopropane-1-carboxylic acid (ACC), the immediate precursor of ethylene. ACC is then transported to the shoot where ACC is converted to ethylene in the presence of oxygen. Flooding enhances ACC synthase in tomato plants, which is accompanied by ethylene synthesis in the leaf (Wang and Arteca 1992). Second, does ethylene involve aerenchyma tissue formation? To test this hypothesis, three approaches were used:

1. measurement of endogenous ethylene.
2. observation of aerenchyma tissue formation when ethylene is applied exogenously.
3. application of the ethylene inhibitor to solution.

The observations on the evolution of ethylene in Mango trees after two days of anaerobic treatment showed that ethylene increases several fold (Larson et al. 1993). The enhancement of ethylene production dose not appear to be related to the flooding tolerance of plants (Voesseneks et al. 1993). Exogenous application of ethylene showed varied responses in the formation of aerenchyma tissue. A low concentration of ethylene (0.1 µl/l) promotes collapse and lysis of cortical cells and the gas space formation (Drew et al. 1981). The involvement of ethylene in the formation of aerenchyma have been extensively supported by the application of ethylene inhibitors. Drew et al. (1981) showed as low as 0.6 µM Ag inhibited ethylene action in Zea mays.
Kawase (1981) also found the ethylene effect was absent when 100 ppm AgNO₃ was applied to sunflower. AOA, AVG were also used as inhibitors for ethylene in flooded plants. Some research has indicated that nitrogen and phosphorus deficiency could also induce aerenchyma tissues even in aerobic plants. However, the action seems to be dependent on the responses of root cortical cell to endogenous ethylene (He et al. 1992).

Third, how does the ethylene involve the aerenchyma tissue formation? Some research has shown that cellulase activity is enhanced by ethylene (Kawase 1981). However almost nothing seems to be known of biochemical events that leads to lysigenous cavitation (Jackson and Pearce 1991).

METABOLIC RESPONSE OF PLANTS TO ANAEROBIC CONDITION

Plants maintain energy and structural material supply by respiration. Under aerobic conditions, plants obtain their energy by an active Tricarboxylic Acid (TCA) cycle. Under anaerobic, flooded environments, although some internal aeration may play an important role in continuation of aerobic respiration, there is not always enough energy supply from aerobic respiration. For many species, engagement of anaerobic respiration is considered an indicator for plant tolerance to anoxic conditions. The respiration metabolism in the absence of oxygen can be simply described.

A molecule of glucose is first converted to 2 molecules of pyruvate with 2 ATP produced in the process. Pyruvate may go to TCA cycle in the presence of oxygen as the terminal oxidase in electric transport chain needs oxygen to reduce NAD+. Under anaerobic conditions, pyruvate either goes to ethanol or lactate (Dennis and Turpin 1990). McManmon and Crawford (1971) proposed that plants may produce alternative products such as malate instead of ethanol. So, the flood tolerant plants had lower alcohol dehydrogenase (ADH) activity. According to this view, ethanol was toxic to
plant metabolism and nontoxic malate would be produced in tolerant plants. Recent studies indicate this is not true. High levels of ethanol may be toxic to some plant organs (Drew et al. 1981). However, ethanol often can diffuse out of plants. The supposed alternative metabolites such as malate, may not have significant function in some flood tolerant plants (McKee and Mendelssohn 1987). Systematic research on coastal species, Spartina spp, do show that ADH was stimulated in flood tolerant Spartina alterniflora (Mendelssohn et al. 1981, Mendelssohn and McKee 1987, Andrew et al. 1993). However, elevated ethanol levels were not observed in many studies because of the rapid diffusion (McKee and Mendelssohn 1987). The mutants of ADH showed limited ethanol production which supplied evidence for the hypothesis (Saglio et al. 1983). More recently, the action of lactic acid was studied by Xia and Saglio (1992). The early engagement of lactate dehydrogenase (LDH) seems to create an acidulous environment in cell and trigger ethanol fermentation (Miemyk 1990).

Based on the above discussion, an interesting question is raised. What's the relative importance of aerobic and anaerobic respiration in flood tolerant plants? Burdick and Mendelssohn (1990) examined ADH activity in Spartina patens. They measured both ADH activity and specific gravity of the plant roots. In the first 10 days of hypoxia, ADH activity rapidly increased. Then ADH activity decreased as the specific gravity declined after 10 days of hypoxia. The proposed mechanism is that during short term flooding, plants have a high level of fermentation activity as the aerenchyma tissue are not developed yet. Anaerobic respiration may play a more important role in energy production during this period. After a period of acclimation, the ethylene induced aerenchyma would enhance aerobic respiration.

Even for plants which have well developed internal aeration systems, specialized metabolism such as fermentation is necessary (Miernyk 1990). Changes in carbohydrate metabolism may be crucial in surviving anaerobiosis. Besides the
production of ADH, other anaerobic stress proteins (ASP's) are also induced by
anaerobic stress. The characterized ASP include sucrose synthase, glucose-6-phosphate
isomerase, aldolase, cytosolic glyceraldehyde-3-phosphate dehydrogenase, and LDH
(Kennedy et al. 1992). All of these ASP’s are glycolytic enzymes although not all
enzymes of the glycolytic pathway show enhanced activity during \( O_2 \) deficiency (Drew
1990, Mujer et al. 1993). It seems that the flood intolerant plants may produce fewer
ASP’s which may be traced to the different gene responses in flood tolerant and
intolerant plants (Kennedy et al. 1992).

An often observed phenomenon in carbohydrate metabolism is starch
accumulation in the shoots of anaerobic plants (Wample and Davis 1983, Waters et al.
1991). The inhibition of phloem transport is considered as the major reason for starch
accumulation (Waters et al. 1991, Schumacher and Smucker 1985). It seems that the
inhibited action is associated with the leakage of \( K^+ \) in flooded plants (Castonguay et al.
1993). However, there is at least one species \( Nicotiana tabacum \) that does not show
starch accumulation under anaerobic treatments (Weei and Kao 1993). An interesting
part is that sucrose accumulation occurs in flooded alfalfa roots (Barta 1988). This
suggests that carbohydrate availability does not appear to be a limiting factor in root
tolerance to anoxia in alfalfa (Barta 1988, Castonguay et al. 1993).

**PHYSIOLOGICAL AND GROWTH RESPONSES OF PLANTS TO FLOODING**

Morphological and metabolic changes in flooded plants will eventually affect
their physiological performance in whole tissues or at the whole plant level. Survival
and growth of plants are affected as well. Water relation of plants, stomatal behavior,
and photosynthetic characteristics are probably the most monitored parameters in
physiological performance of flood stressed plants. The understanding of physiological
performance plus the observations in metabolic and morphological aspects will be valuable in the accurate assessment of flood tolerance.

Stomata serve as a control gate in water and CO$_2$ movement in plants. So it is natural to examine stomatal behavior in stressed plants. Many studies have shown a decline in stomatal conductance in tree species response to flooding (Bradford and Yang 1980, Tang and Kozlowski 1982, Pezeshki and Chambers 1985, Beckman et al. 1992). In early reports, stomatal closure was attributed to the inhibition of water uptake in roots. However, some studies found stomatal closure in flooded plants was not a direct result of hydraulic status of plant leaf (Pezeshki and Chambers 1985, Pezeshki and Chambers 1986). A nonhydraulic reason has also been hypothesized in the literature.

The involvement of ABA (abscisic acid) in stomatal behavior is perhaps the most prevalent view (Zhang and Davis 1987, Castonguay et al. 1993). A close correlation of ABA concentration increase in the root and stomata closure is often found (Zhang et al. 1987). A chemical signal hypothesis was proposed to explain the stomatal action (Zhang and Davies 1987). The main hypothesis is that stress induces ABA concentration increase in the root system, which is then transported to the leaf and in turn regulates stomatal closure. However, recent research has shown that ABA might not accumulate in roots and ABA transport to the shoot is also non-significant (Jackson et al. 1988). The ABA concentration in the shoot itself is high enough to induce stomatal closure. So a possible mechanism is the reallocation of ABA in cell wall and cytosol in guard cells. The concomitant movement of K$^+$ and H$^+$ seems to be associated with stomatal action as well. Another interpretation involving stomata closure is the inhibition of phloem transport, which leads to higher ABA concentration as assimilate accumulation occurs in leaf (Castonguay et al. 1993).

The water potential status of flooded plants has also often produced controversy. Some research has shown a drought stress symptom in flooded plants (Bradford and
Hsiao 1982). Water uptake is inhibited in the root, by reduced root membrane
permeability caused by oxygen deficiency during soil flooding (McLeod et al. 1986).
The limitation of energy supply and lower water conductivity in roots are considered as
the main reason for decreased water potentials. However, several studies do not show a
change in leaf water potential or show less negative water potentials during flooding
(Pereira and Kozlowski 1977, Pezeshki and Chambers 1985, Olien 1989, Everard and
Drew 1989). Reece and Riha (1991) did not detect the decline in water conductance
during flooding of eastern larch roots. They suggested that chemical messengers might
induce the response. However, contrasting results were reported by Markhart and Smit

Transpiration of plants under flooded conditions seems to decrease (Parker
1950, Pezeshki and Chambers 1985). Part of the reason is lower stomatal conductance.
Lower conductance resulting in lower transpiration may help prevent water deficits.

The photosynthetic rate is observed to decrease in most studies (Regehr et al.
observed that photosynthesis rates of *Populus deltoides* Bartr. ex Marsh. seedlings
decreased by about a half in 28 days of root flooding. However, differences in flood
tolerance creates large variations in photosynthetic responses. Photosynthetic rates in
flood tolerant plants are often less affected (Zaerr 1983). For example, Ps was little
affected by flooding of Scots pine. However, CO$_2$ uptake in Douglas fir and Norway
Spruce are strongly inhibited (Zaerr 1983). The decline in Ps rate can be affected by
stomatal and non-stomatal processes. Kozlowski and Pallardy (1984) attributed the
decline in Ps rate primarily as the stomatal closure. However, some non-stomatal
processes such as enzyme activity, reduced chlorophyll content, or leaf senescence may
also be involved. Vu and Yelenosky (1992) found Rubisco activity was a significantly
lower in flooded citrus. The feed-back inhibition from accumulated assimilates in shoot might also be involved (Vu and Yelenosky 1992).

SUBMERGENCE ON PLANTS

The responses of plants mentioned previously are mainly those caused by shallow water flooding or soil waterlogging. In nature, small plants and young tree seedlings are often submerged by flood waters. Setter et al. (1987) defined submergence as complete coverage of whole plants by water. The differences between shallow water flooding or waterlogging and submergence are dramatic. Voesenek et al. (1992) summarized significant changes resulting from 1) changes in quantity and quality of irradiation, 2) reduced carbon availability, and 3) reduction in gas diffusion into and out of the plants, including the complete blockage of oxygen entrance into plants.

Although foresters were among the pioneers in the study of submergence effects (Demaree 1932), detailed examinations of tree species are limited. Hosner (1960) tested submergence tolerance in fourteen bottomland tree species. His results indicated that variation existed among species. Silver maple, buttonbush, boxelder and black willow were the most submergence tolerant species. Most of the tested seedlings survived thirty days of submergence. Shumard oak (Quercus shumardii Buck), sycamore (Platanus occidentalis L.), and red maple (Acer rubrum L.) were found to only survive ten days submergence. Cherrybark oak (Q. falcata var. pagodifolia Elliott) only survived about five day of submergence. The growth of all submerged intolerant seedlings are severely retarded after flood water was removed. However the submergence tolerant species usually resumed their growth rapidly after release from submergence. Conifer species seem to be more sensitive to submergence. McCaughey
and Weaver (1991) found no Douglas fir (Pseudotsuga menziesii Franco), lodgepole pine (Pinus contorta Dougl.), blue spruce (Picea pungens Engelm), or Engelmann spruce (Picea engelmannii Parry) seedlings survived twenty eight days submergence. Loucks and Keen (1973) tested the submergence tolerance for 10 tree species. The seedlings of the ten species received one week, two weeks, and four weeks submergence treatments and a flooded only control. Their results indicated that green ash (Fraxinus pennsylvanica Marsh.), baldcypress (Taxodium distichum (L.) Rich.) and silver maple (Acer saccharinum L.) were the most submergence tolerant species. Pecan, eastern cottonwood (Populus deltoides Bartr. ex Marsh.), honeylocust (Gleditsia triacanthos L.), and bur oak (Q. macrocarpa Michx.) were in an intermediate group. The least tolerant species were boxelder (Acer negundo), Siberian elm (Ulnus pumila), and black walnut (Juglans nigra L.). However, all studies discussed above focused on survival. The growth parameters measured were limited. No physiological parameters were recorded after release from submergence treatments. So, the addition of information on growth processes and physiological performance for submergence treated plants is needed to understand how species recover and perhaps how they tolerate submergence.

Intensive research on submergence effects on plants are limited to only a few species (Mitchell 1976). Some of rice cultivars and plants in the genus Rumex have received relatively heavy study (Setter et al. 1987, Jackson et al. 1987, Laan and Blom 1990). Researchers have shown that there is a great variation in submergence tolerance among plant species. Under submergence, a strong reduction in the growth rates were recorded in Rumex (Laan and Blom 1990). Plant responses seem to be toward maintaining survival and biomass. However, the strategies are different among species. The rapid elongation of shoot or coleoptiles have been observed in many deep rice cultivars and Rumex species (Atwell et al. 1982, Bleecher et al. 1986, Laan and Blom. 1990, Laan et al. 1991). The purpose of rapid elongation has been interpreted as an
avoidance mechanism which can help plants to reach the oxygen rich atmosphere more quickly. Careful examination found wetland *Rumex* species accumulated large amounts of ethylene in intercellular spaces (Voesehek et al. 1992), which may be related to fast elongation of the shoot. However, Raskin and Kende (1983) found deep-water rice may have an external air layer to help move oxygen to the roots even for totally submerged seedlings. Another important aspect of plant response to submergence is under-water photosynthesis. Under-water photosynthesis not only produces photosynthate but also serves as an important oxygen source. Laan and Bloom (1990) found more than 50% of root-utilized oxygen may come from the photosynthetic processes in *Rumex martimus*. For rice species, limiting CO₂ supply became the limiting factor for under-water photosynthesis (Setter et al. 1989).

**SUMMARY**

Flooding is common in the natural environment. The rapid depletion of oxygen in the root environment occurs with the association of dramatic changes in soil physical and chemical properties. Morphological, metabolic and physiological responses to flooding are routinely observed in plants. Although internal aeration may serve as an important characteristic for plants to deal with oxygen-deficient environments, metabolic adaptations are also important. Physiological performance seems to be closely related with flood tolerance as well. Submergence as one special case of flooding shows more detrimental effects on plants. However, only limited information on submergence effects on trees is available in the literature. To successfully manage the bottomland forests and to restore or create successful wetland forest ecosystems, more studies on flood tolerance mechanisms are needed. In particular, the investigation on submergence effects on tree species is needed.
CHAPTER TWO

SUBMERGENCE IMPACTS SURVIVAL AND GROWTH OF THREE BOTTOMLAND TREE SPECIES

INTRODUCTION

Bottomland forests are some of the most productive and diverse ecosystems in the United States (Clatterbuck and Meadows 1992). More than seventy tree species in these forests are important to the commercial timber supply in the southern United States (Putnam et al. 1960). Although large scale acreage once in bottomland hardwood forests have been shifted to agricultural use during this century, the tendency for change has slowed down in recent years (McWilliams and Rosson 1990, Wilen and Tiner 1993). The multiple functions of these forests are highly recognized today (Kennedy 1992, Allen and Kennedy 1989).

Periodic inundation is a critical factor in bottomland forest ecosystems (McKnight et al. 1981, Huffman and Forsythe 1981). The stand composition, structure, and regeneration success of these forests are heavily related to flood conditions. Water depth, timing, duration, frequency, and physical and chemical composition of flood waters are major attributes related to the impact of flood responses (Broadfoot and Williston 1973, Teskey and Hinckley 1977, Whitlow and Harris 1979, Wharton et al. 1982, Allen and Kennedy 1989).

Submergence is a component in the initial stages of many of these forest ecosystems and has been defined as complete coverage of plants by a water body (Setter et al. 1987). The resulting environment significantly affects the quantity and quality of irradiation, carbon availability, gas diffusion rates into and out-of the plants, and the
density of the plant's immediate surroundings (Voesenek et al. 1992). Traditionally, submergence has received little attention in research compared with that of root flooding and anoxic soil conditions. Rice and some weed plants have received most of the terrestrial plant research attention related to submergence (Atwell et al. 1982, Raskin and Kende 1983, Schat 1984, Setter et al. 1987, Voesenek et al. 1993, and Bleecher et al. 1986).

Submergence is common in wetland forest ecosystems. Foresters were among early researchers paying attention to submergence effects. As early as in 1932, Demaree found that baldcypress seedlings were dead after two weeks of submergence. Briscoe (1957) examined submergence tolerance of several tree species. He showed that tolerance of seedlings to submergence varied with species, and was also correlated with frequency of flooding and the age of seedlings. Hosner (1960) tested the relative tolerance of 14 bottomland tree species to complete inundation. He also found considerable variation in the ability of bottomland tree species to withstand submergence. The oak species had low submergence tolerance. However, black willow (Salix nigra Marsh), eastern cottonwood (Populus deltoides Bartr. ex Marsh) and green ash (Fraxinus pennsylvanica Marsh) survived 30 days while submerged. Several others have provided information on submergence effects (Broadfoot and Williston 1973, Loucks and Keen 1973, McKnight et al. 1981, Loucks 1987, McCaughey and Weaver 1991).

This pioneer work enriched our understanding on submergence tolerance among species. However, these studies did not supply an interpretation of the mechanism for submergence tolerance differences. The quantitative description of the recovery processes that wetland/bottomland tree species undergo is also very limited in the literature although it is important to the understanding of submergence tolerance (Loucks 1987).
This study was aimed at providing more detailed data on submergence responses for wetland/bottomland tree species. This chapter will present the results for survival, shoot growth, root growth, and biomass production of three wetland bottomland tree species during submergence and after water removal.

RESEARCH MATERIALS AND METHODS

Three wetland/bottomland tree species, baldcypress (*Taxodium distichum* (L.) Rich), swamp chestnut oak (*Quercus michauxii* L.), and Nuttall oak (*Q. nuttallii* Palmer) were selected for this study since they represent a range of flood tolerance in bottomland tree species. The seeds of these three species were obtained from Southern Hardwoods Laboratory of the USDA Forest Service, Southern Forest Experiment Station, in Stoneville, Mississippi. The baldcypress cones were air-dried, then washed with ethyl alcohol to remove resins in the cones and the seeds were removed. The washed seeds were mixed with wet sand and put in plastic bags. The seed and sand mixture was then stored in a cold room at 3 °C. The seeds of the two oaks species were soaked in water, placed in plastic bags and also cold stored at 3 °C from January until April, 1993.

At the end of April, seeds of the three species were put on plastic trays which were filled with 3 cm deep vermiculite. The seeds were covered with an additional 1 cm of vermiculite, watered and placed in a seed germinator (ConViron). Media was kept moist by watering regularly. The temperature in the germinator was set at 28° C for day time, and 20° C for night time. Light/dark cycle was set 12/12 hr and relative humidity was kept above 90 percent.

When the young seedlings reached about 5 cm in height, they were transplanted to pots. The median used in this study was a sintered-clay (Terra-Green, Oil Dry
Corporation). Terra-Green was used because roots are easy to wash-out and roots are visible when tracing root growth on rhizotron walls. This technique has been used successfully in previous studies in our lab. The pots were made of PVC pipe split lengthwise and a transparent polycarbonate sheet cemented on the open face. The bottom part of the pot was sealed with a water permeable nylon mesh sheet which prevented outgrowth of the root.

A total of 240 seedlings were transplanted. These seedlings were then cultured in a plastic house with open end walls to stimulate near natural temperature and humidity conditions. All seedlings were grown in about 50% shade. Water was supplied as needed. Peter’s water soluble 20-20-20 (N-P-K) mix and trace elements was applied twice.

Twelve plastic-lined wooden tanks were used in this experiment. Each tank was 175 cm long X 70 cm wide X 85 cm high. Before receiving any submergence treatment, all seedlings were kept in soil saturated conditions (root flooding only) for two days during acclimation to the tanks. The 30 day submergence treatment was initiated on July 11, 1993, the 20 day submergence treatment was started on July 21, and the 10 days submergence treatment was started on July 31 (Fig 2.01). During treatment period, all seedlings were kept in saturated soils only (control) except those which were receiving submergence treatment. The submergence treatments covered all portions of the seedlings. After release from the submergence treatments, the plant root zone was kept saturated until the final harvest in October of 1993. Each treatment was replicated three times. Each replication was randomly assigned to one of the twelve wooden tanks. Each tank contained 6 to 7 seedlings of each species. A general layout of the experiment is shown in Figure 2.02.
Fig. 2.01. Timing of submergence (sub) treatments

<table>
<thead>
<tr>
<th>sub 30 days</th>
<th>sub 20 days</th>
<th>sub 10 days</th>
<th>recovery period</th>
</tr>
</thead>
<tbody>
<tr>
<td>July 11</td>
<td>July 21</td>
<td>July 31</td>
<td>Aug. 11</td>
</tr>
</tbody>
</table>

(submergence ends for all treatments)

Fig. 2.02. General layout of submergence treatments and replicates

<table>
<thead>
<tr>
<th>submerged 20 days</th>
<th>control</th>
<th>submerged 20 days</th>
<th>submerged 10 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>control</td>
<td>submerged 20 days</td>
<td>submerged 10 days</td>
<td>submerged 30 days</td>
</tr>
<tr>
<td>submerged 30 days</td>
<td>submerged 10 days</td>
<td>submerged 30 days</td>
<td>control</td>
</tr>
</tbody>
</table>
Seedling heights were measured with a meter stick and diameters were measured with a digital caliper. Measurements were made before submergence treatments, immediately after release from the submergence treatments, and during final harvest period. New roots along the transparent side of pots were marked on clear acetate sheets with colored ink. Root length and root number were measured five times during this study. Root length was measured with the GS-ROOT root measurement system (PP Systems, Bradford, Maine) from images traced onto acetate and scanned by computer. The root images from the tracing plastic were automatically measured by the computer software. At the final harvest date, heights, and diameters were measured. Root volumes were measured by water displacement as modified from Burdett (1979). The leaves, shoots, and roots of all seedlings were separated at harvest, then dried in an oven at 65°C for 48 hours. Dry weights were recorded with an analytical balance. Leaf areas were measured prior to drying with a Li-Cor 3000 leaf area meter (Li-Cor Inc, Lincoln, Nebraska).

A complete randomized design was used in the experiment. A GLM procedure (SAS Institute) was run for the statistical analysis. Tukey’s multiple comparison test was used to compare the differences among treatments. Tests were conducted at the 5% significance level.

RESULTS

Survival

Survival is considered as an indicator of stress impacts and is also a useful in indication of stress tolerance. Survival of seedlings was assessed at 5, 20, 36, 55 days after release from submergence treatments (Table 2.01). After removal of submergence treatments, variation in tolerance to submergence period was obvious. Survival was
Table 2.01. Changes in survival (percent) of three bottomland tree species submerged for 10, 20, or 30 days, and after release.

<table>
<thead>
<tr>
<th>Species / Submergence time</th>
<th>Time since release from submergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>5 days</td>
</tr>
<tr>
<td>Baldcypress</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>100</td>
</tr>
<tr>
<td>Submerged 10 days</td>
<td>100</td>
</tr>
<tr>
<td>Submerged 20 days</td>
<td>100</td>
</tr>
<tr>
<td>Submerged 30 days</td>
<td>100</td>
</tr>
<tr>
<td>Nuttall oak</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>100</td>
</tr>
<tr>
<td>Submerged 10 days</td>
<td>95</td>
</tr>
<tr>
<td>Submerged 20 days</td>
<td>91</td>
</tr>
<tr>
<td>Submerged 30 days</td>
<td>28</td>
</tr>
<tr>
<td>Swamp chestnut oak</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>100</td>
</tr>
<tr>
<td>Submerged 10 days</td>
<td>100</td>
</tr>
<tr>
<td>Submerged 20 days</td>
<td>29</td>
</tr>
<tr>
<td>Submerged 30 days</td>
<td>0</td>
</tr>
</tbody>
</table>
100 percent for all baldcypress seedlings submerged for up to 30 days. About 95 percent and 91 percent of the Nuttall oak seedlings survived the 10 days and 20 days of submergence respectively. Only 28 percent of the Nuttall oak seedlings remained alive after being submerged for 30 days. Swamp chestnut oak had the poorest survival performance under survive submergence treatments. All swamp chestnut oak seedlings could survive 10 days of submergence treatment, but only 29 percent seedlings could survive 20 days of submergence, and none survived for 30 days while submerged.

During the recovery period, species performances also varied. Baldcypress seedlings maintained 100 percent survival in all treatments. A slight decline of Nuttall oak survival was observed after release from submergence. Mortality of swamp chestnut oak seedlings in submerged treatments was higher during the recovery period. At 55 days after release, swamp chestnut oak had no seedlings surviving the 20 day or 30 day submergence treatments.

Height and Diameter Growth

Height and diameter growth are sensitive to some extreme environmental stresses. In this study, the heights (Table 2.02) and diameters (Table 2.03) were measured on July 6 (five days before treatments), August 11 (immediately after release from the treatment), and Oct. 10 (at the final harvest). The results on July 6 showed there were no significant differences within species for height or diameter prior to submergence (Table 2.02, 2.03). Nuttall oak was the tallest and had a diameter close to that of swamp chestnut oak. Baldcypress was the smallest in height and diameter of the three species.

The measurement data on August 11 showed that different responses in height and diameter for different treatments. For baldcypress, there were significant
Table 2.02. Mean heights for seedlings of three species subjected to flood submergence on three measurement dates

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Pre submergence (July 6) (cm)</th>
<th>1 day after water removed (Aug. 11) (cm)</th>
<th>Final harvest (Oct. 10) (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baldcypress</td>
<td>Control</td>
<td>10.8±0.6(^1)(^2)(a)(2)</td>
<td>18.9±1.1 (a)</td>
<td>23.4±1.2 (a)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>10.1±0.4 (a) (100)</td>
<td>15.3±1.1 (b) (151)</td>
<td>22.3±0.6 (a) (221)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>10.3±0.4 (a) (100)</td>
<td>13.0±0.7 (b) (126)</td>
<td>20.9±0.9 (a) (203)</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>9.8±0.4 (a) (100)</td>
<td>10.0±0.5 (c) (102)</td>
<td>19.9±1.2 (a) (203)</td>
</tr>
<tr>
<td>Nuttall oak</td>
<td>Control</td>
<td>16.8±1.1 (a) (100)</td>
<td>18.6±1.1 (a) (111)</td>
<td>18.8±1.1 (a) (112)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>17.0±1.4 (a) (100)</td>
<td>17.9±1.5 (a) (100)</td>
<td>18.1±1.6 (a) (106)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>16.2±0.9 (a) (100)</td>
<td>16.5±1.3 (a) (102)</td>
<td>17.5±1.3 (a) (108)</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>15.1±1.2 (a) (100)</td>
<td>—</td>
<td>11.0±1.5 (a) (72.8)</td>
</tr>
<tr>
<td>Swamp chestnut</td>
<td>Control</td>
<td>14.3±0.7 (a) (100)</td>
<td>15.2±0.7 (a) (106)</td>
<td>15.3±0.8 (a) (107)</td>
</tr>
<tr>
<td>oak</td>
<td>Sub-10</td>
<td>15.0±0.7 (a) (100)</td>
<td>15.6±0.9 (a) (104)</td>
<td>16.3±0.8 (a) (109)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>15.5±0.8 (a) (100)</td>
<td>16.4±1.3 (a) (105)</td>
<td>all dead</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>15.0±0.8 (a) (100)</td>
<td>all dead</td>
<td>all dead</td>
</tr>
</tbody>
</table>

1. Means ± s.e.
2. Same letters within species at the same measurement time are not significantly different at the 5% level.
3. Relative height compared to pre-submergence height (%).
Table 2.03. Baldcypress, swamp chestnut oak and Nuttall oak mean diameters under saturated soil conditions (control) and three submergence periods on three measurement dates

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Pre submergence (July 6) (mm)</th>
<th>1 day after release from submergence (Aug.11)(mm)</th>
<th>Final harvest (Oct. 10) (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baldcypress</td>
<td>Control</td>
<td>1.19±0.05 (^1) a (^2) (100) (^3)</td>
<td>1.79±0.08 a (150)</td>
<td>3.10±0.15 a (261)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>1.22±0.05 a (100)</td>
<td>1.97±0.08 a (161)</td>
<td>2.60±0.08 b (213)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>1.19±0.05 a (100)</td>
<td>1.77±0.08 a (149)</td>
<td>2.60±0.08 b (210)</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>1.24±0.04 a (100)</td>
<td>1.48±0.05 b (119)</td>
<td>2.60±0.16 b (210)</td>
</tr>
<tr>
<td>Nuttall oak</td>
<td>Control</td>
<td>2.53±0.11 a (100)</td>
<td>2.99±0.13 a (118)</td>
<td>3.90±0.22 a (119)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>2.73±0.07 a (100)</td>
<td>3.14±0.15 a (115)</td>
<td>3.60±0.15 a (132)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>2.56±0.09 a (100)</td>
<td>2.91±0.10 a (114)</td>
<td>3.30±0.09 a (129)</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>2.62±0.11 a (100)</td>
<td>—</td>
<td>2.50±0.19 b (95)</td>
</tr>
<tr>
<td>Swamp chestnut oak</td>
<td>Control</td>
<td>2.53±0.06 a (100)</td>
<td>2.79±0.09 a (110)</td>
<td>3.00±0.11 a (114)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>2.77±0.08 a (100)</td>
<td>2.94±0.10 a (106)</td>
<td>3.10±0.08 a (112)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>2.69±0.09 a (100)</td>
<td>3.00±0.23 a (112)</td>
<td>dead</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>2.59±0.07 a (100)</td>
<td>dead</td>
<td>dead</td>
</tr>
</tbody>
</table>

\(^1\) Mean ± s.e.
\(^2\) Same letters within species at the same measurement day are not significantly different at the 5% level.
\(^3\) The relative diameter compared to pre-submergence diameter (%)
differences among the four treatments. The height and diameter of baldcypress seedlings in the control treatment increased 75 percent and 50 percent respectively, compared with that on July 6. The data showed the longer the submergence time, the smaller increment in height and diameter in baldcypress seedlings (Table 2.02, 2.03). Nuttall oak seedlings in the control treatment showed a change in height and diameter during the period from July 6 to August 11, while Nuttall oak seedlings in submergence treatments showed very limited height increment during the same period (Table 2.02, 2.03). There were no significant differences in height or diameter among treatments for Nuttall oak on August 11. Swamp chestnut oak growth followed a similar pattern (Table 2.02, 2.03).

During the recovery period (August 11 to October 10), baldcypress had a strong recovery in height and diameter growth in the submergence treatments. All seedlings at least doubled their height and diameter even seedlings submerged for 30 days. There were no significant differences in heights among treatments, however, significant differences remained among treatments for diameter. The control seedlings of baldcypress had the largest mean diameter (Table 2.03). Nuttall oak showed a limited increment in height and diameter for the control, the 10 day submergence, the 20 day submergence treatments. Die-back and mortality occurred in Nuttall oak seedlings submerged for 30 days, which resulted in a reduced mean height and diameter growth (Table 2.02 and Table 2.03). Swamp chestnut oak in the control and submerged 10 days treatment had almost no height increment and only a slight increment in diameter during the same period. No significant differences were found between control and submergence 10 day treatment. However, for swamp chestnut oak, complete mortality occurred in the other two submergence treatments.
Root Growth

Root adaptations are critical to the plant's ability to survive flooding and have been used to assess the relative flood tolerance for a number of tree species (Hosner and Boyce, 1962). The number of new roots and root lengths were monitored several times during the study. The observation periods have been divided into two periods. The stages are the submergence treatment period, a period during which all seedlings except controls, experience some period of submergence, (10 days, 20 days, or 30 days) and the recovery period which was a period during which seedlings were allowed to recover from submergence treatments.

During the submergence treatment period, the root growth pattern of the three species were similar but levels of root growth were different. For baldcypress, the number of new roots and root elongation were significantly different among treatments (Fig. 2.03). Seedlings in the control treatment initiated a significantly large number of new roots, while seedlings in the 10 day submergence treatment had a second largest numbers of new roots. The number of new roots was not significantly different between 20 day submergence and 30 day submergence treatments for baldcypress. Root elongation followed a similar pattern to new root development for baldcypress (Fig. 2.03). The mean root elongation of control baldcypress seedlings was 16.87 cm. Mean increments of 9.15 cm, 4.10 cm, and 2.39 cm in root elongation were observed for submerged 10 days, submerged 20 days, and submerged 30 days treatments respectively. Nuttall oak in the control treatment had a greater number of new roots than that of submerged seedlings. There was more root elongation in control Nuttall oak seedlings as well (Fig 2.03). For swamp chestnut oak, there was very limited new root formation and elongation. However, the seedlings in the control treatment had significantly more new roots and root elongation (Fig. 2.03).
Fig. 2.03. New root elongation (A) and mean number of new roots (B) for baldcypress (BCY), Nuttall oak (NUT), and swamp chestnut oak (SCO) for the period of July 11 to August 16. Same letters within species indicate no significant difference at the 5 percent level. Submergence water removed from all treatment on August 11.
There were three observations of root growth during the recovery period. For the period of August 16 - September 1, baldcypress resumed rapid root growth in the previously submerged 20 and 30 day treatments. The number of new roots for 10 days, 20 days, and 30 days submergence reached 6.6, 8.8, and 9.6 respectively, compared to 8.9 new roots in the control treatment. These new roots elongated 6.34 cm, 8.86 cm, and 9.91 cm in the 10 day, 20 day, and 30 day submergence treatments respectively, compared with the 8.08 cm in the control treatment. There were no longer significant differences found in the number of new roots or root elongation for baldcypress among the four treatments by the end of this measurement period.

Root growth recovered more slowly in Nuttall oak. Both the number of new roots and root elongation were limited in the submergence treatments compared to the control treatment (Fig. 2.04). The number of new roots of swamp chestnut oak in control treatment was more than that of 20 days submerged treatment, however, no differences were detected in root elongation rate among treatments for swamp chestnut oak (Fig. 2.04).

For the period of September 1 - September 17, a strong increment in new root initiation and root elongation was observed in baldcypress in all treatments. No significant differences were found for root initiation or root elongation among treatments (Fig. 2.05) during this period. Both oak species had low new root initiation and elongation during this period (Fig. 2.05). There were no significant differences among treatments for Nuttall oak or swamp chestnut oak. Root initiation and root elongation was always much greater in baldcypress than in the oaks.

For the period of September 17 - October 6, baldcypress root initiation and root elongation remained high. There were no significant differences among treatments for baldcypress seedlings (Fig. 2.06). Root initiation and elongation continued to decline in both oak species during this measurement period (Fig. 2.06). No root growth difference
Fig. 2.04. New root elongation (A) and mean number of new roots (B) for baldcypress (BCY), Nuttall oak (NUT), and swamp chestnut oak (SCO) for the period of August 16 to Sept. 1. Same letters within species indicate no significant difference at the 5 percent level. Submergence water removed from all treatment on August 11.
Fig. 2.05. New root elongation (A) and mean number of new roots (B) for baldcypress (BCY), Nuttall oak (NUT), and swamp chestnut oak (SCO) for the period of Sept. 1 - Sept. 17. Same letters within species indicate no significant difference at the 5 percent level. Submergence water removed from all treatment on August 11.
Fig. 2.06. New root elongation (A) and mean number of new roots (B) for baldcypress (BCY), Nuttall oak (NUT), and swamp chestnut oak (SCO) for the period of Sept. 17 to Oct. 6. Same letters within species indicate no significant difference at P<0.05 level. Submergence water removed from all treatment on August 11.
Table 2.04. The root volume and dry weight of baldcypress, Nuttall oak, and swamp chestnut oak at the final harvest.

<table>
<thead>
<tr>
<th>Species</th>
<th>Treatment</th>
<th>Volume (cm³)</th>
<th>Root (g)</th>
<th>Shoot (g)</th>
<th>Leaf (g)</th>
<th>Total (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Baldcypress</td>
<td>Control</td>
<td>4.238(a)¹</td>
<td>0.517(a)</td>
<td>0.359(a)</td>
<td>0.191(a)</td>
<td>1.067(a)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>2.874(b)</td>
<td>0.254(b)</td>
<td>0.193(b)</td>
<td>0.126(a)</td>
<td>0.573(b)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>3.468(ab)</td>
<td>0.272(b)</td>
<td>0.158(b)</td>
<td>0.143(a)</td>
<td>0.572(b)</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>3.093(b)</td>
<td>0.300(b)</td>
<td>0.190(b)</td>
<td>0.126(a)</td>
<td>0.616(b)</td>
</tr>
<tr>
<td>Nuttall oak</td>
<td>Control</td>
<td>4.350(a)</td>
<td>0.901(a)</td>
<td>0.974(a)</td>
<td>0.502(a)</td>
<td>2.337(a)</td>
</tr>
<tr>
<td></td>
<td>Sub-10</td>
<td>4.616(a)</td>
<td>0.942(a)</td>
<td>0.767(a)</td>
<td>0.507(a)</td>
<td>2.216(a)</td>
</tr>
<tr>
<td></td>
<td>Sub-20</td>
<td>4.295(a)</td>
<td>0.809(ab)</td>
<td>0.576(ab)</td>
<td>0.332(b)</td>
<td>1.717(a)</td>
</tr>
<tr>
<td></td>
<td>Sub-30</td>
<td>3.450(a)</td>
<td>0.495(b)</td>
<td>0.235(b)</td>
<td>0   (b)</td>
<td>0.73(b)</td>
</tr>
<tr>
<td>Swamp chestnut</td>
<td>Control</td>
<td>8.447(a)</td>
<td>1.945(a)</td>
<td>0.631(a)</td>
<td>0.637(a)</td>
<td>3.212(a)</td>
</tr>
<tr>
<td>oak</td>
<td>Sub-10</td>
<td>8.495(a)</td>
<td>2.113(a)</td>
<td>0.561(a)</td>
<td>0.678(a)</td>
<td>3.352(a)</td>
</tr>
</tbody>
</table>

¹. Same letters are not significantly different at P≤0.05 level within species in a same column.
existed but all swamp chestnut oak had died by Oct. 6 in the submerged 20 day and 30
day treatments.

**Final Harvest Results**

**Root volume** The root volumes for the three species were measured at the final
harvest, and results are shown in Table 2.04. Baldcypress, seedlings in the control
treatment had the largest root volume which was significantly larger than that for
seedlings in the submergence treatments. The root volume of baldcypress in the
submerged 10 days, submerged 20 days, and submerged 30 days treatments were 67.8
percent, 81.8 percent, 73.0 percent of the control respectively. For Nuttall oak, the
mean root volumes in control, submerged 10 days, and submerged 20 days treatments
were close to each other and yielded values of 4.35 cm³, 4.616 cm³, and 4.295 cm³
respectively. The mean root volume for submerged 30 days treatment was only 3.45
cm³. However, no significant differences were detected for Nuttall oak. For swamp
chestnut oak, the control and submerged 10 days seedlings had similar root volumes
which were 8.447 cm³, and 8.495 cm³ respectively for the two treatments. Complete
mortality had occurred in swamp chestnut oak in the other treatments.

**Biomass** Dry weight of roots, shoots, and leaves of seedlings in final harvest are
shown in Table 2.04. The mean root dry weight of baldcypress seedlings in the control
treatment was 0.517 g, which was significantly larger than that of submerged seedlings
(Table 2.04). The mean root dry weights for baldcypress seedlings in 10 day, 20 day,
and 30 day submergence treatment were close to each other and not significantly
different. Nuttall oak seedlings had intermediate root dry weights compared with that of
baldcypress and swamp chestnut oak. Root dry weights for Nuttall oak seedlings were
0.901 g, 0.942 g, 0.809 g, and 0.495 g for control, submerged 10 day, submerged 20
day, and submerged 30 day treatments respectively. The Nuttall oak seedlings that were
submerged 30 days had a much lower mean root dry weight. Swamp chestnut oak had much larger mean root dry weights than Nuttall oak. They were 1.945 g and 2.113 g for the control and submerged 10 day treatments. However, no significant differences existed between the two treatments. In submerged 20 and 30 day treatment seedlings were all dead.

The mean shoot dry weight of baldcypress seedlings in the control treatment was significantly larger than that of submergence treated seedlings, but there were no statistically significant differences among the 10 day, 20 day, and 30 day submergence treatments (Table 2.04). Submergence seemed to have similar impacts regardless of length. In Nuttall oak, seedlings in control and submerged 10 day treatments had a significantly larger shoot dry weight than submerged 30 day treatment (Table 2.04). Dry weight values of shoot of swamp chestnut oak were similar in the control and submerged 10 days treatments.

There were no statistical differences among leaf dry weights of the four treatments for baldcypress (Table 2.04). However, leaf dry weights of Nuttall oak seedlings in control and submerged 10 day treatments had significantly larger values than those of submergence 20 day, submergence 30 day treatments (Table 2.04). Similar leaf dry weight were found in swamp chestnut oak seedlings in the submerged 10 days and saturated soil control treatments (Table 2.04).

**Root/Shoot ratio** Root/Shoot ratio may indicate the allocation of carbon between assimilation and absorption organs and may also indicate the surviving strategy under stress. Root / Shoot ratio (R/S) of different species seemed to have similar tendency (Fig. 2.07). The control seedlings tended to have a lower R/S ratio than that of submerged treatment seedlings. The ratio increased in the submerged treatments. For example, in Nuttall oak, control had a R/S ratio of 0.933. The submerged 10 day
Fig. 2.07. Root/Shoot ratio of seedlings on a weight basis for baldcypress (BCY), Nuttall oak (NUT) and swamp chestnut oak (SCO) at final harvest (Oct.).
treatment ratio was 1.43, and submerged 20 day seedlings R/S ratio was 1.51. The largest R/S ratio was found in submerged 30 day treatment, and reached 2.15.

**Leaf area** Significant difference in leaf area occurred in baldcypress and Nuttall oak but not for swamp chestnut oak (Fig. 2.08). For baldcypress, the leaf areas of submerged 30 day seedlings was significantly lower than that of other treatments. For Nuttall oak, the submerged 30 day seedlings had significantly lower leaf area which was resulted from the leaf loss, while other treatments yielded similar leaf areas. For swamp chestnut oak, the leaf areas were similar for plants in control and 10-day submergence treatments.

**Leaf number** Differences in mean leaf number at the final harvest time are shown in Fig. 2.09. Baldcypress averaged more leaves than both of Nuttall oak and swamp chestnut oak by the final harvest. The average leaf number for baldcypress seedlings ranged from 15.9 to 18.3 for seedlings in submerged treatments and control. No significant differences among treatments were found (Fig. 2.09). Nuttall oak seedlings had a mean leaf number about eight, and no difference observed among treatments. However, leaves of Nuttall oak in submerged 30 day treatment were new initiated to replace the dropped leaves. The new leaves were much smaller and the leaf area data indicated this. Swamp chestnut oak seedlings had less than 5 leaves in control and submergence 10 days treatments. No difference in leaf number in swamp chestnut oak was found.
Fig. 2.08. Mean leaf area of seedlings at final harvest time (Oct.) for baldcypress (BCY); Nuttall oak (NUT); and swamp chestnut oak (SCO). The same letter within species are not significantly different at the 5% level.
Fig. 2.09. Mean number of leaves per seedling at final harvest for baldcypress (BCY); Nuttall oak (NUT); and swamp chestnut oak (SCO). The same letters within species are not significantly different at the 5% level.
**Specific weight of root**  Specific weight of roots may indicate carbon storage in plant roots. The higher specific weight of roots, the more carbon storage may have in root systems. For baldcypress, the control had a higher specific weight (Fig. 2.10). The value was 0.121 g/cm³. However, the values for submergence treated plants were smaller, which were 0.089 g/cm³, 0.076 g/cm³, 0.099 g/cm³ respectively. For Nuttall oak, the control, submerged 10 days, and submerged 20 days yielded close specific weight. However, the submerged 30 day seedlings had a lower value in specific weight. For swamp chestnut oak, seedlings in both control and submerged 10 day treatments had close values, which was 0.228 g/cm³ and 0.246 g/cm³ respectively.

**DISCUSSION**

The significant impacts of submergence on the three wetland tree species caused differentiation in survival among species. Baldcypress was able to maintain 100 percent survival in all submergence treatments. Nuttall oak had high survival in submerged 10 day, and submerged 20 day treatment. However, the seedlings of Nuttall oak submerged for 30 days had a much lower survival immediately after submergence water removed and during the subsequent recovery period. Swamp chestnut oak experienced high mortality in submerged 20 day, and submerged 30 day treatments. By the final harvest time, no seedlings of swamp chestnut oak in submerged 20 day or submerged 30 day treatments survived.

Past research has indicated that baldcypress is a submergence tolerant species, which could survive at least four weeks of submergence (Loucks and Keen 1973). There
Fig. 2.10. Specific weight of root for baldcypress (BCY), Nuttall oak (NUT), and swamp chestnut oak (SCO) at final harvest.
have not any reports about the submergence tolerance for Nuttall oak and swamp chestnut oak seedlings. Usually, oak species are less submergence tolerant (Hosner 1960). In a study to examine the submergence tolerance for 14 bottomland tree species, Hosner (1960) found that silver maple (Acer saccharinum L.) and buttonbush (Cephalanthus occidentalis L.) were two of the most submergence tolerant species. The two species could survive 30 day submergence. Pin oak (Quercus palustris Muenchh), shumard oak (Q. shumardii Buckl.), and cherrybark oak (Q. falcata Michx.) were the species with lower submergence tolerance to submergence. Few seedlings of the three species could survive the 20 day submergence treatment (Hosner 1960). The direct reason for the tolerance differences for these tree species was not found in the literature. In root flooding situations, baldcypress is a flood tolerant species, and Nuttall oak and swamp chestnut oak have a weaker tolerance to flooding (Teskey and Hinckley 1977), which seems to be coincident with submergence tolerance for the three species found in the current study.

Submergence also greatly affected shoot growth and root growth for baldcypress, Nuttall oak and swamp chestnut oak. However, the growth responses varied with species. During submergence treatment period, shoot growth of baldcypress in submerged 30 days was completely inhibited (Table 2.02 and Table 2.03), while shoot growth of the baldcypress in submerged 20 days and submerged 10 days were only partially inhibited (Table 2.02 and Table 2.03). The retardation effects of retardation of submergence treatments on shoot growth may be related to the lower PPFD under water and blockage of CO₂ and O₂ supply to plants. This seems not to be the same as occurred in rice and some Rumex species. When plants were submerged, a rapid shoot elongation is often observed in rice and some Rumex species. This is probably caused by induced ethylene increment in submerged plants (Voesenek et al. 1993). The purpose of rapid shoot elongation was considered as a resistance
mechanism to help plants to obtain oxygen supply from aerial environment. It seems that the study species do not present this avoidance mechanism to deal with submergence stress because no shoot elongation was observed during submergence.

The growth responses during the recovery period were also different between the baldcypress and the two oak species. The data shown earlier indicate that baldcypress regains strong shoot growth in all three submergence treatments after release. Partial reasons for renewed growth may be the rapid recovery of root growth. Research done by Van der Sman et al. (1991) found the extra ethylene production accrued after de-submergence and might be related to a continuation of growth of the shoot above the water surface. Such reactions need to be researched for wetland/bottomland tree species. Instead of rapid height growth, the control seedlings of baldcypress seem to allocate more photosynthate to diameter growth and root storage.

For both oak species, very limited height and diameter growth occurred in submergence treatments. In general, plant growth depends on maintaining of turgor, wall extendibility and structure material supply (Nobel 1991). This means plants have to produce more assimilation products which can meet the maintenance respiration requirements for plants and extra carbohydrates can be invested in a growth process. In anaerobic conditions, the lower efficiency of energy use in flood intolerant species always creates a growth barrier for plants (Jackson and Drew 1984). The low height growth rate of the two oaks suggested they are either unable to produce more assimilate or retain a low level of maintenance respiration. Such responses of submerged seedlings were similar with that of the control. Hosner (1960) also indicated that submergence tolerant species, such as silver maple, bottonbush, and black willow recovered rapidly after removal of submergence, while submergence intolerant species such as pin oak and cherrybark oak recovered slowly. Metabolic processes may be
unable to adjust or accumulation of toxic end products may prevent rapid new growth in intolerant species.

Flooding will have significant impacts on soil properties. Soil pores will soon be filled by water. The oxygen level in the root zone will rapidly decline due to consumption of plant roots and microorganism (Drew, 1990). The slow diffusion of gas into water is another reason. The activity of anaerobic microorganism lead to a decline in soil redox potential (Gambrell et al. 1991). Some toxic materials such as Mn++, Fe++, H2S will accumulate in soil (Crawford 1982). Even ethylene, an important plant hormone in flooding conditions may accumulate in the root environment (Jackson 1985). These dramatic physical and chemical changes will no doubt affect root growth and development. The acclimation of root system to anaerobic environment was very important for plants to grow successfully in flooded condition. The ability to initiate new roots and elongate were key to the growth vigor of shoot (Loucks 1987). Hook and Brown (1973) suggested that flood tolerance in tree species was largely dependent upon a combination of root adaptations. Only a few studies have been conducted for root growth process in flooded tree species (Chambers et al. 1993). Studies of root growth of tree species released from submergence were not found in the literature. This study revealed that during the submergence treatment period, submergence inhibited new root initiation and elongation for baldcypress. The longer the submergence time, the more inhibitory the effect on root development. During the recovery period, seedlings of baldcypress rapidly resumed root initiation and root elongation which was accompanied by the rapid growth in height and diameter. A strong increment in new root growth continued until near the final harvest time in October. Contrary to baldcypress root growth, the two oak species showed only limited activity during the same period. This observation was similar with that of Hosner (1959). He found that under submergence, the secondary roots of pin oak and cherrybark oak died and new roots
were weakly developed after submergence treatment. He attributed the differences of survival and growth of several tree species to the formation of adventitious roots and ability to produce new roots. For plants, ion absorption and transportation is an energy demanding process. The energy supply from fermentation is very limited. The inability of plants, such as oak species, to invest in root growth will affect their absorption and transportation capabilities (Jackson and Drew 1984). Further, the interruption of membrane properties will also affect ion movement among cells. The arrest of root initiation and elongation probably contributed to the slow shoot growth of both oak species.

Very limited information is available in literature about biomass production for tree species during a de-submergence period. The biomass data of baldcypress, Nuttall oak and swamp chestnut oak in this study did reveal a different response pattern. Baldcypress maintained active shoot and root growth during the recovery period in all submergence treatments. However, root volumes and dry weights indicate a significantly smaller root size in submerged seedlings than in the control. Setter et al. (1987) showed submergence decreased the carbohydrate concentration in rice, especially a low soluble sugar concentration occurred in the roots. A high photosynthetic rate may help to increase the size of shoot and root in baldcypress seedlings during de-submergence. However, it might be the results of a lower carbohydrate storage in the seedlings which were subjected to submergence treatment. The root specific weight of baldcypress seedlings also indicated that seedlings in control treatment had larger root specific weight than that of submerged seedlings. For Nuttall oak and swamp chestnut oak, a lower growth in shoot and roots were observed. The seedlings of both oak species have to depend more on the carbohydrate storage to support their survival during de submergence. If such supply was not enough to meet the metabolism need, loss of leaves or mortality would be resulted. Nuttall oak
seedlings submerged for 30 days had significant lower root and shoot dry weight which indicated that Nuttall oak may survive by use of stored carbohydrates. Swamp chestnut oak may not have such a tolerance mechanism.

We might summarize the above discussions. There was a difference in the survival of the three tested species to submergence. Baldcypress had the highest survival and ranked as the most submergence tolerant species of the three species. Nuttall oak was an intermediate submergence tolerant species, while swamp chestnut oak ranked as a submergence intolerant species. The arrest of shoot growth was observed in all submerged seedlings. However, the rapid regain of shoot growth was observed in submergence treated baldcypress seedlings and was accompanied by strong new root initiation and root elongation during the recovery period. The two oak species had a relatively slow recovery in both shoot and root growth. In oaks, the survival mechanism may mainly depend on carbon storage prior to submergence. Once such storage supply of carbohydrate was limited, loss of dry weight and mortality might be the results.
CHAPTER THREE

PHYSIOLOGICAL RESPONSES OF TWO BOTTOMLAND TREE SPECIES TO SUBMERGENCE

INTRODUCTION

Profound impacts of submergence on woody plants have been observed by several researchers (Hosner 1958, Hosner 1960, Loucks and Keen 1973, Misra et al., 1986, McCaughey and Weaver 1991). Some direct effects of submergence on tree species include decline in survival, reduced growth rate and leaf senescence (Demaree 1932, Kennedy 1970, Hosner 1960, Scarano and Crawford 1992). Root growth is also greatly retarded in some cases. However, the resumption of new growth after plants are released from submergence is species dependent (Hosner 1960). The growth of some submergence tolerant species can recover rapidly and the growth of submergence intolerant species may never recover (Hosner 1960, Loucks 1987). A detailed examination of the physiological performance of woody plants following water removal is lacking in the literature. This study will supply some information on the physiological responses of two wetland tree species after removal of flood waters (de-submergence).

Photosynthetic rate is routinely used to indicate health status of plants and the tolerance of plants to stresses (Kovach et al. 1992, Larcher 1994). In research related to shallow water flooding, the photosynthetic rate of many species has often been observed to decline although the degree of decline is species dependent (Zaerr 1983, Pezeshki and Chambers 1985, Vu and Yelenosky 1992, Karim et al. 1993). Potential reasons for the
decline in photosynthetic rate have been attributed to reduced stomatal function and some non-stomatal effects, such as the decrease in Rubisco activity and changes in source-sink relationships (Pezeshki 1990). Recently, some non-destructive techniques used to detect effects on the photosynthetic process have been used to assess stress impacts. One of these techniques is to use fluorescence parameters to indicate the effects on the light reaction process in plants (Sharkey 1985, Strasser et al. 1988, Krause and Weis 1991). However, such studies have not been used thus far to reveal the impact of submergence or the ability of species to repair physiological capability during the recovery period from submergence.

This study examined photosynthetic rate, stomatal conductance, and fluorescence parameters to describe impacts of submergence on photosynthetic rate. Changes in chlorophyll content and leaf xylem water potential were also monitored at the same time. The aim of this study was to test the null hypotheses that the submergence period has no impact on physiological performance of baldcypress or Nuttall oak.

RESEARCH METHODS AND MATERIALS

Seedling Care

Two wetland species were studied in this experiment. Baldcypress (Taxodium distichum (L.) Rich.), a very flood tolerant species and Nuttall oak (Quercus nuttallii Palmer), a species with intermediate flood tolerance were used in this experiment. The Nuttall oak acorns and baldcypress cones were obtained from USDA Forest Service, Southern Forest Experiment Station, Southern Hardwoods Laboratory at Stoneville, Mississippi.
The baldcypress cones were washed with ethyl alcohol to erase resins in the cones and allow seed extraction. The seeds were mixed with sand and stored in a cold room at a temperature of 3°C from January, 1993 until April, 1993. Seeds of both species were germinated in a ConViron E-15 growth chamber. The light period was set to 12 hours. The temperature was set to 25°C for day and 20°C for night. Humidity was maintained above 90 percent. As the seedlings reached approximately 5 cm in height, they were transplanted to black PVC pots with 6.2 cm diameter and height of 25 cm, then transported to a glasshouse to culture for two months. Seedlings were watered daily and fertilizer was applied as needed.

There were four treatments applied to the seedlings. Treatments included submergence for 30 days, which was started on July 11, 1993, submergence for 20 days, which was started on July 21, 1993, and submergence for 10 days, which was initiated on July 31, 1993. Completely Randomized Design was used in this experiment. A control treatment was maintained with root flooding only (soil saturation). During the submergence period, all seedlings in submergence treatments were covered completely by clear water. Three replicates were used for each treatment. Each replicate contained seven seedlings of each species, and occupied a single tank. Water above the soil surface was removed from all treatments on August 11, 1993 (Fig. 2.01). During the recovery period, the seedlings were maintained in saturated soil conditions until the final harvest in October, 1993.

During each period of measurement, three seedlings of each species were randomly selected from each treatment, then moved to a ConViron growth chamber to acclimate for at least 24 hours before measurement of physiological parameters. The growth chamber was set to a 12 hr/12 hr day/night cycle with a day temperature of 28°C and night temperature at 25°C. The light level at mid canopy position averaged about 500 μmol s⁻¹m⁻².
Measurements

Photosynthetic rate was measured with an ADC-LCA-3 (Analytical Development Company, Inc) potable photosynthesis system. The instrument was calibrated with a standard CO$_2$ source at the beginning of each measurement day. The sampled leaves of baldcypress were chosen as the tenth leaf counting down from the top of plants, and sampled Nuttall oak leaves were chosen from the fully expanded healthy leaves within the upper canopy. Photorespiration was measured by supplying the same system with a CO$_2$ source having an oxygen concentration of 1.8 percent and comparing measurements with those made at 21% oxygen. Stomatal conductance was also measured with the ADC-LCA-3 photosynthesis system. The calculated results are shown on a leaf area basis.

Fluorescence measurements were made with a CF-1000 chlorophyll fluorescence measurement system (P.K. Morgan Instruments, Inc). Minimal fluorescence (Fo), maximal fluorescence (Fm), and variable fluorescence (Fv) were measured at the same time. The ratio of variable fluorescence (Fv) and maximal fluorescence (Fm) was also calculated by Fv/Fm. Photon flux density of the actinic light was set to 500 umol s$^{-1}$m$^{-2}$. The dark acclimation time for measuring leaf fluorescence was at least 10 minutes for all samples. Xylem water potentials of leaves were measured with a pressure chamber (PMS Instrument Company, Corvallis, Oregon).

Chlorophyll content was measured with the N,N-Dimethyl-formamide (DMF) method (Moran and Porath 1980, Spezial. 1984). About 100-200 mg fresh leaves were put in 3.5 ml of DMF, then stored at 3 °C for at least 24 hours. The extract was then measured at 665 and 647 nm spectrometrically. The content of chlorophyll a, b, and chlorophyll ab were calculated by the formula supplied by Inskeep and Bloom (1985).
Statistical Analysis: Data was analyzed as a complete randomized design. The General Linear Model procedure was used for the analysis (SAS Institute, Inc.). Tukey's multiple comparison technique was used to compare the treatment differences. The significance level for testing hypotheses was chosen at the 5% level.

RESULTS

Photosynthesis at 21 percent Oxygen Level and 1.8 percent Oxygen Level.

Photosynthetic rate at normal oxygen level Two parameters were measured after the seedlings were removed from submergence treatments. The photosynthetic rate (Ps) at normal oxygen (≈ 21 percent) and photosynthetic rate with 1.8 percent oxygen are reported in Fig. 3.01 and Fig. 3.02. On August 13, 1993, the second day after water was removed from the submergence treatments, the mean photosynthetic rate of baldcypress was the highest in control plants, and seedlings of the submergence treatments had lower mean photosynthetic rates. Differences were not significant. Mean photosynthetic rates of baldcypress on August 13, 22 and 30 seemed to suggest recovery for the submergence treatments but again differences were not significant (Fig. 3.01b, 3.01c, 3.01d). Mean photosynthesis measured at 1.8 percent oxygen were higher than at 21 percent oxygen but seemed to closely parallel this same pattern. The closely parallel responses indicates effects of submergence on photorespiration.

The photosynthetic rates of Nuttall oak are shown in Fig. 3.02. Two days following release from submergence, the mean Ps rate of Nuttall oak seedlings at the control treatment appeared to be higher than that of seedlings in the submergence treatments. The longer the submergence treatment, the lower mean Ps rate observed (Fig. 3.02a). However, such difference in Ps rates were not significantly different. As with baldcypress no effects on photorespiration were apparent.
Figure 3.01. Net photosynthetic rate of baldcypress at 21 percent oxygen (●) and 1.8 percent (■) on four measurement days after termination of submergence treatments. a). Aug. 13; b). Aug. 22; c). Aug. 30; d). Sept. 08. Treatments were 1). control; 2). Submergence 10 days; 3). Submergence 20 days; 4). Submergence 30 days. Vertical bars indicate standard error.
Figure 3.02. Net photosynthetic rate of Nuttall oak at 21 percent oxygen (●) and 1.8 percent oxygen (■) on four measurement days after termination of submergence treatments. a). Aug. 13; b). Aug. 22; c). Aug. 30; d). Sept. 08. Treatments were 1). control; 2). Submergence 10 days; 3). Submergence 20 days. Vertical bars indicate standard error.
Stomatal Conductance

Mean stomatal conductance during the recovery period was highly variable in all treatments. By the second day following release from submergence, the mean stomatal conductance of baldcypress and Nuttall oak seedlings in submerged treatments seemed to be higher than that of control (Fig. 3.03a, Fig. 3.04a). A similar relationship existed on the other measurement days but levels were inconsistent (Fig. 3.03b-d, 3.04b-d). However, no statistically significant difference was found among treatments at 0.05 level.

Chlorophyll Content

In this experiment, the content of chlorophyll a, chlorophyll b, and chlorophyll ab were monitored on three measurement dates (Table 3.01). On the day immediately after removal of water coverage, the chlorophyll a, b, and total chlorophyll content in all treatments were not significantly different for either baldcypress or Nuttall oak seedlings (Table 3.01). However, the total chlorophyll content in Nuttall oak on August 22 was significantly different (Table 3.01). The seedlings submerged 20 day treatment had significantly lower total chlorophyll content than that of control and submergence 10 day treatment. After being released from submergence for three weeks, baldcypress seedlings showed no significant difference in chlorophyll a, chlorophyll b, and total chlorophyll content (Table 3.01). Baldcypress gradually showed a slightly higher mean chlorophyll level for greater exposure to submergence although the difference was not significant. However, there were treatment differences on chlorophyll a and total chlorophyll content in Nuttall oak seedlings on Aug. 30 (Table 3.01).
Fig. 3.03. Stomatal conductance of baldcypress on four measurement days. a). 8/13; b). 8/22; c). 8/30; d). 908. Treatments were 1). control; 2). submergence 10 days; 3). submergence 20 days; 4). submergence 30 days. Vertical bars indicate standard error.
Fig. 3.04. Stomatal conductance of Nuttall oak on four measurement days. a). 8/13; b). 8/22; c). 8/30; d). 9/08. Treatments were 1). control; 2). submergence 10 days; 3). submergence 20 days; 4). submergence 30 days. Vertical bars indicate standard error.
Fluorescence Parameters

Some non-destructive methods of monitoring photosynthesis are attractive for use by physiologists. In this study, the leaf which was used in the photosynthesis measurement was also used to assess fluorescence parameters (Table 3.02). Two days after release from submergence, there were no significant differences in Fo and Fm for baldcypress. However, a significantly lower Fv/Fm ratio was detected in submerged 30 day treatment compared with that of control, submerged 10 day, and submerged 20 day treatment for baldcypress (Table 3.02). For Nuttall oak, there were no significant differences in Fo and Fm among treatments (Table 3.02) on Aug. 13. The Fv/Fm ratio of Nuttall oak in submerged 20 day and 30 day treatments seemed to have lower mean values however no significant differences were detected in this case. In the later recovery stage, there were no significant differences found in Fo, Fv, and Fv/Fm ratio among treatments for baldcypress and Nuttall oak (Table 3.02).

Water Potential

Water potential of seedlings was measured after measurement of the fluorescence parameters (Fig. 3.05 and Fig. 3.06). Leaf xylem water potentials of baldcypress in the control, submerged 10 day, submerged 20 day and submerged 30 day treatments were similar to each other after release from submergence (Fig. 3.05a). This pattern remained similar in the later stage of recovery for baldcypress and no significant difference among treatments was detected for baldcypress (Fig. 3.05b, 3.05c, and 3.05d). The leaf xylem water potential of Nuttall oak in submergence treatments was more varied than that of baldcypress seedlings. Mean leaf xylem water potentials tended to decrease with exposure time to submergence but was not significantly different among treatments. Means were similar by Sept. 8. However, no significant difference was detected among treatments for Nuttall oak were detected.
Table 3.01. Chlorophyll content of baldcypress and Nuttall oak for three measurement days following removal of submergence water on August 11.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Species</th>
<th>Date</th>
<th>chl$^{1}$ ug/g fwt</th>
<th>chl$^{2}$ ug/g fwt</th>
<th>chl$^{3}$ ug/g fwt</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Aug. 14</td>
<td>705±148</td>
<td>249±60</td>
<td>954±207</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Baldcypress</td>
<td>Aug. 14</td>
<td>924±73</td>
<td>474±60</td>
<td>1398±122</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Aug. 14</td>
<td>981±42</td>
<td>578±81</td>
<td>1559±83</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Aug. 14</td>
<td>944±26</td>
<td>505±7</td>
<td>1449±19</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.2899)</td>
<td>(0.0506)</td>
<td>(0.0993)</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Aug. 14</td>
<td>743±77</td>
<td>534±181</td>
<td>1277±245</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Aug. 14</td>
<td>768±102</td>
<td>438±212</td>
<td>1205±313</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Aug. 14</td>
<td>838±31</td>
<td>458±116</td>
<td>1295±86</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.5691)</td>
<td>(0.9183)</td>
<td>(0.9545)</td>
</tr>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Aug. 22</td>
<td>810±88</td>
<td>537±121</td>
<td>1347±199</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Baldcypress</td>
<td>Aug. 22</td>
<td>847±28</td>
<td>708±44</td>
<td>1554±17</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Aug. 22</td>
<td>894±72</td>
<td>491±49</td>
<td>1385±104</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Aug. 22</td>
<td>857±27</td>
<td>585±42</td>
<td>1442±16</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.7602)</td>
<td>(0.2088)</td>
<td>(0.5161)</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Aug. 22</td>
<td>851±101</td>
<td>894±146</td>
<td>1743±219 ab</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Aug. 22</td>
<td>893±17</td>
<td>959±89</td>
<td>1850±74 a</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Aug. 22</td>
<td>730±37</td>
<td>392±68</td>
<td>1121±59 b</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.2705)</td>
<td>(0.0500)</td>
<td>(0.0371)</td>
</tr>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Aug. 30</td>
<td>1065±143</td>
<td>477±66</td>
<td>1541±181</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Baldcypress</td>
<td>Aug. 30</td>
<td>1380±136</td>
<td>509±56</td>
<td>1890±189</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Aug. 30</td>
<td>1156±216</td>
<td>434±74</td>
<td>1589±290</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Aug. 30</td>
<td>1359±136</td>
<td>523±31</td>
<td>1882±166</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.5861)</td>
<td>(0.7693)</td>
<td>(0.6431)</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Aug. 30</td>
<td>780±38 b</td>
<td>819±84</td>
<td>1599±74 b</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Aug. 30</td>
<td>781±57 b</td>
<td>986±87</td>
<td>1767±43 ab</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Aug. 30</td>
<td>1032±11 a</td>
<td>1102±60</td>
<td>2133±49 a</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(0.0149)</td>
<td>(0.3107)</td>
<td>(0.0431)</td>
</tr>
</tbody>
</table>

1. chla: chlorophyll a.
2. chlb: chlorophyll b.
3. chlab: total chlorophyll.
4. The same letters were not significantly different at the 5% level within the same species, column and measurement day. All values without letters were also non-significant.
Table 3.02. Fluorescence parameters for baldcypress and Nuttall oak on four different measurement dates during the recovery period after submergence treatments

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Species</th>
<th>Date</th>
<th>$F_o$</th>
<th>$F_m$</th>
<th>$F_v/F_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Aug.13</td>
<td>131</td>
<td>580</td>
<td>0.7765 a</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Baldcypress</td>
<td>Aug.13</td>
<td>180</td>
<td>685</td>
<td>0.7385 a</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Aug.13</td>
<td>125</td>
<td>450</td>
<td>0.7170 ab</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Aug.13</td>
<td>244</td>
<td>754</td>
<td>0.6743 b</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Aug.13</td>
<td>215</td>
<td>790</td>
<td>0.7263</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Aug.13</td>
<td>276</td>
<td>1050</td>
<td>0.7380</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Aug.13</td>
<td>239</td>
<td>702</td>
<td>0.6527</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Nuttall oak</td>
<td>Aug.13</td>
<td>304</td>
<td>911</td>
<td>0.6660</td>
</tr>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Aug.22</td>
<td>144</td>
<td>540</td>
<td>0.7343</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Baldcypress</td>
<td>Aug.22</td>
<td>108</td>
<td>521</td>
<td>0.7933</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Aug.22</td>
<td>118</td>
<td>555</td>
<td>0.8000</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Aug.22</td>
<td>172</td>
<td>751</td>
<td>0.7613</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Aug.22</td>
<td>165</td>
<td>731</td>
<td>0.7870</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Aug.22</td>
<td>176</td>
<td>743</td>
<td>0.7587</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Aug.22</td>
<td>225</td>
<td>939</td>
<td>0.7663</td>
</tr>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Aug.30</td>
<td>106</td>
<td>393</td>
<td>0.7290</td>
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<td>Baldcypress</td>
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<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Aug.30</td>
<td>128</td>
<td>582</td>
<td>0.7933</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Aug.30</td>
<td>200</td>
<td>730</td>
<td>0.7467</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Aug.30</td>
<td>123</td>
<td>557</td>
<td>0.7847</td>
</tr>
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<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Aug.30</td>
<td>131</td>
<td>627</td>
<td>0.8050</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Aug.30</td>
<td>117</td>
<td>631</td>
<td>0.8263</td>
</tr>
<tr>
<td>Control</td>
<td>Baldcypress</td>
<td>Sept.08</td>
<td>87</td>
<td>376</td>
<td>0.7610</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Baldcypress</td>
<td>Sept.08</td>
<td>87</td>
<td>392</td>
<td>0.7807</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Baldcypress</td>
<td>Sept.08</td>
<td>154</td>
<td>602</td>
<td>0.7383</td>
</tr>
<tr>
<td>Sub-30</td>
<td>Baldcypress</td>
<td>Sept.08</td>
<td>56</td>
<td>321</td>
<td>0.8140</td>
</tr>
<tr>
<td>Control</td>
<td>Nuttall oak</td>
<td>Sept.08</td>
<td>146</td>
<td>726</td>
<td>0.7966</td>
</tr>
<tr>
<td>Sub-10</td>
<td>Nuttall oak</td>
<td>Sept.08</td>
<td>120</td>
<td>590</td>
<td>0.7987</td>
</tr>
<tr>
<td>Sub-20</td>
<td>Nuttall oak</td>
<td>Sept.08</td>
<td>121</td>
<td>476</td>
<td>0.7633</td>
</tr>
</tbody>
</table>

1. sub-10: submerged 10 days; sub-20: submerged 20 days; sub-30: submerged 30 days.
2. Parameters with the same letters are not significantly different within species on the same date at the 5% significant level.
3. $F_o$: Minimal Fluorescence
4. $F_m$: Maximal Fluorescence
5. $F_v/F_m$: Ratio of Variable Fluorescence and Maximal Fluorescence
Figure 3.05. Xylem water potential of baldcypress on four measurement days after termination of submergence treatments. a). Aug. 13; b). Aug. 22; c). Aug. 30; d). Sept. 08. Treatments were 1). control; 2). submergence 10 days; 3). submergence 20 days; 4). submergence 30 days.
Fig. 3.06. Leaf xylem water potential of Nuttall oak on four measurement days after termination of submergence treatments. a). Aug. 13; b). Aug. 22; c). Aug. 30; d). Sept. 08. Treatments were 1). control; 2). submergence 10 days; 3). submergence 20 days.
DISCUSSION

Physiological responses in most flooding experiments have shown a reduction in photosynthetic rates in flooded plants although the reason for this phenomenon is not completely clear (Teskey and Hinckley 1977, Beckman et al. 1992). The photosynthetic rates during submergence were measured in rice by Setter et al. (1987) and in *Rumex* by Blom (1990). The underwater photosynthetic rate of rice and *Rumex* species seems to depend on PPFD and CO$_2$ supply for plants. The significance of this physiological function is not only for carbohydrate supply, but also for oxygen supply in flooded plants (Laan and Blom 1990). There was a report about photosynthetic responses of three *Fucus* species after submergence (Beer and Kautsky 1992). However, the photosynthetic rate (Ps) of woody plants during submergence was not found in the literature. The Ps rates of tree species after submergence water are removed are also not readily available in the literature. The data in this study revealed a decline in photosynthetic rate in the seedlings which were exposed to different submergence treatments. The control seedlings had the highest mean photosynthetic rate in both tree species. The longer the time of submergence, the lower the mean photosynthetic rate upon immediate release from submergence although no significant differences were detected. The high variation within treatment and small sample size probably contributed to the low efficiency of the statistical test. Nuttall oak seedlings also seem to be injured by the longer submergence periods. Few Nuttall oak seedlings survived 30 days of submergence (Chapter 2). The Ps rate of surviving Nuttall oak seedling in 30 days of submergence was very low. No Nuttall oak seedlings in submerged 30 day treatment survived by Aug. 22. The data indicated that submergence treated baldcypress seedlings had similar Ps rates on Aug. 22, Aug. 30, and Sept. 8 compared with that of control. The Ps rate of Nuttall oak fluctuated more than that of
baldcypress. Although there were possibly some trends showing submergence impacts on $P_s$ rate for baldcypress and Nuttall oak, the great variation due to stress treatments, small sample size due to the limited plant material, and limited growth chamber space are some major causes for a weak statistical inference about photosynthetic rates.

When supplied with a lower ambient oxygen air source, the photosynthetic rate of plants usually is stimulated by the suppression of photorespiration (Musgrave et al. 1991). The results in this experiment fit this general pattern. A parallel increase in photosynthetic rate in 1.8 percent oxygen level for baldcypress was observed. However, for seedlings of Nuttall oak in submerged treatment, less stimulation was observed on the day immediately after release from submergence (Fig. 3.04a). The insensitivity of oxygen in photosynthesis was observed in root flooding situations by Musgrave et al. (1991). A limitation in the rate of triose phosphate utilization was suggested by Sharkey (1985), and Musgrave et al. (1991).

Stomata control of gas and water exchange in plants has been noted for long time (Cowan 1994). The examination of stomatal conductance showed that submergence seems to enhance stomatal opening when the seedlings were released from submergence. But responses were not significant. Stomatal opening has been traditionally attributed to the hydraulic status of the leaf. The more negative water potentials observed in flooded situations in some plant species (Olien 1989), have often been considered a direct reason for stomatal closure. Due to the large variation in the stomatal conductance data of this experiment, no determined relationship between hydraulic status and stomatal conductance can be concluded. Recent literature which shows that some plant regulators may play an important role in stomata functions when plants were under stress (Zhang et al. 1987, Jackson and Hall 1988, Smit et al. 1989, Smit et al. 1990). Zhang and Davies (1987) suggested that abscisic acid (ABA) was a direct messenger to induce stomata closure in flooded peas. Sudden changes in ABA or
ABA/other regulator ratio may be responsible for stomata movement once submergence has been removed.

Although most studies have found chlorosis in flooded seedlings (Hosner 1959, Jackson and Hall 1988), there was no evidence to show that submergence treatment had caused lower chlorophyll content in the current study. In fact the data showed a slightly higher chlorophyll a, b, and total chlorophyll content in submerged plants although the differences did not reach a significant level (P<0.05) on Aug. 13. Both species maintained similar values in the above parameters. Differences in chlorophyll a and chlorophyll ab content on Aug. 30 were detected. Reasons for higher chlorophyll content in submerged 20 day treatment are not clear. However a similar trend was seen in baldcypress and Nuttall oak. This suggests some recovery or stimulation in chlorophyll content during the recovery.

Portions of the photosynthetic process of plants can be monitored by chlorophyll fluorescence kinetics which are related to the photochemistry of photosystem II (Gnojek 1992, Kao and Forseth 1992, Moffatee et al. 1990, Schreiber et al. 1994). Observation of chlorophyll fluorescence kinetics is especially useful as it supplies an non-destructive means to indicate changes in the photosynthetic process (Kooten and Snel 1990). The Fo values indicate the activity of photosynthesis system II reaction center (Schreiber et al. 1994). A higher Fo value is often associated with an increase in inactive photosynthesis II reaction centers. This experiment indicated that submerged seedlings had similar Fo values with that of the control treatment. This means the photosynthesis II system functions well or at least is not damaged in submerged baldcypress. The ratio of Fv/Fm is a particularly useful parameter since it relates to the quantum yield of the photosystems primary photochemistry (Hipkinds and Baker 1986). The lower Fv/Fm values in baldcypress seedlings which were submerged for 30 days did have a lower photosynthetic rate. There was a weak evidence to show that Fv/Fm ratio of Nuttall oak
also showed a similar trend when seedlings were immediately removed from submergence. The Fv/Fm ratio of both species was restored in the later part of the recovery period. No significant differences were found in the Fo, Fm, Fv/Fm ratio in all treatments on Aug. 22, Aug. 30, and Sept. 8, 1993. The low power of fluorescence parameters to detect the differences in salinity stressed treatments of baldcypress and control treatment was also observed by Allen (personal communication).

Although there were some trends in the measured physiological parameters, no significant difference among treatments was detected for most physiological parameters in this study. The large variations within treatment, small sample size, hardship in selecting samples all may have contributed to the failure to detect differences. Large differences in below ground responses may figure to a larger degree in controlling response to submergence stress. Important impacts on physiological parameters may be occurring only during the period of submergence itself.
CHAPTER FOUR

STRESS TOLERANCE INDICES

INTRODUCTION

Plants experience a variety of stresses in the natural environment. About two-thirds of the earth's land area experiences drought sometime during a year. In the United States, about 25.3 percent of the land area is affected by drought stress, 16.5 percent of the area is affected by cold stress, and 15.5 percent of the land area is affected by flooding (Boyer 1982). Other stresses are also common in certain natural habitats. The impacts of stress on plant health and yield of agricultural and forest crops are tremendous. Great variations in stress tolerance exist among species. Therefore, a means to quantitatively describe and evaluate stress tolerance of plant species is important.

Although stress and stress tolerance are key terms used in plant stress physiology, there is no universally agreed upon definitions for either term. There are some generally accepted concepts applied to stress physiology. One of them is supplied by Osmond et al. (1987), who defined stress as any factor that decreases plant growth and reproduction below the genotype's potential. However, there is much variation in the definition of stress tolerance. Tolerance is often considered the ability of plants to maintain high metabolic activity or reduce the activity under stress conditions (Osmond et al. 1987).

The tolerance of plants can be assessed by a plant's response to a stress. A plant's responses to various stresses might be found at the molecular, cellular, tissue,
and whole plant levels. In theory, the responses at one or more levels can be used to
describe the tolerance of plants. However, most scientists in applied science areas
prefer to use easily measured responses such as survival or growth to address the
problem. In practice, the survival of plants exposed to a specified stress is perhaps the
most commonly used attribute to describe the tolerance of the plants. McKnight et al.
(1981) ranked the flood tolerance for several dozen wetland tree species. They stated
that flood tolerant species are the species that are able to survive and grow on sites in
which the soil is saturated or flooded for long, indefinite periods during the growing
season, and the intolerant species are the species unable to survive even short periods of
soil saturation or flooding during the growing season. The above approach was also
used by several others (Hosner and Boyce 1962; Teskey and Hinckley 1977).
However, there are several limitations in this method. First, field observations are main
data sources for tolerance classification, so there are no standardized tolerance criteria.
Therefore it is hard to compare the tolerance of a species on one site or in one study
with the results from other studies. Second, some classification systems are based on
qualitative parameters (e.g. color of plants). Third, there is no standard system for
ranking tolerance to stresses. Different levels of stress exposure and duration affect the
tolerance rankings in different ways. In many cases, the methods of ranking do not
provide a clear-cut difference among the tolerance groups. There is also difficulty in
integrating the tolerance term into quantitative models. Some quantitative stress indices
can be found in the literature. A general approach to the study of tolerance in plants is
to subject plants to different levels of a stress. The survival of plants during a stress
period is often considered a quantitative description of tolerance for a given level of
stress. Crawford (1982) listed the survival time under inundation for some flood
tolerant species. It is possible to assess tolerance of the listed tree species by the
absolute length of time a species can survive flooding. However, the low resolution of
this method to rank tolerance of plants is obvious. A more detailed quantitative measurement of tolerance of a plant can be assessed by the environmental discrimination coefficient which was used by McGraw and Antonovics (1983). McGraw and Antonovics defined the environmental discrimination coefficient as $1 - \frac{a}{b}$, where $a$ is survival of a given ecotype in a given environment, and $b$ is survival of that ecotype in an environment giving maximum survival. Treacy (1984) developed a salt resistance index which was defined by comparing combined values of relative height and relative diameter growth of a genotype treatment in a stressed family relative to the combined growth of the same genotype in a control treatment. The salt resistance index he developed was used to rank the 12 live oak families (Treacy 1984). Taylor and Foy (1985 a) defined a root tolerance index (RTI) and a shoot tolerance index (STI) to evaluate the tolerance of wheat cultivars to aluminum (AL). RTI and STI were calculated by dividing the root or shoot yield of plants grown with AL by that of plants grown without AL. Taylor and Foy have used these two indices to screen the AL tolerance for 20 wheat cultivars. This approach has been used by several researchers (Taylor and Foy 1985 b, Sivaguru et al. 1992, Sivaguru and Paliwal 1993). A common drawback for these indices is that they ignore the polymorphic characteristics of plant responses to a stress. These indices may not accurately indicate the tolerance of a species or a cultivar to a particular stress. I will therefore present two new quantitative indices of plant tolerance, which are based on the performance of plants exposed to stress conditions for a specific time period and performance of plants under multiple stress conditions.
GENERAL STRESS TOLERANCE INDICES METHODS

For the purpose of this work, stress will be defined as the level of any environmental factor which will reduce plant growth or development. Tolerance will be defined as the ability of the plant to survive the particular environmental stress. To simplify the discussion, I focus on a single stress here.

In this chapter, I introduce two new concepts to describe stress tolerance. The first one, Chronic Stress Tolerance Index (CSTI), is defined as a relative ability of plants to survive a particular stress during the applied stress or after release from the stress. Calculation of the Chronic Stress Tolerance Index is presented in formula (1)

\[
CSTI = \frac{\sum_{i=1}^{P} t_{mi}}{N \sum_{i=1}^{P} t_{i}}
\]

where: CSTI = Chronic Stress Tolerance Index

\( t_{i} \) = time since a stress was applied (assesses tolerance during stress) or time since the release from the stress (assesses ability to recover from stress).

\( n_{i} \) = number of the plants surviving at the given time \( t_{i} \).

\( N \) = total number of plants before the stress treatment was initiated.

\( P \) = number of times that plant survival is measured during and following removal of stress.

Chronic Stress Tolerance Index as calculated in (1) will be a number between 0 and 1. A value of zero indicates that plant can not survive to the first measurement period after the stress is introduced. A value of one suggests that the change in survival of the plant species will not be affected by the application of a particular stress.

Therefore, the larger CSTI value, the more tolerant the plant.
The second new index, Variant Stress Tolerance Index (VSTI), is defined as changes in survival of plants once plants are released from different levels of a stress (e.g. salinity levels). The formula for Variant Stress Tolerance Index is shown in (2)

\[
VSTI = \frac{\sum_{i=1}^{P} a_{ni}}{N \sum_{i=1}^{P} a_{i}}
\]

where: VSTI = Variant Stress Tolerant Index

\( a_{ij} \) = level of intensity of a particular stress (e.g. salinity level, \( SO_2 \) concentration)

\( n_{ij} \) = the number of plants surviving after release from the ith level stress

\( N \) = total number of plants before in ith level of stress before treatment applied

\( P \) = number of levels of stress

The VSTI value is also a number from 0 to 1. A larger VSTI value indicates a higher tolerance of the plant to a particular stress.

RESULTS OF STRESS TOLERANCE

Example of Submergence Tolerance

A study of tree seedling tolerance to submergence was initiated in the School of Forestry, Wildlife, and Fisheries at Louisiana State University. The purpose of the study was to address the responses of three wetland tree species to submergence and develop a means of ranking the tolerance of these species to submergence. Baldcypress, swamp chestnut oak, and Nuttall oak were tested in this experiment. The three species were submerged for 10 days, 20 days and 30 days plus one treatment was subject to root flooding only and served as a control. The survival of seedlings in all treatments was recorded just after release from the submergence treatments and again after 5 days, 20 days, 36 days, and 55 days since release. Survival is reported in Table 4.01.
Table 4.01. Numbers of the baldcypress, Nuttall oak, and swamp chestnut oak seedlings surviving for different periods of submergence and the associated Chronic Stress Tolerance Index (CSTI).

<table>
<thead>
<tr>
<th>Species/Treatment</th>
<th>5 days</th>
<th>Number of days after release from submergence</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>20 days</td>
<td>36 days</td>
</tr>
<tr>
<td><strong>baldcypress</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>control</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>10 days sub</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>20 days sub</td>
<td>21</td>
<td>21</td>
</tr>
<tr>
<td>30 days sub</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td><strong>Nuttall oak</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>control</td>
<td>19</td>
<td>19</td>
</tr>
<tr>
<td>10 days sub</td>
<td>20</td>
<td>19</td>
</tr>
<tr>
<td>20 days sub</td>
<td>22</td>
<td>20</td>
</tr>
<tr>
<td>30 days sub</td>
<td>18</td>
<td>5</td>
</tr>
<tr>
<td><strong>Swamp chestnut oak</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>control</td>
<td>18</td>
<td>18</td>
</tr>
<tr>
<td>10 days sub</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>20 days sub</td>
<td>21</td>
<td>6</td>
</tr>
<tr>
<td>30 days sub</td>
<td>20</td>
<td>0</td>
</tr>
</tbody>
</table>

1. Number of days submerged.
2. N = initial number of seedlings.
The Chronic Stress Tolerance Index was calculated with formula (1). The results are shown in Table 4.01. For example, the CSTI value for swamp chestnut oak seedlings in the submerged for 10 day treatment can be calculated as

\[
\text{CSTI} = \frac{\sum_{i=1}^{P} t_{ini}}{N} \sum_{i=1}^{P} t_{i} = 0.96
\]

where:

\[
\sum_{i=1}^{4} t_{ini} = (5)(20) + (20)(20) + (36)(19) + (55)(19), \quad N \sum_{i=1}^{4} t_{i} = 20(5 + 20 + 36 + 55)
\]

Other index values are also included in Table 4.01. The results in Table 4.01 can be either used to compare the CSTI values within species or to compare the changes of the CSTI values among species. For example, at a given stress level (submerged 20 days), the CSTI value for baldcypress was 1.00, Nuttall oak was 0.91, and swamp chestnut oak was 0.29. The ranking of submergence tolerance would then be baldcypress > Nuttall oak >> swamp chestnut oak.

**Example of Salt Tolerance of 15 Families of Baldcypress**

Since evaluation of the effects of various levels of stress may be needed in some cases, VSTI was developed. For the purpose of illustration of the use of Variant Stress Tolerance Index, data from Allen et al. (in press) are used. The survivals of 15 families of baldcypress subjected to different salinity levels serve as an example for VSTI application.

In their study, the seeds of fifteen families of baldcypress were collected from southern Louisiana and Mobile Bay, Alabama. The seedling culture procedure has been described previously (Allen et al. 1994). Five salinity levels (0, 2, 4, 6, 8 g/l) were applied to the 15 families. Survival was measured after release from the salinity treatments (Table 4.02). VSTI was calculated from their data and is listed in Table 4.02.
Table 4.02. Family survival and Variant Stress Tolerance Index of 15 families of baldcypress exposed to five levels of salinity

<table>
<thead>
<tr>
<th>Family</th>
<th>Salinity (g/l)</th>
<th>Variant Stress Tolerance Index</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>LS1</td>
<td>100</td>
<td>97</td>
</tr>
<tr>
<td>FA1</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>VE2</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>FA2</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>SG2</td>
<td>100</td>
<td>97</td>
</tr>
<tr>
<td>FA3</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>FA4</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>SW1</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>CB2</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>BO2</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>SW2</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>CB3</td>
<td>100</td>
<td>97</td>
</tr>
<tr>
<td>VE3</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>PR1</td>
<td>100</td>
<td>94</td>
</tr>
<tr>
<td>PB1</td>
<td>100</td>
<td>94</td>
</tr>
</tbody>
</table>
Fig. 4.01 Results of cluster analysis of 15 families of baldcypress according to VSTI value
Fig. 4.02. Results of cluster analysis of 15 families of baldcypress according to survival percentage
Based on the results in Table 4.02, it is easy to rank salinity tolerance of 15 families of baldcypress. We can rank the families into three survival tolerance groups by the absolute VSTI values. The most tolerant families included: LS1, FA1, and VE2 (VSTI > 0.90). The moderately tolerant group contained FA2, SG2, FA3, FA4, CB2, BO2, SW1, and SW2 (0.8 < VSTI < 0.9). The intolerant families included CB3, VE3, PR1, and PB1 (VSTI < 0.8).

How good does the stress tolerance index describe the survival process? The data for survival and VSTI values in Table 4.02 were used in a cluster analysis (average linkage). Fig. 4.01 and Fig. 4.02 show the classification results. Cluster analysis is often used for a classification based on multiple parameters. Generally, the closest subjects based on the classification parameters are classified into the same group. The use of cluster analysis here is based on an assumption that the survival of seedlings at different stress levels is a more accurate than based on a single stress level. It is supposed to provide a standard method to produce a relative tolerance ranking for plants. Therefore, we can compare how well the VSTI system works at the ranking salinity tolerance for the 15 tested baldcypress families with the standard. Suppose we want to have five tolerance groups, by survival percentage at different salt levels, the cluster analysis results show the most salinity tolerant seed source is LS1. The salinity tolerant group includes FA1, FA2, VE2, SG2, FA3 (Fig. 4.02). The intermediate salinity tolerant group included SW1, FA4, CB2. The slightly tolerant seed source contains VE3, BO2, SW2, and CB3. The intolerant group includes PB1, PR1. Based on Variant Tolerance Index, the very tolerant group would include LS1. The tolerant group would have FA1, FA2, SG2, VE2. The intermediate tolerant group would have SW1, FA4, CB2, FA3, BO2. The slightly tolerant group included VE3, SW2, CB3. The intolerant group would include PB1, PR1 (Fig. 4.01).
DISCUSSION

There are many different ways available to describe plant tolerance to a particular stress. Crawford (1989) thought survival was a true indicator for plant tolerance. The survival does indicate stress tolerance to some degrees but is only useful when a stress level and time of exposure are also shown. Usually, a single survival value does not describe different effects that exposure time and exposure level may have on plants. It should be noted that plant response to a stress often has polymorphic characteristics (different shapes of response curves). A hypothetical set of survival curves under a stress may be depicted as in Fig. 4.03. Fig. 4.03 indicated that relative tolerance ranking of seedlings based on survival can be highly variable depending on the stress level and the percent mortality at which tolerance is judged. For example, in Figure 4.03, if relative stress tolerance is based on survival at stress level 2, the stress tolerance of the five species will be: species a > species b > species c > species d > species e. However, if relative stress tolerance is based on survival at stress level 6, then the species would be ranked in the order: species a > species d > species c > species b > species e. Therefore the chosen level of stress affects the ranking since species or genotype have different survival response curves to a stress. Similar problems are encountered if we evaluate stress tolerance based on a fixed survival level. Relative tolerance ranking of seedling survival can be highly variable depending on the stress level and the percent mortality at which tolerance is judged. For example, in Figure 4.04, if relative stress tolerance is based on survival at the 20% mortality level, then the species would be ranked in the order: species a > species b > species c > species d > species e. However, if relative stress tolerance is based on a 60% mortality level then the species would rank in the order: species a > species d > species c > species e. The selection criteria for judgment of tolerance affects the outcome. Both of
Fig. 4.03. Hypothetical representation of different survival response for five hypothetical species in response to a stress. •). species a; ◆). species b; ■). species c; ▲). species d; ▼). species e.
Fig. 4.04. Hypothetical representation of different survival response for five hypothetical species in response to a stress. ( ) surviving line. ( ) species a; ( ) species b; ( ) species c; ( ) species d; ( ) species e.
these approaches have this inherent shortfall. The stress indices presented in this paper solve this problem by combining the stress tolerance over a range of exposure times (CSTI) and over several stress exposure levels (VSTI). The proposed stress tolerance indices here are basically a relative measurement of stress tolerance. Plants of a species that survive the longer stress exposure at a given level should have a greater tolerance to the stress (Chronic tolerance). It is also true that plants of a species that survive a higher intensity of a stress will have a greater tolerance to the stress (acute tolerance). More weight should be assigned to the plants which either can survive longer stress exposure time or survive greater stress intensity. The weight related to the survival time is provided by formula 1 (CSTI). The weight related to stress intensity was provided by formula 2 (VSTI). So, CSTI and VSTI are more accurate than the absolute survival or absolute survival time and are also easier to interpret in short term studies. The numerator in (1) can be viewed as the performance of plants exposed to a stress, and denominator can be considered as the maximum performance when no stress is applied.

There is a pretty good match between clusters (Fig. 4.02) based on VSTI and survival percentages. However, the classification results based on cluster analysis of survival percentages were dependent on some arbitrary judgment. The classification by VSTI provided a decisive result.

The basic difference of CSTI and VSTI is that CSTI is calculated as the surviving number of the plants at the different times when they are exposed to a particular stress level, while VSTI is calculated based on the surviving number of the plants when the plants are exposed to different stress levels. Both can be used to indicate the tolerance of the plants.

In the example presented for CSTI, days are used as the measurement unit of time. In fact, other time units can also be used in (1). For both CSTI and VSTI, the index values are sensitive either to measured time unit or applied stress levels. The
choice of which time units or stress levels will depend on how sensitive the plants respond to the stress. If we are interested in comparing in the tolerance of a large number of plant species to a stress, a standard exposure time or stress exposure levels should be used to observe changes in plant survival.

In formulas (1) and (2), survival is used to calculate the tolerance indices. However, we can easily calculate the tolerance using growth measurements by a slight modification of the formula. For example, if we are interested in relating the tolerance to the height growth, the following modification can be used for this purpose.

\[
GSTI = \frac{\sum_{i=1}^{P} t_i h_i}{\sum_{i=1}^{P} t_i H_i}
\]

where: GSTI = stress tolerance index based on growth parameter.

\[t_i = \text{time since a stress was applied.}\]
\[h_i = \text{plant height at ith time.}\]
\[H_i = \text{plant height of the unstressed control plants at ith time.}\]
\[P = \text{number of times that growth measurements were taken.}\]

The choice of parameters used in tolerance indices calculations mainly depends on the purpose of the research and the sensitivity of plants to the environmental stress. In some cases, the growth or physiological response parameters are perhaps more sensitive to a stress and are easier to measure.

When survival in the control treatment is not 100 percent, an adjusted ratio might be used to correct the impacts of un-equal base survival. We suggest the survival value be divided by the survival in the control treatment. Then formula (1) or (2) can be applied. The use of tolerance indices have several advantages. The first advantage of using tolerance indices is the creation of a quantitative estimate of tolerance. If we use
standard measurement time intervals and standard levels of stress, we can easily compare the tolerance of different species or genotypes. The second advantage is that we can also use the indices to study the correlation of tolerance in young seedlings to mature plants. Finally it is easy to introduce these indices in quantitative models where stress responses are needed. One thing needs to be noted that the prediction of stress tolerance by such indices is only valid for studies which have conditions similar with those for which the indices are developed. Prediction out of measurement range should be done with caution.
SUMMARY AND CONCLUSIONS

Flooding causes stress on a variety of plant species in natural environments. The impacts of flooding on bottomland forests in the southern United States are well documented (Putnam et al. 1960). The successful management of bottomland forests is greatly dependent on an understanding of flood effects on tree species in these forests, since the composition, structure, and regeneration success of bottomland forests are closely related to the flood conditions (Barrett 1980).

Changes in soil physical and chemical conditions produced by flooding have profound impacts on plants. These effects are observed extensively at the whole plant level, and include morphological changes, physiological changes, growth decline in roots and shoots, and in severe situations, mortality (Teskey and Hinckley 1977). The varied responses of plants are attributed to the species and flood produced environmental factors, such as season, duration, frequency, and depth of flooding (Broadfoot and Williston 1973, Kozlowski 1984). To deal with flood stress, plants either develop avoidance mechanisms, tolerance mechanisms or both. These mechanisms may be expressed as changes in anatomical, morphological, and metabolic aspects of plant life. In general plant tolerance to flooding is closely related with these changes (Chapter One).

Submergence has been defined as the total coverage of plants by water (Setter et al. 1987). Modifications by submergence on the physical surroundings of exposed plants is tremendous compared to those exposed to shallow water flooding. The changes in PPFD, and gas diffusion into and out plants are obvious (Voesenek et al. 1992). The
impacts of the changing environment during submergence on woody plants have received relatively limited attention. The main body of knowledge of submergence effects on wetland tree species comes from research by Hosner (1960), Hosner and Boyce (1962), and Loucks and Keen (1973). Only survival and some morphological changes were recorded in their research (Chapter One).

This dissertation provides a more detailed examination of submergence impacts on three bottomland tree species. Measurements included survival, shoot growth, root growth, and biomass production (Chapter Two). The physiological performances of baldcypress, and Nuttall oak seedlings during a recovery period (the period after water removal from shoots of the seedlings) were also monitored (Chapter Three). To more precisely assess submergence tolerance, two stress indices are proposed. Such indices might also have application to describe the tolerance for other stresses. The justification of such approaches is also supplied (Chapter Four).

One of the most notable effects of submergence was the survival difference among the three tested species. Baldcypress seedlings could survive 30 days of submergence period, while only 17 percent of the Nuttall oak survived 30 days of submergence. No swamp chestnut oak seedlings survived 20 days of submergence (Table 2.01). The survival data indicate that a difference in submergence tolerance existed among the three species.

Evident inhibitory effects of submergence on height and diameter growth of baldcypress seedlings were observed during the submergence period. However, the rapid recovery of shoot growth (both height and diameter) in baldcypress during the recovery period is an evidence of its relative tolerance to submergence. The relative height growth of baldcypress in submerged seedlings was more rapid than that of the control. The results of this study indicate rapid new root initiation and elongation also occurred in baldcypress during the recovery period. Growth responses of both oak
species were similar, and characterized by a very limited increment in root and shoot growth for surviving seedlings. The results seem to indicate baldcypress is well adapted to a short term submergence period. Once the water is removed from shoots, the rapid resumption of shoot and root growth will help baldcypress seedlings. This submergence tolerance and rapid shoot growth after de-submergence is an advantage for them in wetland or frequently flooded habitats. The two oak species would be in a less favorable position to compete on wetland or flood prone sites.

Can the responses of these species to submergence be interpreted by some physiological parameters? The research reported in Chapter Three attempted to supply part of answer to this question. Due to the great variation in responses within treatments and the small sample size, the major physiological parameters did not show many significant differences among treatments. The relationship between growth performance and physiological responses in different treatments was not conclusive based on the current data. The high variability in physiological response may be a result of the lingering effects of stress and variable response rates during recovery. Continued mortality during the recovery period suggests that lingering effects may be large.

Assessment of stress tolerance has practical values and different approaches have been proposed to rank the tolerance of plants to various stresses. The majority of previous tolerance indices currently available have been based on the performance of plants under stress compared with the performance of plants not under stress (Treacy 1984, Taylor and Foy 1985 a, Crawford 1989). Such approaches have not considered the polymorphological characteristics of plant responses to stress. So, previous indices have not done an adequate job of assessing or ranking plant tolerance to a particular stress. In this dissertation, two stress tolerance indices are proposed (Chapter Four). Chronic Stress Tolerance Index (CSTI) considers the plants performance relative to the time that plants are exposed to a particular stress. Variant Stress Tolerance Index
(VSTI) incorporates stress intensity into a stress tolerance index. Both indices yield a value between 0 and 1, and the larger the value is, the more tolerant the plant to a stress. Using first of those indices (CSTI), baldcypress was ranked as the most submergence tolerant species, and Nuttall oak was ranked as an intermediate submergence tolerance species. Swamp chestnut oak was a submergence intolerant species according to the CSTI index. The salinity tolerances of 15 families of baldcypress were ranked by the VSTI index. The VSTI values provided a clear-cut tolerance difference among families. The two indices proposed in Chapter Four supply a quantitative description or means for ranking stress tolerance. The consideration of multiple ranges of stress intensity provide a more precise assessment of stress tolerance. The incorporation of growth and physiological performance into similar stress tolerance assessment indices is also possible.

In summary, baldcypress seedlings in this study were submergence tolerant, and could survive more than 30 days submergence. The rapid recovery of growth in shoot and roots greatly help baldcypress to resist future submergence impacts. Nuttall oak was somewhat submergence tolerant but less capable of surviving 30 days of submergence. In this study, swamp chestnut oak seedlings were incapable of surviving even 20 day submergence. The slow growth recovery of swamp chestnut oak in roots and shoots may create further problems for survival during the period when water is removed from shoots.

The concern about conservation and restoration of bottomland/wetland forest ecosystems has increased in recent years. Forested wetlands are important components of bottomland ecosystems. In the southern United States, only 20 percent forest wetlands of the pre-European settlement remain. Several federal agencies and local state agencies are involved in conservation and restoration of wetland forests. The success of such efforts is greatly dependent on the knowledge of flooding effects on tree
species. The submergence impacts on tree species are less available in the literature. The data in this study provided some basic understanding of survival, growth, and tolerance of three important bottomland tree species subjected to different periods of submergence. However, more studies on other tree species are needed and several areas are worthy of future research. One area of needed study is the study submergence tolerance of different plant organs, such as shoots, roots, and leaves. A second area of viable research includes investigation of biochemical, and physiological properties which are related to tolerance mechanisms. To more precisely indicate stress tolerance, multiple stresses need to be incorporated into stress indices. An increase in submergence tolerance data for a wider variety of bottomland species and incorporation of this data into quantitative stress tolerance indices such as those presented in this dissertation, will enhance restoration efforts.
LITERATURE CITED


VITA

Jian Sun was born in Chongqing, Sichuan province, P.R. China, on November 3, 1961. He completed high school, Chongqing, in June, 1978. Sun entered Beijing Forestry University in September, 1978, where he received a B.S. degree in Forestry and a M.S. degree in Silviculture.

In June, 1990, Sun entered the Graduate School at Louisiana State University for a Ph.D. degree in Tree Ecophysiology.

Sun is currently a candidate for the degree of Ph.D. in Forestry.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Jian Sun

Major Field: Forestry

Title of Dissertation: Submergence Impacts on Selected Wetland/Bottomland Tree Species

Approved:

[Signature]
Major Professor and Chairman

[Signature]
Dean of the Graduate School

EXAMINING COMMITTEE:

[Signature]

[Signature]

[Signature]

Date of Examination: 12-01-1984