EVALUATING FLOOD TOLERANCE MEASURES FOR MISSOURI OAK SPECIES

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by
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The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

EVALUATING FLOOD TOLERANCE MEASURES FOR
MISSOURI OAK SPECIES

Presented by Mark Vose Coggeshall

A candidate for the degree of Doctor of Philosophy

And hereby certify in their opinion it is worthy of acceptance.

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DEDICATION

The love and support received from my entire family was critical to the successful completion of this work. I cannot recall all of the many times that my wife Bettina, lifted me up with her encouraging words during my graduate school experience. None of my success would be possible without her presence in my life. No words can fully express my thanks to her for all that she has done and sacrificed for me. This work is dedicated to her.

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ABSTRACT

The aim of this research was to determine the effects of four flooding treatments on survival of seedlings from 45 seedlots of seven oak species at two sampling dates using logistic analysis, and to quantify growth responses to flooding of seedlings from 27 seedlots of swamp white oak (*Quercus bicolor*). Flooding treatments were initiated at the completion of the first growth flush. Significant species and flood treatment differences were detected at the end of the growing season (15 week post-flood) and again in the following year (45 weeks post-flood). Logistic analysis demonstrated that *Q. bicolor* was the most flood tolerant species, followed by *Q. palustris* and *Q. macrocarpa*. Seedlings of *Q. shumardii*, *Q. rubra*, *Q. alba* and *Q. muehelenbergii* were less flood tolerant based on survival odds ratios at 45 weeks post-flood.

Genetic differences in growth responses to flooding were detected among 27 seedling families of swamp white oak. No significant gains in flood tolerance were achieved using acorns derived from specific seed sources (or stands) along a hydrologic gradient. Flood tolerant swamp white oak families were identified in the “recovery” year following flooding by a flood tolerance index, which integrated four growth response variables. Of these four variables, the total number of elongating shoots and total leaf number after an over wintering flush were most highly correlated with flood tolerance.

CHAPTER 1

INTRODUCTION

From 1993 to 2005, bottomland hardwood restoration work has been conducted on an estimated 160,000 to 182,000 ha of former agricultural cropland in the Lower Mississippi Alluvial Valley (LMAV) using a combination of direct seeding and seedling planting practices (Lockhart et al., 2003). In addition, similar afforestation efforts have been targeted along the Missouri and Mississippi Rivers in Missouri, following the devastating floods of 1993 and 1995 (Kabrick et al., 2007). In spite of this significant focus on hardwood restoration, particularly for former bottomland hardwood sites in the southern U.S. (Gardiner et al., 2002), widespread planting success has remained elusive (Stanturf et al., 2001; Allen, 1997). This lack of understanding of how to predict success on such planting sites is indicative of their complexity, especially in terms of their hydrology. Highly variable spatial and/or temporal flooding conditions have resulted in different survivorship rates for a range of hardwood tree species (Hodges, 1997).

In a review of current bottomland afforestation practices in the southern U.S., Stanturf et al. (2003) listed criteria that ensure improved planting success including a focus on seedling stock size and quality. Further, these authors emphasized the need for protocols on the of transfer “well-adapted genetic material capable of surviving in potentially flood prone sites”. Similarly, Connor et al. (1998) stated that use of maladapted planting stock was a potential cause of poor planting success on bottomland sites. To date, the potential contribution of maladapted seed sources to plantation failures on flood prone sites has not been a focus for land managers in the Midwestern U.S. (Coggeshall et al., 2007). However, based on previous research, significant levels of genetic variation for flood tolerance appear to exist within a range of native oak species commonly used in bottomland reforestation programs in both the LMAV and Midwestern U.S. (Coggeshall et al., 2004; Coggeshall et al., 2007; Coggeshall and Van Sambeek, 2008).

Some physiological and/or morphological adaptations utilized by temperate North American oak species to accommodate flooding include the use of stored carbohydrate reserves during flooding and/or the development of morphological adaptations, such as hypertrophied lenticels, aerenchyma and adventitious roots. The majority of flooding research conducted with oaks has been based on small scale, greenhouse trials using non-source identified seedlings.

Recently, research has focused on determining the genetic basis for flood (water-logging) tolerance within *Quercus robur* L., a major European oak species. Parelle et al. (2007) tentatively identified five quantitative trait loci (QTL) that were associated with specific morphological traits induced by flooding. The focus of the present research is to quantify the *intraspecific genetic responses* of planted seedlings to controlled flood events for seven North American oak species including: white oak (*Q. alba* L.), swamp white oak (*Q. bicolor* Willd.), bur oak (*Q. macrocarpa* Michx.), chinkapin oak (*Q. muehlenbergii* Engelm.), pin oak (*Q. palustris* Muenchh.), northern red oak (*Q. rubra* L.) and shumard oak (*Q. shumardii* Buckl.).

The specific objectives of this research were: 1) to determine the effects of four flooding treatments on the survival of seedlings from 45 seedlots of seven oak species over two sampling dates using logistic analysis and 2) to quantify the intraspecific variation in growth responses among seedlings from 27 seedlots of swamp white oak.

CHAPTER 2

LITERATURE REVIEW

THE GENUS *QUERCUS*

The oaks, members of the genus *Quercus*, are one of the most ecologically important groups of trees in the world (Burns and Honkala, 1990). Approximately 400 species, primarily trees and tall shrubs, are included in the genus. Their distribution is mainly confined to the northern hemisphere with 90 different species in North America (Nixon, 1997). Of these, 43 species grow east of the 100° meridian (Miller and Lamb, 1985). At least 20 different oak species are native to Missouri (Kurz, 2003), and, of these, nine are found on bottomland sites in the state (Steyermark, 1974).

Oaks are a dominant component of the forest landscapes in the Midwestern U.S. and valued for their high quality wood products as well as food and cover for a number of wildlife species. Oak acorns are an important part of the diet consumed by 49 different species of birds and mammals in the Eastern hardwood forests (Miller and Lamb, 1985). Several native oak species are also prized as ornamental trees in urban landscape settings (Dirr, 1998), and a number of species are commonly found in bottomland sites that are prone to flooding (Hook, 1984).

Many tree species are capable of growing on an array of sites within their native ranges (Battaglia et al., 2004). Some species exhibit wide amplitude in terms of their capacity to occupy a range of positions along a hydrologic gradient. The presence or absence of a particular tree species in a bottomland hardwood forest is primarily dependent upon soil moisture gradients, stream deposition patterns, and flooding season and duration (Hodges, 1997) as well as seed size and dispersal mechanisms (Battaglia et al., 2004). These bottomland forests are extremely productive in terms of wood productivity and wildlife diversity (Connor, 1994; Clawson et al., 2001; Twedt and Wilson, 2002). Furthermore, they function as riparian buffers, which provide significant environmental benefits such as improved water quality, stream channel stabilization and improved wildlife habitat (Schultz et al., 2000).

FLOODING EFFECTS ON SOILS

When a soil is flooded, a series of physical and chemical changes occur that can influence plant growth processes. The magnitude of these changes is influenced by soil microbial activity and the length and depth of flooding. During flooding, gas-filled soil pores are replaced with water, resulting in the elimination soil oxygen, except within a few millimeters at the soil-water interface (Kozlowski, 1997). In non-flooded soils, oxygen and carbon dioxide, as well as other gasses, are maintained in the soil through gas diffusion. Upon flooding, this diffusion process ceases and gas transport is replaced by molecular diffusion from the air through the flood water into the soil profile. This type of diffusion is $\approx 10^4$ times slower and less efficient than through air, resulting in a restricted oxygen flow into the soil (Ponnamperuma, 1984). Molecular diffusion rates are further decreased with increased water depth and/or reduced rates of water flow. As oxygen from the air is depleted, it is also consumed by plant roots and soil microorganisms which depend on aerobic respiration. Subsequently, aerobic soil microbes are rapidly replaced in flooded soils by anaerobic bacteria, which scavenge essentially all available soil oxygen (Kozlowski, 2002). As a consequence, soil oxygen is consumed within a few hours following flooding, except at the soil surface, which remains somewhat oxidized through direct contact with flood waters and the maintenance of aerobic bacteria and algae. These organisms colonize flooded soils to a depth of 1 centimeter (Ponnamperuma, 1984). Below this surface layer, soil oxygen is rapidly consumed through aerobic respiration. Anaerobes, especially bacteria, utilize various substrates for respiration During flooding, anaerobic respiration by-products (methane, acetic and butyric acid, and ethylene) can become toxic within the soil profile. The concentration of these by-products is dependent upon soil temperatures and the availability of carbon and other specific mineral substrates required for anaerobic respiration (Drew, 1990).

The effects of flooding on soil conditions can be quantified using soil redox potential (Eh), which is used as an indicator of the severity of the flooding on a number of soil processes. Redox potential is a measure of the tendency to accept or donate electrons in a soil. It is normally measured in millivolts and standard values can range from -300 to +700 mV. Well aerated soils are > 400 mV, while non-aerated soils are < 350 mV (Pezeshki, 2001). Eh values can range as low as -250 to -300 mV in waterlogged soils (DeLaune et al., 1998). Oxygen is a strong oxidizer, since it accepts electrons from a number of different elements. In non-flooded soils, aerobic organisms oxidize organic carbon sources for energy. An oxidized soil readily accepts electrons, while a reduced soil supplies electrons.

Specific chemical reactions can be expected to occur at specific redox levels. However, it is important to recognize that reactions shift in response to a change in soil pH. As soil pH increases, Eh values decrease. For example, the reduction of FeOOH to Fe^{2+} occurs at 65 mV in a soil with 4.0 pH, while the same reaction would shift to 25 mV in a soil with 6.0 pH (Brady and Weil, 2002). The slope of this downward shift will be greater or lesser depending upon the specific reaction. Therefore, it is important to record soil pH at the same time soil redox is determined (Pezeshki, 1991). Such reduced soil Eh values are significantly correlated with both reduced plant gas exchange g_s and reduced net photosynthetic rates P_N in flooded oak seedlings (Anderson and Pezeshki, 1999).

In flooded soil profiles, the conversion of organic nitrogen to inorganic forms (ammonification) ends with ammonium (NH_4^+) due to a lack of oxygen, which is needed to ultimately convert ammonium to nitrate (NO_3^-). Any nitrate that is present within a soil at the onset of flooding will become highly unstable and is ultimately lost as either NO or N_2 through denitrification. The rate of denitrification is dependent on the flooding interval, soil organic matter content and soil temperature. High soil temperatures, alternating flooding patterns and high levels of soil organic matter will increase denitrification rates (Ponnamperuma, 1984). For ammonium, some will become immobilized due to chemical fixation within the flooded soil, depending on pH and soil texture. In addition, some ammonium is also immobilized by anaerobic soil bacteria, especially at the onset of flooding. Also, nitrogen can be lost from a flooded soil through volatilization. Finally, some N_2 is fixed in flooded soils in the form of ammonium by blue-green algae and/or anaerobic bacteria, depending upon the soil pH and organic matter content (Ponnamperuma, 1984).

FLOODING EFFECTS ON PLANTS

The response of a plant to flooding has been described as "simultaneous and complex" (Pezeshki and Chambers, 1985). Higher plants are dependent upon adequate supplies of oxygen to maintain normal growth and reproductive functionality. As a result, they have developed a number of adaptations that facilitate the uptake and internal distribution of oxygen, including leaf stomata and a high leaf surface to mass ratio. In addition, intercellular spaces allow for the distribution of oxygen within the plant (Vartapetian and Jackson, 1997). Also, as a result of photosynthesis, a limited supply of oxygen is produced internally during daylight hours. Oxygen exchange between the soil and air is dramatically disrupted as a result of soil flooding. If the supply of soil oxygen becomes deficient (hypoxia), or completely absent (anoxia) due to flooding, plant root systems are rapidly compromised, leading to disruption of such oxygen-dependent processes as photosynthesis and subsequent carbon assimilation. Also, functional relationships between root and stem organs become compromised over time. While it is possible to quantify the levels of anaerobic respiration that are triggered by flooding, such rates do not explain why roots can survive anoxic conditions for more than a few hours (Vartapetian and Jackson, 1997).

Flood tolerance can differ depending upon plant age, and both among and within species (Kozlowski, 1997). Also, the season of the year and internal carbohydrate reserve status will influence survival rates in response to flooding (Crawford and Braendle, 1996). McManmon and Crawford (1971) proposed a "metabolic theory", which stated that flooding tolerance in plants was based on the avoidance of alcohol dehydrogenase (ADH) production. ADH production initiates the alcoholic fermentation process, leading to an accumulation of ethylene which triggers a suite of hormonal changes within the plant. These changes have been associated with the formation of arenchyma and adventitious roots in certain wetland plants (Pierik, et al., 2007).

Some flood tolerant plants produce high levels of non-toxic compounds such as malate as a result of the fermentation process (Crawford, 2003). In comparison, non-flood adapted plants exhibited the tendency to rapidly produce high levels of ADH, with a concomitant increase in alcohol fermentation rates and subsequent ethylene production, leading to cell death. Ethylene production has also been linked to several other flood-induced plant responses, including premature leaf abscission and formation of hypertrophied lenticels and adventitious roots (Kozlowski, 2002).

Vartapetian (2006) reported that the roots of flood-prone plant species did not express a hypotolerance to the products of alcoholic fermentation. Rather, they exhibited a hypersensitive reaction. He concluded that the root systems of such species actually expressed an "apparent tolerance" to flooding, rather than true tolerance. Such tolerance was dependent upon the development of intercellular aerenchyma in the root systems of flood-prone species. This facilitated oxygen transport from the aerated shoots, which enabled the maintenance of aerobic respiration in the root system of flooded plants through oxidation of the rhizosphere. Rhizosphere oxidation occurs when oxygen is secreted into the adjacent flooded soil profile, leading to a detoxification of a number of potentially lethal elements such as Fe^{2+} and Mn^{2+} (Ponnamperuma, 1984). Roots of wetland plants cannot react to flooding through the production of even limited anaerobic respiration pathways. Rather, they are solely dependent upon the production of arenchyma and/or adventitious roots near the air-water interface to facilitate the long distance oxygen transport to the roots. In contrast, plant species that are exposed to occasional flooding have the capacity to develop limited anaerobic respiration functionality.

Vartapetian (2006) stated that "true tolerance" to flooding involves the development of altered protein synthesis and energy metabolism pathways in plants. In many species, anaerobic protein synthesis is initiated during soil hypoxia, not anoxia (Drew et al., 1994). This phenomenon, "hypoxic acclimation" (Andrews, 1997) results in an increase in cell tolerance to subsequent soil anoxia. This transition from aerobic to anaerobic respiration occurs within several hours or up to two days, depending upon the plant species involved (Drew, 1992). Other responses to soil hypoxia may include development of arenchyma, hypertrophied lenticels, adventitious rooting and modification of intracellular pH. In addition, true flood tolerance is not defined by the capacity of a plant to avoid poisoning from reduced, toxic soil products or the lack of oxygen. Rather, tolerance to flooding requires metabolism and utilization of stored carbohydrates, such as starch. The demand for stored carbohydrates in flooded plants is based on the difference in production of energy equivalents (ATPs) via alcoholic fermentation compared to respiration (Kreuzwieser et al. 2004). Through the avoidance of toxic soil products, increasing carbohydrate consumption, and a reduction in energy-consuming processes (i.e. root growth), fermentation can be maintained for extended time periods and thus allow the plant to survive hypoxic and/or anoxic conditions (Vartapetian, 2006). However, such changes in energy metabolism pathways provide only a short term alternative to aerobic respiration. Long-term flood tolerance requires additional morphological adaptations (e.g. arenchyma) to avoid the negative consequences associated with soil anoxia (Vartapetian and Jackson, 1997).

Plant recovery from soil anoxia is dependent upon the length of exposure to flooding and also air temperature (Crawford and Braendle, 1996). Extended anoxia coupled with high temperatures results in “oxidative stress”, which is caused by the oxidation of accumulated metabolites following flooding (Vartapetian, 2006). Plants susceptible to such post-anoxic damage are called reactive oxygen species, or ROS (Crawford, 2003). In ROS plants, cell membrane damage results from the transfer of the electrons accumulated as a result of cell respiration under oxygen deficiency to molecular oxygen. This electron transfer leads to the production of several products including acetaldehyde, which is rapidly oxidized by hydrogen peroxide and catalase. Acetaldehyde damages plant cells by denaturing proteins and nucleic acids, and attacking unsaturated fatty acids associated with cell walls. Plants tolerant of this oxidative stress neutralize these free radicals through the production of antioxidants, such as ascorbic acid and other phenolic compounds (Blokhina et al., 2003).

A number of responses are elicited in plants by flooding and no single mechanism ensures long term survival post-flood. This suite of changes, called a "stress resistance syndrome" (Chapin et al., 1993), involves altered hormonal levels, including increased levels of foliar abscisic acid (ABA). This hormonal response leads to decreased root hydraulic conductance and tissue turgor. In addition, a lower demand for carbon results from a lack of new leaf growth in response to elevated ABA levels. Lower carbon demand results in an increase in carbohydrate accumulation, leading to decreased photosynthesis to match the lower plant demand for carbohydrates. Kreuzweiser et al. (2004) reported that as soil oxygen levels decrease, flooded plants switch from respiration to lactic acid production, leading to an acidification of the cell cytoplasm. Once a critical pH threshold was reached, lactic fermentation ceased due to lactate dehydrogenase (LDH) inhibition. Alcoholic fermentation was subsequently initiated in response to the production of ADH and other enzymes in response to the lower cytoplasmic pH levels.

Kozlowski (2002) described several major physiological responses to flooding. At the onset of flooding, roots begin to respire aerobically and anaerobically. However, the products derived from anaerobic respiration become inadequate to support prolonged plant growth. Photosynthesis is also inhibited due to rapid stomatal closure and decreased carbon dioxide diffusion into the leaves. In the long run, this decrease in photosynthetic rate results in a reduction in leaf chlorophyll, which leads to a corresponding decrease in translocation of photosynthetic products to apical meristems. Additionally, plant mineral nutrition is altered in response to flooding. Mineral absorption requires metabolic energy, which is inadequate under anaerobic respiration conditions in flooded soils, especially for flood-intolerant plants.

As a consequence, both total nitrogen content and nitrogen concentration are reduced in flood intolerant plant tissues due to a limited capacity to absorb nitrate and /or ammonium, which become limited in flooded soils (Kreuzwieser et al., 2002). In addition to nitrogen, absorption rates of phosphorous and potassium are also diminished in flooded soils. This reduction in macronutrient absorption rates has been associated with a lack of mycorrhizae, which are highly aerobic and are not readily found in flooded soils (Kozlowski, 2002).

Similarly, Crawford and Braendle (1996) outlined responses that coincide with flooding stress. As previously mentioned, flooding leads to at least four different consequences including: an increase in soil microbial pathogens, altered plant hormonal distributions, production of reduced (and potentially toxic) ions such as Fe^{2+} and Mn^{2+}, and oxygen deprivation to plant organs, especially roots. Within the category of oxygen deprivation, the authors list three additional consequences: post-flood developmental injuries due to root system dieback, post-anoxia cell wall damage resulting from oxidative stress reactions, and anoxic injury. Categories of anoxic injury include hormonal dysfunction, accumulation of toxic ions, reduction in ATP production levels, and a depletion of carbohydrate reserves.

SEED SOURCE STUDIES

There has been limited research focused on intraspecific patterns within bottomland hardwood tree species in response to flooding. Significant differences in growth were detected among red maple (*Acer rubrum* L.) seedlots when exposed to controlled flooding treatments (Baurle et al., 2003). Mesic-origin seedlings suffered greater growth losses due to flooding than seedlings from more flood prone (hydric) provenances. Similarly, Anella and Whitlow (2000) detected seed source differences in photosynthetic recovery rates for wet vs.

dry site red maple seedlings three months after flooding. Will et al. (1995) reported a differential response to flooding among red maple seedlots derived from a range of provenances across a hydrological gradient in Virginia. However, they concluded that there was no true ecotypic variation in flood tolerance for red maple; rather, the variation in this trait was due to phenotypic plasticity in the variables they chose to measure. However, as pointed out by Pigliucci (2005), this lack of a significant genotype x environment interaction may actually reflect a common response across all populations to flooding that has no direct (mechanistic) analog on an individual tree basis. Others (de Kroon et al., 2005) suggested that phenotypic plasticity should not be based on a whole-plant response, but on a series of morphological responses of individual meristems.

Keeley (1979) investigated the effects of flooding on a series of black gum (*Nyssa sylvatica* Marsh.) seed sources collected from various hydrologic positions. After a short term flood, root systems of upland seed sources deteriorated rapidly, while swamp and floodplain seed sources successfully regenerated new roots. Although increased ethanol production was associated with the flooding treatment across all seed sources, it appeared that the floodplain and swamp provenances adapted to elevated ethanol production during the flood while the upland seed source could not. Seedlings of upland seed sources used in this study had greater root biomass and higher root respiration rates than seedlings from floodplain and swamp seed sources. In contrast, trees adapted to flood-prone conditions allocated less biomass to roots and transported oxygen to the roots via hypertrophied lenticels and/or newly developed adventitious roots. Similar seed source-related, morphological adaptations to restricted oxygen in the root zone have also been reported in other hardwood (Cao and Connor, 1999; Smit 1988) and conifer species (Topa and McLeod, 1986). However, such seed source investigations have not been conducted for any oak species in North America with the exception of the recent investigations by Coggeshall et al. (2004; 2007), Walsh et al. (2007) and Coggeshall and Van Sambeek (2008).

FLOOD TOLERANCE RATINGS FOR OAK SPECIES

Responses of oak species to flooding, or waterlogging, have been described by several authors (Allen et al., 2001; Whitlow and Harris, 1979; Hook, 1984; Sykes, 1993; Kabrick and Dey, 2001). Variation in flood tolerance rankings are influenced by plant age and season of flooding (Kozlowski, 1997), as well as flow rate (Kabrick et al., 2007) and depth (Hook, 1984). Seedlings are more susceptible to flooding in low soil redox conditions than mature trees (Pezeshki et al., 1999). Further, flood tolerance on a species level was defined by Hook and Brown (1973) as the difference in secondary root mortality rates for newly planted seedlings.

Kabrick et al. (2007) investigated the flood tolerance of several hardwood species in an outdoor flood tolerance laboratory as described by Van Sambeek et al. (2007). This study compared survival, shoot growth (or dieback) and overall leaf health of flooded seedlings and non-flooded controls. Similarly, Coggeshall et al. (2004) evaluated cherrybark oak (*Q. pagoda* Raf.), water oak (*Q. nigra* L.) and willow oak (*Q. phellos* L.) for their flood tolerance by comparing survival, number of new shoots and cumulative shoot length of flooded seedlings versus their non-flooded controls. Willow oak seedlings had better survival, greater new shoot length and less taproot dieback than water oak or cherrybark oak seedlings when flooded at spring budbreak. In a later study, Coggeshall et al. (2007) used survival, number of shoots, and their cumulative length to develop a “flood tolerance index” to assess family (or seedlot) differences in flood tolerance. Within each species, flood tolerance index values were determined by multiplying three ratios composed of observed divided by maximum values for each trait for each family (survival and total number and cumulative length of new shoots). Differences among families of three oak species were detected for all variables. This suggests that flood tolerance has a genetic basis and that positive gains in both field survival and growth could be realized through selection of more flood tolerant families of these species for planting on frequently flooded sites.

Hook (1984) defined tolerance to flooding as the ability of a species to tolerate soil inundation (waterlogging) and/or partial/complete inundation by flood waters during the growing season. This definition is species-based and includes seedlings to mature trees. Kabrick and Dey (2001) categorized flood tolerance from 1 (intolerant = plants that do not survive flooding events during the growing season) to 4 (very tolerant = plants survived over two or more growing seasons). Similarly, Allen et al. (2001) assigned flood tolerance rankings based on four categories. They further defined these categories based on the morphological adaptations of tree species in response to flooding (hypertrophied lenticels). Flood tolerant trees were capable of producing adaptations while intolerant species did not. In contrast, Sykes (1993) used five flood tolerance rankings from 1 (least tolerant = species that survived waterlogged soil for a few days) to 5 (most tolerant = species survived continual soil waterlogging over multiple years, except for short durations of drying due to drought).

SEEDLING SURVIVAL

Angelov et al. (1996) reported that long term survival of oak seedlings was dependent upon re-foliation following the flood event and before winter. Neither swamp chestnut oak (*Q. michauxii* Nutt.) nor cherrybark oak survived a two-year continuous flood. In contrast, swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.), sweetgum (*Liquidambar* *styraciflua* L.) and swamp chestnut oak had 90-100% survival when flooded during the dormant season, followed by a three-month, non-flood treatment during the growing season (June through October). The survival rate for the cherrybark oak seedlings was only 49%. Leaves of the surviving oak seedlings that formed during the dry period were 3 to 4 times larger than previously-formed “flood” leaves. These “dry” leaves had higher photosynthetic rates than those formed either during the flood or on non-flooded control seedlings. The authors concluded that the development of new leaves during the dry season was necessary to replenish stored starch reserves before to winter. Similarly, Gravatt and Kirby (1998) showed that flood tolerant green ash (*Fraxinus pennsylvanica* Marsh.) and water tupelo had higher pre-flood root starch levels than non flood tolerant white oak (*Q. alba* L.) seedlings.

Frye and Grosse (1992) assessed the survival of 22 deciduous tree species during the growing season following the year of flooding. In their study, flooded English oak (*Q. robur* L.) and pin oak (*Q. palustris* Muenchh.) seedling survival rates exceeded 90% in the year following flooding. In contrast, sessile oak (*Q. pretraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.), had 45 and 10% survival, respectively, in the year following a 120 day flood during the growing season.

CHAPTER 3

LOGISTIC ANALYSIS OF POST-FLOOD SURVIVAL FOR SEVEN MISSOURI OAK SPECIES

INTRODUCTION

In a recent review of artificial regeneration methods for oak (*Quercus* L.) species in the eastern U.S., Dey et al. (2008) listed some challenges associated with the successful establishment of newly planted oak seedlings on flood prone sites. These included problems with micro-site heterogeneity associated with poor internal drainage, elevated soil pH levels and irregular flooding frequency. Responses of different oak species to flooding, or waterlogging, have been reported by several authors (Hook, 1984; Sykes, 1993; Kabrick and Dey, 2001; Allen et al., 2001; Whitlow and Harris, 1979). Variation in flood tolerance rankings are dependent on specific the parameters evaluated, such as plant age, season of flooding (Kozlowski, 1997; Vreugdenhil et al., 2006), as well as water flow rate (Kabrick et al., 2007), and depth (Hook, 1984) . Further, seedlings have been shown to be more susceptible to the flooding consequences resulting from low soil redox conditions than mature trees (Pezeshki et al., 1999).

Kabrick et al. (2007) investigated the flood tolerance of several hardwood species using an outdoor flood tolerance laboratory described by Van Sambeek et al. (2007). In their study, Kabrick et al. (2007) defined flood tolerance as the relative performance of flooded seedlings compared to their non-flooded controls using several criteria, including survival, shoot growth (or dieback) and overall leaf health. Similarly, Coggeshall et al. (2007) evaluated the flood tolerance of three southern oak species comparing survival, number of new shoots and cumulative length of new shoots for flooded seedlings and non-flooded controls.

Hook (1984) defined tolerance to flooding as the ability of a species – including seedlings to mature trees - to tolerate partial flooding or complete inundation during the growing season. Kabrick and Dey (2001) used four definitions to assign species to specific flood tolerance categories ranging from "very tolerant" (survival over two or more growing seasons of flooding) to "intolerant" (lack of capacity to survive any flooding events during the growing season). Similarly, Allen et al. (2001) assigned flood tolerance rankings based on four categories, including the development of morphological adaptations (e.g. hypertrophied lenticels). In contrast, Sykes (1993) ranked flood tolerance from 1 (least tolerant = species that can only survive in waterlogged soil for a few days) to 5 (most tolerant = species that can survive continual soil waterlogging conditions over multiple years, except for short durations of drying due to drought). Since the criteria used to assess flood tolerance can differ based upon which rating scheme is employed, assessments of flood tolerance for different oak species reported in the literature have been inconsistent (Table 3-1).

Effects of flooding on soil conditions can be quantified using several standardized measures. Redox potential (Eh) is one measurement that indicates the severity of the flooding impact on a number of soil processes. It is a measure of the tendency of a soil to accept or donate electrons, which can be used to assess nutrient availability within flooded soils (Unger et al., 2008). It is normally measured in millivolts and standard values can range from -300 to +700 mV. Well aerated (oxic) soils have an Eh value of >414 mV at pH 7, while non-aerated (suboxic) soils range from 120 to 414 mV. Anoxic soils have Eh readings of <120 mV (Essington, 2004). Soil Eh values can range as low as -250 to -300 mV in waterlogged soils (DeLaune et al., 1998).

Table 3-1. Past flood tolerance ratings for seven oak species used in the present study.

		Flood Tolerance Rating[1]			
Species	Name	Kabrick[2] and Dey 2001	Allen[3] et al. 2001	Sykes[4] 1993	Whitlow[5] and Harris 1979
Quercus alba	White Oak	1	1-2	1	1
Q. bicolor	Swamp White Oak	3	3	4	2
Q. macrocarpa	Bur Oak	2	1	4	4
Q. muehlengergii	Chinkapin Oak	--	--	4	4
Q. palustris	Pin Oak	2	3	3	3
Q. rubra	Northern Red Oak	--	--	2	1
Q. shumardii	Shumard Oak	2	2	2	1

[1] Refer to cited authors for specific definitions.
[2] Kabrick and Dey (2001): 1 (intolerant) to 4 (very tolerant).
[3] Allen et al. (2001): 1 (intolerant) to 4 (tolerant).
[4] Sykes (1993): 1 (least tolerant) to 4 (most tolerant).
[5] Whitlow and Harris (1979): 1 (intolerant) to 4 (very tolerant).

Various flooding responses among species have been attributed to morphological, physiological and/or metabolic adaptations (Glenz et al., 2006). Angelov et al. (1996) reported that long term survival of oak seedlings flooded during the growing season was dependent upon re-foliation following the flood event before winter. Angelov et al. (1996) found that neither swamp chestnut oak (*Q. michauxii* Nutt.) nor cherrybark oak (*Q. pagoda* Raf.), which are both considered to be flood intolerant oak species, were capable of surviving a two-year long, continuous flood, in contrast to swamp tupelo (*Nyssa sylvatica* var. *biflora* (Walt.) Sarg.) and sweetgum (*Liquidambar styraciflua* L.). Swamp tupelo, sweetgum and swamp chestnut oak had 90-100% survival when flooded during the dormant season, followed by a three-month, non-flood treatment during the growing season (June through October). The survival rate for the cherrybark oak seedlings was only 49%. For the surviving oak seedlings, leaves formed during the dry period were 3 to 4 times larger than previously-formed "flood" leaves. Also, "dry" leaves had higher photosynthetic rates than leaves formed either during the flood or on non-flooded control seedlings. The authors concluded that subsequent survival of flooded oak seedlings is directly linked to the development of new leaves during the dry season to replenish starch reserves prior to winter. Similarly, Gravatt and Kirby (1998) showed that higher pre-flood root starch levels correlated with higher survival rates in flood tolerant green ash (*Fraxinus pennsylvanica* Marsh.) and water tupelo, in contrast to seedlings of white oak (*Q. alba* L.), which is considered a flood intolerant species (Kabrick and Dey, 2001).

Frye and Grosse (1992) assessed survival rates of 22 deciduous tree species the growing season after flooding. In their study, flooded English oak (*Q. robur* L.) and pin oak (*Q. palustris* Muenchh.) exceeded 90 percent survival in the year following flooding. In contrast, sessile oak (*Q. petraea* (Matt.) Liebl.) and European beech (*Fagus sylvatica* L.), both of which are considered to be flood intolerant species (Glenz, 2006), had 45 and 10% survival rates, respectively, a year following a 120 day flood imposed during June through August. In contrast, Kuβner (2003) reported cumulative mortality rates of 55% for naturally occurring English oak seedlings in response to two dormant season flood events in Germany after three years, with most of this mortality (34%) occurring the year of the flooding event. These results suggest that timing of survival assessment after flooding is important. For many planting scenarios, it would be desirable to estimate the number of seedlings that need to be planted on flood prone sites to achieve management goals, based upon species flood tolerance ratings and desired stocking levels. Currently, there are no such estimates available for sites that are prone to flooding. Stanturf et al. (2001) reported efforts to reforest such sites in the southeastern U.S. by plantings primarily hardwood trees seedlings, including oaks. Many of these plantings have had limited success due to a lack of knowledge of species responses to flooding. Also, inconsistencies in the time of assessing flood tolerance for tree species have contributed to poor estimates of expected success rates of reforestation efforts on flood-prone sites. Therefore, the objective of this study was to assess the flood tolerance of seven oak species by examining the survival responses of newly planted seedlings at the end of the flooding season and in the following year at the completion of the first growth flush.

MATERIALS AND METHODS

ACORN COLLECTION AND SEEDLING PRODUCTION

A total of 44 open pollinated seedlots of seven oak species were collected from 23 stands in six counties in central Missouri in fall 2003. Parent trees were chosen based on the presence of >300 sound acorns. One to five individual seedlots (hereafter termed families) represented each stand. Following collection, acorns were soaked in water for 48 hours to insure imbibition of sound acorns and allow for separation and removal of floaters or insect-damaged seeds. Following floating, a sample of 25 acorns from each seedlot was bisected longitudinally to assess the presence of any undetected disease or insect damage. Seeds in each seedlot were subsequently counted and the numbers of filled, undamaged seeds were calculated based on the previous cut test. Each seedlot was divided into three, equal lots for future sowing into three nursery bed replications. Seeds were maintained in plastic bags at 4.5° C until to sown.

Seedlots were hand sown at the Missouri Department of Conservation George O. White Nursery near Licking (37° 34' N, 91° 53' W) on 5 November 2003. Acorns were hand sown in three nursery bed replications at a uniform seedbed density of 75 viable seeds per m^2 based on previous work conducted by Wichman and Coggeshall (1983). Following sowing, seedbeds were maintained using standard weeding, fertility and irrigation nursery practices throughout the 2004 growing season. Seedlings were lifted at a minimum depth of 20 cm on 15 November 2004 and subsequently stored at 4.5° C. Seedlings were individually tagged and measured for total shoot height and root collar diameter data prior to planting.

FLOOD TREATMENTS

On 15 March 2005, a total of 2713 one-year-old seedlings representing 44 different seedlots of seven native oak species were planted into a multi-channel flood tolerance laboratory (Van Sambeek et al., 2007) located at the University of Missouri Horticulture and Agroforestry Research Center in New Franklin, MO (39° 04' N, 92° 74' W). Treatments included: 1) three weeks flowing water (3F); 2) five weeks flowing water (5F); 3) five weeks stagnant water (5S); and 4) a non-flooded control (NF). Water depths were maintained at

≈15cm for the duration of the study. Flooding treatments commenced on 23 May 2005. By this date, all trees had completed their first growth flush, but had yet to initiate a second flush. During the experiment, 199 mm of additional rainfall fell, with the majority occurring during the fourth week of the five week flooding period, resulting in soil saturation in the non-flooded control channels, as well as the three weeks flooded channels. In addition to natural rainfall, seepage from the adjacent flooded channels may have contributed to this waterlogging condition (Unger et al., 2008). Soil redox measurements were recorded using both automated and manual measurements on a bi-weekly basis during the five weeks flooding period. These readings indicated that anoxic levels were achieved by the end of the third weeks of flooding, with the lowest soil redox reading equaling 58 mV. Subsequently, by week five, redox levels became suboxic (mean = 155mV) (Van Sambeek et al., 2007). Flooded channels were drained on 13 May 2005 (three week treatment) and on 27 June 2005 (five week treatment). Soil Eh values in the flooded channels recovered to pre-flood levels within two weeks after draining (VanSambeek et al., 2007).

DATA COLLECTION

On 12 September 2005, end of season survival (15 weeks post-flood) was determined for all seedlings in the flood channels. Subsequently, on 6 June 2006, (45 weeks post-flood), seedling survival was recorded a second time. The timing of this second data collection date coincided with the completion of the first growth flush in the year following flooding. Dead trees at 15 weeks post-flood were removed from the 45 weeks post-flood dataset. As a result, the longer term impact of flooding stress was evaluated.

STATISTICAL ANALYSES

The experimental design was a split plot with flood treatments as whole plots and species as sub-plots. The four flood treatments were arranged in three randomized complete blocks and both flood treatments and species were considered fixed effects. For each species, a total of 5-7 single tree plots per family were established at random within each channel. Data analyses were conducted using PROC GENMOD (SAS, Cary, NC), which provided an analysis of species and treatment differences in survival rates based on calculated odds ratios (Thomas et al., 2008). Seedling survival data had a binomial distribution and was analyzed using the following logistic linear model which included at least one explanatory variable x and $i = 1,\ldots,$ n individuals:

$$\text{Logit}\ (P_i) = \log\ (P_i\ /\ 1 - P_i) = \alpha + \beta_1 x_{i1} \qquad (1)$$

where P_i is the probability of seedling survival, α is the slope intercept and x and β represent the independent fixed variable of interest and its accompanying unknown coefficient, respectively (Allison, 1999). Due to the unbalanced numbers of live seedlings per family at each assessment date, blocking was ignored and a single "live" tree and a single "dead" tree were added to the dataset for each family within each flood treatment before analysis. The addition of these dummy values provided a uniform expression for each family in each species that facilitated comparisons between species, especially in the case of poor survival and/or fewer planted seedlings representing certain species (Maestre et al., 2005) and assured that no family x treatment combination would have 0 or 100% survival. Survival odds ratios ($= P_i / (1-P_i)$) were determined using the ESTIMATE option of the PROC GENMOD procedure. In this study, an odds ratio compared the probabilities of seedling survival rates between two factors by calculating the antilog (e^x) of the estimate (= Logit P_i) values that represent the difference between two species least square means. Differences between two species survival rates were significant if the chi-square *P* value was <0.05. Percent survival data were calculated in the following manner: % survival = odds ratio/(1+odds ratio). This back-transformation method is preferred when the numbers of observations per species are unbalanced (Thomas et al., 2008).

RESULTS

Numbers of seedlings and families planted in this study with accompanying survival data on a species basis at both the end of the growing season (15 weeks post-flood) and first flush after overwinter (45 weeks post-flood) for seven oak species are presented in Table 3-2. In the upper half of the species matrix, odds ratios compare the 15 weeks post-flood survival performance among all seven species. Relative performance between two species was determined by comparing a species in a given row with an alternate species in the appropriate column. Values presented were calculated as the antilog of the difference between the two least square means for each species and can be interpreted as the likelihood of one species to survive 15 weeks post-flood versus the alternate species. Conversely, the odds ratio indicates the number of seedlings that would need to be planted of the less flood tolerant species for every seedling representing the more flood tolerant species to obtain the same survival rate at 15 weeks post-flood. Chi square values were calculated to determine how likely odds ratios were equal to a 1:1 ratio. For example, swamp white oak seedlings survived 12.69 times as often as white oak seedlings at 15 weeks post-flood. This means that to achieve the same species densities after flooding, land managers would need to plant 12.69 more white oak seedlings than swamp white oak seedlings to achieve the same density.

Alternatively, it could be stated that swamp white oak seedlings were nearly 13 times more likely to survive than white oak.

At 45 weeks post-flood, species comparisons are determined by contrasting a species in a given column with an alternate species in a given row in the bottom half of the species matrix. As in the example above, swamp white oak seedlings were 2.40 times as likely to survive at the end of the 45 week study as were white oaks. However, in this case, the value of 2.40 was not significantly different from a 1:1 ratio based on chi-square, which reflects a combination of both differential survival rates and large disparity in numbers of seedlings planted for both species (Table 3-2).

Relative flood tolerance rankings using odds ratios for all seven oak species were determined over both sampling dates (Table 3-2). Although not statistically different, swamp white oak was nominally more flood tolerant than either pin oak or bur oak based upon odds ratios at 15 weeks post-flood. All three of these species were significantly more flood tolerant than chinkapin oak, shumard oak, northern red oak and white oak. There was no difference in survival rates between chinkapin oak seedlings and shumard oak at the end of 15 weeks. However, chinkapin oak seedlings had greater survival than either northern red oak or white oak during the same evaluation period based on species odds ratios. No species survival differences were detected among shumard oak, northern red oak or white oak when evaluated 15 weeks post-flood.

At 45 weeks post-flood, the relative flood tolerance rankings did not change appreciably, with the exception that chinkapin oak, which along with northern red oak, were less flood tolerant than swamp white oak, with odds ratios of 2.61 and 2.38, respectively (Table 3-2). Pin oak, bur oak and shumard oak and all other species had similar flood tolerance rankings based on survival after completion of the first growth flush following overwintering (45 weeks post-flood).

Species with the greatest numbers of seedlings were swamp white oak (n = 1910) and northern red oak (n = 317) (Table 3-2). For swamp white oak, odds ratios across all four flooding treatments over both sampling dates are presented in Table 3-3. As before, in the upper right half of the table, odds ratios within a given row compares a specific flood treatment effect at 15 weeks post-flood with an alternative (second) flood treatment in a given column. For example, swamp white oak seedlings planted in the 5 week flowing (5F) channels were 7.75 times less likely to survive as the non-flooded control (NF) seedlings. Alternatively, to achieve the same species density 15 weeks post-flood as in the control channels, 7.75 times more seedlings would need to be planted in the 5 weeks flowing (5F) channels. Across all four flood treatments, non-flooded control seedlings had greater survival than those in all flooding treatments ($P<0.0001$). However, 3F seedlings had greater survival than 5S ($P = 0.0351$) and 5F ($P<0.0001$) seedlings. Also, 5S seedlings had greater survival than those in the 5 week flowing (5F) channels ($P = 0.0117$).

At 45 weeks post-flood, odds ratios that compare the overwintering survival rates for swamp white oak among the four flood treatments are presented in the lower left half of Table 3-3. Odds ratios for all three flood treatments differed from the non-flooded control (NF) seedlings and their interpretation follows the same logic as the 15 weeks post-flood results. Odds ratios for the 45 weeks post-flood data indicate more mortality occurred at 45 weeks as compared to that at 15 weeks. Percent survival at 45 weeks post-flood ranged from 69.3% to 83.2% (Table 3-3) and survival in all three flooded treatments were significantly lower than in the non-flooded control treatment ($P<0.0001$). These treatment means reflect differences in over winter survival rates when expressed in terms of odds ratios between

Table 3-2. Odds ratios for seven oak species subjected to controlled flooding to assess species survival in Missouri at 15 or 45 weeks after flooding.[1]

		Odds Ratio - 15 weeks post-flood							
	Species[2]	SWO	PIO	BRO	CHO	SHO	REO	WHO	% Survival 15 weeks
Odds Ratio 45 weeks post-flood	SWO	--	1.16 $^{\mathrm{NS}}$	1.83 $^{\mathrm{NS}}$	4.93 ***	9.52 ***	10.89 ***	12.69 ***	77.5 ***
	PIO	**1.18** $^{\mathrm{NS}}$	--	1.57 $^{\mathrm{NS}}$	4.22 ***	8.16 ***	9.33 ***	10.88 ***	74.7 ***
	BRO	**1.40** $^{\mathrm{NS}}$	**1.19** $^{\mathrm{NS}}$	--	2.69 *	5.20 *	5.95 ***	6.94 ***	65.2 $^{\mathrm{NS}}$
	CHO	**2.61***	**2.20** $^{\mathrm{NS}}$	**1.86** $^{\mathrm{NS}}$	--	1.93 $^{\mathrm{NS}}$	2.21 *	2.57 *	41.3 $^{\mathrm{NS}}$
	SHO	**1.87** $^{\mathrm{NS}}$	**1.58** $^{\mathrm{NS}}$	**1.33** $^{\mathrm{NS}}$	**1.39** $^{\mathrm{NS}}$	--	1.14 $^{\mathrm{NS}}$	1.33 $^{\mathrm{NS}}$	26.6 $^{\mathrm{NS}}$
	REO	**2.38 ***	**3.03** $^{\mathrm{NS}}$	**1.70** $^{\mathrm{NS}}$	**1.09** $^{\mathrm{NS}}$	**1.27** $^{\mathrm{NS}}$	--	1.17 $^{\mathrm{NS}}$	24.1 ***
	WHO	**2.40** $^{\mathrm{NS}}$	**2.02** $^{\mathrm{NS}}$	**1.70** $^{\mathrm{NS}}$	**1.09** $^{\mathrm{NS}}$	**1.27** $^{\mathrm{NS}}$	**1.00** $^{\mathrm{NS}}$	--	21.4 ***
	% survival 45 weeks	75.1 ***	71.8*	66.4 $^{\mathrm{NS}}$	53.7 $^{\mathrm{NS}}$	61.6 $^{\mathrm{NS}}$	57.4 $^{\mathrm{NS}}$	55.5 $^{\mathrm{NS}}$	
	No. families	27	1	3	5	1	5	2	
	No. seedlings	1910	72	78	160	33	317	143	

[1] Relative survival performance between two species at the end of the growing season (15 weeks post-flood) is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates after the first growth flush following overwintering (45 weeks post-flood) (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom left half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05, 0.01, 0.001$, respectively).

[2] Species abbreviations: SWO = swamp white oak (*Quercus bicolor*); PIO = pin oak (*Q. palustris*); BRO = bur oak (*Q. macrocarpa*); CHO = chinkapin oak (*Q. muehlenbergii*); SHO = shumard oak (*Q. shumardii*); REO = northern red oak (*Q. rubra*); WHO = white oak (*Q. alba*).

flooded and non- flooded control seedlings at the end of 45 weeks. Unlike at 15 weeks, there were no differences in survival rates at 45 weeks post-flood among the three flood treatments.

Odds ratios of northern red oak seedling survival rates after flooding for two sampling dates are given in Table 3-4. While these results generally reflect the same pattern as the swamp white oak data in Table 3-3, the magnitude of the odds ratios for seedling survival between the three flooded treatments and non-flooded control is much larger (5F = 7.75 for swamp white oak vs. 5F = 25.52 for northern red oak at 15 weeks post-flood). These increased odds ratios across all flood treatments and both sampling dates confirm the conclusion by other authors (e.g. Sykes, 1993) that northern red oak seedlings are less flood tolerant than those of swamp white oak (Table 3-2). Non-flooded control seedlings had greater survival than the other three flood treatments (P<0.0001). Survival rates among the three flooded treatments were similar at 15 weeks. For overwintering survival (45 weeks post-flood), odds ratios for all three flood treatments differed from the non-flooded (control) treatment.

Percent survival treatment means were significantly different at 45 weeks post-flood for northern red oak. Across all four treatments, non-flooded (control) seedlings had greater survival than all other flood treatments (*P*<0.0001). Seedlings in the 3 week flowing (3F) channels had greater survival than the 5 weeks stagnant (5S) channels (*P* =0.0407), as was the case with 5 week flowing (5F) channels in comparison to the 5 weeks stagnant (5S) channels (*P* =0.0478). Seedling survival in the 3 week (3F) and 5 week flowing (5F) treatments was similar (*P* =0.4610). Again, these treatment means represent seedlings that survived during the 15 to 45 weeks post-flood timeline, and were used to reflect differences

Table 3-3. Survival odds ratios for 1910 swamp white oak (*Q. bicolor* Willd.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	4.52 ***	5.86 ***	7.75 ***	92.9 ***
Odds Ratio 45 weeks post-flood	3F	**2.04 *****	--	1.29 *	1.71 ***	74.3 ***
	5S	**2.19 *****	**1.07** $^{\text{NS}}$	--	1.32 *	69.0 ***
	5F	**1.60 *****	**1.27** $^{\text{NS}}$	**1.36** $^{\text{NS}}$	--	62.8 ***
	% survival 45 weeks	83.2 ***	70.8 ***	69.3 ***	75.4 ***	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05, 0.01, 0.001$, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

Table 3-4. Survival odds ratios for 317 northern red oak (*Q. rubra* L.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	15.54 ***	17.71 ***	25.52 ***	74.4 ***
Odds Ratio 45 weeks post-flood	3 F	**2.92 ***	--	1.14 $^{\mathrm{NS}}$	1.64 $^{\mathrm{NS}}$	15.7 ***
	5S	**7.67 *****	**2.62 $^{\mathrm{NS}}$**	--	1.44 *	14.1 ***
	5F	**3.66 *****	**1.25 $^{\mathrm{NS}}$**	**2.09 $^{\mathrm{NS}}$**	--	10.2 ***
	% survival 45 weeks	79.2 ***	56.5 $^{\mathrm{NS}}$	33.1 $^{\mathrm{NS}}$	50.9 $^{\mathrm{NS}}$	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05, 0.01, 0.001$, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

in survival among treatment means when expressed in terms of odds ratios following completion of the first flush in the year following flooding (45 weeks post-flood).

The opportunity to examine the effect of the four flooding treatments on survival rates for individual species was limited due to the small numbers of seedlings planted and/or the extremely poor survival rates for some species included in this study. Thus, results for pin oak, bur oak, chinkapin oak, shumard oak and white oak survival by flood treatment at the end of the growing season and after completion of the first flush after overwintering are presented in the Appendix.

DISCUSSION

Timing of flood assessment is important. If assessed too early, reforestation efforts will likely result in underestimating the numbers of planted seedlings needed to achieve management objectives. Such information is critical for those land managers responsible for the design of large-scale afforestation/reforestation planting programs on flood-prone sites such as riparian zones. Further, studies designed to elucidate patterns of species-specific mortality due to flooding may ultimately clarify environmental factors that affect seedling survival rates, leading to altered species composition patterns over time (Kuβner, 2003).

In the present study, survival differed for non-flooded and flooded seedlings at 45 weeks post-flood, which clearly demonstrated the longer term impact of flooding on survival rates in the year following flooding. Angelov et al. (1996) reported that over winter oak seedling mortality due to flooding was primarily the result of a lack of ability to maintain stored carbohydrate resources to sustain future vegetative growth. In their study, Angelov et al. (1996) observed that oak seedling mortality was associated with growth phases including spring stem elongation (which correlated with flood timing in the present study), summer stem elongation, and during winter dormancy. Likewise, Frye and Grosse (1992) reported second year responses to flooding stress for 22 deciduous tree species exposed to a 17 week flood during the growing season. Flood intolerant species, such as European beech and sessile oak, exhibited greater mortality in the second year in comparison to more flood tolerant species such as English oak. In the present study, similar trends in mortality were observed in both swamp white oak (Table 3-3) and northern red oak (Table 3-4) when odds ratios after overwintering for the three flooded treatments are compared to the non-flooded control treatment. Odds ratios for all three flooding treatments differed from the non-flooded (control) treatment, which demonstrates that many of the flooded northern red oak seedlings failed to fully recover before winter. Therefore, it is recommended that survival assessments should be deferred to the year following flooding. While the number of planted seedlings of the remaining five species included in this study were quite limited (Table 3-2), the same conclusion can be drawn, namely, that survival assessments of newly planted oaks seedlings will be more accurate if conducted in the year following flooding (data not shown).

The ability of a species to survive anoxic soil conditions is primarily a response mechanism based on a number of morphological and physiological adaptations that can be influenced by other spatial and temporal abiotic features including flooding flow and depth, duration and timing (Glenz et al., 2006). In the present study, anoxic conditions based on soil redox Eh values were detected by week 3 in the flooded channels and slowly increased to suboxic levels by week 5 before returning to oxic levels 2 weeks after drainage (Unger et al., 2008).

Coupled with the lack of oxygen in flooded soils, the development (growth) stage when flooding occurs can be of major importance, especially for oak seedlings, which exhibit an episodic pattern of growth. For example, English oak seedlings, which are considered to be very flood tolerant (Glenz et al., 2006), exhibit different survival responses depending upon the season of flooding. Essentially no mortality occurred when English oak seedlings were exposed to a 120 day flood late in the growing season (Kuhne and Bartsch, 2007). In contrast, >50% mortality rates have been reported for this species when flooded during the growing season (Blom, 1999; Vreugdenhil et al., 2006). In the present study, all flood treatments were initiated at the completion of the first growth flush. This timing coincides with the basipetal transport of up to 90% of available photosynthates from first flush leaves to the stem and roots (Dickson et al., 2000). Thus, how oak seedlings survive the effects of flooding at this critical growth period was considered an important component of defining relative flood tolerances for the species included in this study.

Results of other flood tolerance evaluations of oak seedlings using the flood tolerance laboratory have been reported by Kabrick et al. (2007) and Coggeshall et al. (2007). Seedling survival was assessed at the end of the growing season in which the flood treatments were imposed, which is equivalent to survival results obtained at 15 weeks post-flood in the present study. During the 2004 growing season, Kabrick et al. (2007) assessed the flood tolerance of three oak species (swamp white oak, pin oak, bur oak) that were also evaluated during the 2005 growing season in the present study. For these three species, survival rankings were similar in both studies. Swamp white oak was more flood tolerant than pin oak, followed by bur oak, based upon percent survival data by Kabrick et al. (2007) and odds ratios for all three species in the present study (Table 3-2). Swamp white oak seedling survival rates equaled 99% across all flood treatments in the Kabrick et al. (2007) study, but ranged from 62.8 to 92.9% in the present study (Table 3-3). This temporal variation in survival may be attributed to different temperature and rainfall patterns during the two growing seasons, and the genetic origins of the seedlings evaluated. Kabrick et al. (2007) evaluated non-source identified 1-0 bare root seedlings from the Missouri

Department of Conservation, while in the present study, all swamp white oak seedlings were derived from upland and bottomland seed sources.

The assessment of flood tolerances for tree species that will be used in future reforestation/afforestation programs is of critical importance to insure long-term success. Examples can be found in the literature that document poor survival rates across a range of planting sites and species (e.g. Stanturf et al., 2001, among others). Furthermore, as demonstrated in the present study, it is important to conduct such an assessment over more than one growing season to insure accuracy.

The use of odds ratios provided an evaluation tool that can be used when making decisions on deploying specific species in adequate numbers across flood prone sites. The value of this evaluation tool, as compared to percent seedling survival, is that odds ratios incorporate results obtained from the first and second growing season following flooding. This timing has been shown to be a more accurate measure of oak seedling flood tolerance for both tolerant (swamp white oak) and intolerant species (northern red oak). While this odds ratio method provides an assessment of survival in the second year after flooding, longer term studies may be needed to evaluate reforestation efforts over time.

CHAPTER 4

SENSITIVITY ANALYSIS OF FLOOD TOLERANCE FOR SWAMP WHITE OAK SEEDLINGS

INTRODUCTION

Many tree species are capable of growing over an array of sites within their native ranges (Battaglia et al., 2004). Some species exhibit wide amplitude in their capacity to occupy a range of positions along a hydrologic gradient. The presence or absence of a particular tree species in a bottomland hardwood forest is primarily dependent upon soil moisture gradients, stream deposition patterns, and season and duration of flooding (Hodges, 1997), and seed size and dispersal mechanisms (Battaglia et al., 2004). Bottomland forests are extremely productive in terms of wood growth and wildlife diversity (Connor, 1994; Clawson et al., 2001; Twedt and Wilson, 2002). Furthermore, they function as riparian buffers, which provide numerous environmental benefits in terms of improved water quality, stream channel stabilization and improved wildlife habitat (Schultz et al., 2000).

Beginning in the mid-1970s, an estimated 117,000 hectares of flood-prone forests were lost each year in the U.S. due to shifting agricultural land-use patterns (Dahl and Johnson, 1991). More recently restoration of a portion of these areas has been undertaken, especially in the southeastern U.S., through widespread plantings of primarily hardwood trees seedlings, including oaks (Stanturf et al., 2001). Unfortunately, these restoration efforts have had only limited success in many cases due to tree losses after flooding. An increased understanding of the effects of flooding stress will enhance future management recommendations for restoration efforts, which may become increasingly important in the Northern Hemisphere as a result of climate change (Glenz et al., 2006).

Different oak species exhibit biomass allocation patterns that can be linked to their native habitats (Long and Jones, 1996). Changes in oak seedling biomass allocation in response to flooding have been reported by a number of authors (Wagner and Dreyer, 1997; Pezeshki and Anderson, 1997; Pezeshki and DeLaune, 1998; Colin-Belgrand et al., 1991; Kuhne and Bartsch, 2007). Hook and Brown (1973) found flood tolerance differences in secondary root mortality rates among species of newly planted oak seedlings.

Variation in flood tolerance rankings is dependent upon plant age, season of flooding (Kozlowski, 1997), water flow rate (Kabrick et al., 2007) and water depth (Hook, 1984). In addition to using simple survival rates as a measure of flood tolerance, species rankings have also been based on rates of recovery. Seedlings are more susceptible to flooding consequences resulting from low soil redox conditions than mature trees (Pezeshki et al., 1999). Observed responses of oaks to flooding, or waterlogging, have been published by several authors (Hook, 1984; Sykes, 1993; Kabrick and Dey, 2001; Allen et al., 2001; Whitlow and Harris, 1979). Tolerant oak species exhibit the capacity to maintain root functionality and even limited growth in the presence of flooding (Burke and Chambers, 2003). However, there is a lack of understanding of the role of genetic origin in determining flood tolerance within this genus (Parelle et al., 2007).

The flood tolerance of several hardwood tree species was investigated by Kabrick et al. (2007) in an outdoor flood tolerance laboratory described by Van Sambeek et al. (2007). In their study, Kabrick et al. (2007) defined flood tolerance in terms of survival, shoot growth (or dieback) and overall leaf health. Similarly, Coggeshall et al. (2004) evaluated three southern oak species for their flood tolerance by comparing the survival, number of new shoots and their cumulative length of flooded seedlings versus their non-flooded controls following a three week flood. More recently, these same three variables were used to develop a "flood tolerance index" to assess intraspecific differences in flood tolerance (Coggeshall et al., 2007). Index values were determined as the product of three ratios for survival, number of new shoots and their cumulative length, where the observed mean for each family (or seedlot) was divided by the mean for the best family.

Hook (1984) defined tolerance of both seedlings and mature trees of various species as the capacity to tolerate different levels of soil inundation (waterlogging) during the growing season. Kabrick and Dey (2001) rated flood tolerance of trees from 1 (intolerant = species that are unable to survive flooding events during the growing season) to 4 (very tolerant = ability to survive over two or more growing seasons). Similarly, Allen et al. (2001) assigned flood tolerance rankings based on four categories, including the development of morphological adaptations in response to flooding (e.g. hypertrophied lenticels). In contrast, Sykes (1993) assessed flood tolerance from 1 (least tolerant = species that survive in waterlogged soil for a few days) to 5 (most tolerant = species that survive continual soil waterlogging conditions over multiple years, except for short durations of drying due to drought).

Frye and Grosse (1992) evaluated flooding impacts on growth and survival rates during the growing season following flooding for 22 deciduous tree species. Based on seedling shoot growth, flooded sessile oak (*Q. petraea* (Matt.) Liebl.) and pin oak (*Q. palustris* Muenchh.) seedlings recovered from flooding in the second year, while flooded English oak (*Q. robur* L.) seedlings did not. However, English oak seedlings had 90% survival at the end of the growing season following flooding in comparison to sessile oak, where only 9 of 20 seedlings (45%) survived. Such studies demonstrate the various methods used to assess the flood tolerance of newly planted seedlings, including the differing times when assessments were conducted.

Parelle et al. (2007) suggested that seedling survival after flooding could be a function of genetic variability within species to develop flood-induced responses, such as hypertrophied lenticels and adventitious rooting. The ability of a genotype to express alternative phenotypes in different environments is termed phenotypic plasticity (Sultan, 2000) and such responses have a firm genetic basis (Schlichting, 1986). This type of variation reflects a shift in growth allocation patterns, and/or differential expressions in morphology that are cued by abiotic conditions, such as flooding. Measures of plasticity can be used to describe patterns and amounts of phenotypic variability but do not necessarily define the potential "selective impact" of such variability in the future (Vallardes et al., 2000).

While phenotypic plasticity has been well documented on a species level for several traits (Vallardes et al., 2006; Vallardes et al., 2002), relatively few investigations have attempted to quantify intraspecific patterns. Niinemets et al. (2003) detected plastic responses in leaf morphology within two European shrub species in response to light. Nielsen and Jorgensen (2003) observed plasticity in diameter growth increments of flooded European beech (*Fagus sylvatica* L.) seedlings. While stand level plasticity, as measured by coefficient of variation, increased with increasing water content, the opposite trend was noted based on a subset of 10 seedling families derived from a single Danish provenance. These data highlight the challenges associated with the scaling of plastic responses within and among individual trees, families and stands when planted across a soil moisture gradient.

There has been limited research focused on defining potential intraspecific patterns of genetic variation within bottomland hardwood tree species in response to flooding. Keeley (1979) investigated the effects of flooding on a series of black gum (*Nyssa sylvatica* Marsh.) seed sources collected from various hydrologic positions. After a short term flood, the root systems of the upland seed sources deteriorated rapidly, while the swamp and floodplain seed sources successfully regenerated new roots. Upland seed source trees allocated more biomass to their roots and had higher root respiration rates than trees from either the floodplain or swamp seed sources. While flood tolerant trees allocated less biomass to roots, they also transported oxygen to the roots via hypertrophied lenticels and/or newly developed adventitious roots. Similar seed source-related, morphological adaptations to restricted oxygen in the root zone have been reported in other hardwood (Cao and Connor, 1999; Smit, 1988) and conifer species (Topa and McLeod, 1986). However, similar investigations have not been conducted for any oak species in North America with the exception of recent investigations by Coggeshall et al. (2004; 2007), Coggeshall and Van Sambeek (2008), and Walsh et al. (2007).

The flood tolerance ratings of swamp white oak (*Q. bicolor* Willd.) have ranged from "tolerant", "moderately tolerant", and "somewhat tolerant" (Teskey and Hinckley, 1977; Whitlow and Harris, 1979; Haynes et al., 1988; Allen et al., 2001). These inconsistent ratings may be attributed to differences in the genetic origins (i.e. seed sources) of the seedlings used in such studies or the use of varying methods to assess flood tolerance. Therefore, the objectives of this study were to use a sensitivity analysis to assess the flood tolerance of swamp white oak seedlings grown from several seed origins, and to quantify the levels and sources of plasticity in response to flooding.

MATERIALS AND METHODS

ACORN COLLECTION AND SEEDLING PRODUCTION

A total of 27 swamp white oak open pollinated seedlots were collected from eight stands in five different counties in central Missouri in the fall 2003. Each of the parent trees used in this study were chosen based upon the presence of >300 acorns and slope position.

Two to five individual seedlots (families) represented each of the following slope positions: upper (xeric), middle (mesic), or lower (hydric) slopes. Source location and soils information for all seedlots used in this study are given in Table 4-1. All soils data were derived from the Center for Applied Research and Environmental Systems website (http: //www.cares.missouri.edu).

Collected acorns were soaked in water for 48 hours to insure full imbibition and to remove all floaters or insect-damaged seeds. A sample of 25 acorns from each seedlot was cut longitudinally to assess the actual percentage of filled, undamaged seeds. Each seedlot was divided into three, equal lots for future sowing into three nursery bed replications. Moistened seeds were maintained in plastic bags at 4.5° C until sown.

All seedlots were hand sown at the Missouri Department of Conservation George O. White Nursery near Licking (37° 34' N, 91° 53' W) on 5 November 2003. Acorns were sown approximately 2.5 cm deep in three nursery bed replications at a uniform seedbed density of 75 seeds per m^2 based on previous work conducted by Wichman and Coggeshall (1983). Following sowing, seedbeds were maintained using standard weeding, fertility and irrigation nursery practices throughout the 2004 growing season. Seedlings were lifted at a minimum depth of 20 cm on 15 November 2004 and subsequently stored at 4.5° C. Total height and root collar diameter data were recorded for each seedling prior to planting.

FLOOD TREATMENTS

On 15 March 2005, 1963 one year old swamp white oak seedlings representing 27 different half-sib families were planted in the 12-channel Flood Tolerance Laboratory (Van Sambeek et

Table 4-1. Seed origins and local soil descriptions of the 27 swamp white oak (*Quercus bicolor* Willd.) seedling families collected in Missouri for the flood tolerance sensitivity analysis.

Stand	County	No. Families	Latitude	Longitude	Slope Position	Flooding Frequency	Soil Series[1]	Drainage Class[2]
DAL	Boone	4	38° 53' 56"	92° 20' 31"	Mid	None	Weller SL	MWD
GBR	Boone	3	38° 55' 58"	92° 25' 07"	Lower	Frequent	Wilbur SL	VPD
JVS	Boone	1	38° 53' 58"	92° 20' 23"	Mid	None	Weller SL	MWD
KVL	Adair	5	40° 10' 20"	92° 34' 35"	Upper	None	Gara L	MWD
MCN	Macon	5	39° 46' 40"	92° 30' 58"	Mid	Rare	Chariton SL	SPD
MDW	Boone	1	38° 58' 20"	92° 25' 42"	Mid	None	Weller SL	MWD
OFR	Howard	4	39° 00' 41"	92° 45' 20"	Lower	Occasional	Carlow SC	SPD
SCR	Boone	2	38° 57' 48"	92 °14' 42"	Mid	None	Keswick SL	MWD
FKN[3]	--	1	--	--	--	--		
FRK[3]	--	1	--	--	--	--	--	--

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[1] Soil series: SL= Silt Loam, L= Loam, SC= Silty Clay

[2] Drainage class: MWD = moderately well drained; VPD = very poorly drained; SPD = somewhat poorly drained. <u>Source</u>: Center for Applied Research and Environmental Systems website (http://www.cares.missouri.edu).

[3] Commercial seed sources from east central Missouri.

et al., 2007) at the Horticulture and Agroforestry Center in New Franklin, MO (39° 04' N, 92° 74' W). The experimental design was a split plot. Whole plots were four flood treatments arranged in three randomized complete blocks and sub-plots were half-sib families within stands. Flood treatment, stand and family were considered fixed effects. A total of 5-7 single tree plots per family were established randomly within each channel. Treatments included: 1) three week flowing water (3F); 2) five week flowing water (5F); 3) five week stagnant water (5S); and 4) a non-flooded control (NF). Flooding treatment was initiated on 23 May 2005. By this date, all trees had completed their first growth flush, but had yet to initiate a second flush. All water depths were maintained at ~15cm for the duration of the study. Unfortunately, 199 mm of additional rainfall occurred during the flooding period, with the majority occurring during the fourth week of the five week flooding period. This caused the soils in the non-flooded control and three week flooded channels to become temporarily saturated. Also, some seepage from the adjacent flooded channels may have contributed to this waterlogging condition (Unger et al., 2008). Flooded channels were drained on 13 June 2005 (three week treatment) and on 27 June 2005 (five week treatment).

DATA COLLECTION

On 6 June 2006, (12 month post-flood), above-ground portions of surviving seedlings were harvested from the flood channels and evaluated. The number of elongating shoots, length of the terminal shoot and all other shoots, number of leaves and total leaf area of terminal shoot and all other shoots were determined. By this date, all seedlings had completed their first spring growth flush, but had yet to initiate a second flush. Stand and family(stand) means by treatment and block were calculated for each of the following variables: total length of 2005 terminal shoot (TLTS5), total length of 2006 terminal shoot (TLTS6), total length all shoots in 2006 (TLAS6), total length all shoots in both 2005 and 2006 (TLAS56), total number of 2006 branches (TNBR6), total area of 2006 terminal shoot leaves (TATSL6), total area all leaves in 2006 (TALV6), total number of terminal shoot leaves (TNTSL6), and total number of 2006 leaves (TNLV6). Basal sprout data were not included in these analyses because less than 1% of seedlings produced any basal sprouts.

Two approaches were used to assess seed source variation among the 27 swamp white oak families after flooding. First, an index value was constructed on a family mean basis by integrating the four most sensitive flood variables (number of branches, shoot length, number of leaves and leaf area). For each family, a flood tolerance index (F.T.I.) value was calculated using the following formula: observed mean minus minimum mean divided by the maximum mean minus minimum mean for each trait [(observed-min)/(max-min)]. This product of the four variables was then multiplied by 100 to determine the F.T.I. value for each family. Secondly, an index of phenotypic plasticity was calculated for each variable by family as the difference between the maximum and minimum observed values divided by the maximum observed value [(max-min)/max] for each trait across the four flood treatments. The mean phenotypic plasticity index was then determined for each family by averaging the phenotypic plasticity index values obtained for each of the four variables (Vallardes et al., 2000).

STATISTICAL ANALYSES

Due to unbalanced numbers of live seedlings per family, data analyses were conducted using PROC GLM (SAS, Cary, NC) and means were separated using Duncan's new multiple range test (*P* <0.05). To insure normality (Shapiro-Wilkes test) and minimize coefficients of variation for each variable, data were transformed using both square root and log transformations on each family mean by channel. Further, the numbers of quartile outliers were also noted. For each variable, the percent contribution of block, treatment, stand, family(stand), and their interactions, to the total sums of squares were calculated. Based on these analyses, leaf area, leaf number, branch number and shoot length were selected as flood tolerance variables to be included in the sensitivity analyses because they exhibited maximum sensitivity to flooding.

To determine if initial seedling size affected flood tolerance, family rankings based on basal diameters at outplanting in March 2005 were compared with corresponding family mean flood tolerance index values in June 2006. There was a limited, non significant correlation between these rankings (Spearman's ranked correlation $r = 0.2646$) which eliminated the necessity of adjusting for initial seedling size variations prior to analysis of variance.

RESULTS

Swamp white oak seedlings exhibited wide amplitude in their growth responses to the flooding treatments. Based on the Shapiro-Wilkes test, both square root and log transformations improved the normality of family means, reduced the number of outliers and lowered coefficients of variation (Table 4-2). Analysis of variance revealed a consistent lack of interaction between flooding treatment and stand and also, family within stand (Table 4-3). Thus, each stand, or family within stand, produced a similar response to the flooding treatments while maintaining genetic differences in overall growth rates during the study period. Treatment differences were detected for eight variables while family(stand) differences were detected for 14 variables (Table 4-3).

The swamp white oak seedlings used in this study were produced from acorns collected across a hydrologic gradient, and it was anticipated that slope position (or stand) level differences in growth rates as a response to flooding stress would be detected in this study. However, the importance of "stand" as a source of variation in all analyses of variance was negligible when expressed as a percent contribution to total sums of squares (Table 4-3). In contrast, significant family(stand) levels of variation were detected for all measured variables, except terminal shoot leaf area in 2006 (TATSL6S, TATSL6L, P = 0.1212 and P = 0.1897, respectively). Across all measured variables, the amount of genetic variation attributable to family versus stand sources of variation, as defined by analysis of variance, ranged from 2.9:1 for leaf area, 3.0:1 for branch number, 3.2:1 for leaf number and 4.0:1 for shoot length (Table 4-3). This lack of a significant stand component as a source of variation in the analysis of variance allowed for the determination of differences among the 27 swamp white oak families as the sole genetic basis for defining flood tolerance in this species using sensitivity analysis techniques. Family means for the four variables used in calculating flood tolerance index values are given in Table 4-4.

To determine F.T.I. values on a family basis, a single variable was chosen for each category of interest: shoot length, branch number, leaf area and leaf number. Selection of each variable was based on a minimum number of outliers, minimum coefficient of variation, maximum family percent contribution to total sums of squares, maximum treatment percent contribution to total sums of squares, and a normal distribution of the family mean data, as defined by the Shapiro-Wilkes test of normality (Table 4-2). Based on these criteria, the following variables were identified: total length of all new shoot growth in 2005 and 2006 (TLAS56L), total number of elongating shoots in 2006 (TNBR6S), total area

Table 4-2. Test statistics used in a flood tolerance sensitivity analysis of 27 swamp white oak (*Quercus bicolor* Willd.) seedling families in Missouri.

	No. Quartiles		S-W[1]						
Variable	>3.0	1.5 - 3.0	Test	C.V.[2]	N	Mean	Min	Max	Variance
Shoot Length (cm)									
TLTS5[3]	1	12	0.9593	44.21	304	9.68	0.50	27.25	18.32
TLTS5S	0	8	0.9931^{NS}	22.23	304	3.02	1.00	5.19	0.45
TLTS5L	0	2	0.9875	23.98	304	0.90	0.22	1.42	0.05
TLTS6	3	17	0.8084	76.27	306	5.70	0.50	31.50	18.93
TLTS6S	2	5	0.9344	32.01	306	2.27	1.00	5.50	0.53
TLTS6L	0	3	0.9897*	40.82	306	0.64	0.08	1.45	0.07
TLAS6	5	9	0.8299	61.48	306	18.56	2.00	83.25	130.16
TLAS6S	0	11	0.9569	26.88	306	4.08	1.58	8.26	1.20
TLAS6L	0	4	0.9962^{NS}	19.39	306	1.16	0.40	1.81	0.05
TLAS56	3	6	0.8883	50.46	306	38.26	7.00	137.50	372.65
TLAS56S	0	5	0.9683	23.39	306	5.91	2.74	11.27	1.91
TLAS56L[4]	0	3	0.9980^{NS}	13.18	306	1.50	0.88	2.09	0.04
Branches (Number)									
TNBR6	0	3	0.9586	44.82	306	4.51	1.00	13.60	4.08
TNBR6S	0	3	0.9891	20.16	306	2.15	1.22	3.66	0.19
TNBR6L	0	11	0.9827	28.19	306	0.63	0.18	1.11	0.03
Leaf Area (cm^2)									
TATSL6[3]	5	20	0.8602	55.87	306	234.85	18.00	915.50	17219.30
TATSL6S	0	13	0.9552	26.44	306	14.40	4.30	28.03	14.50
TATSL6l	1	6	0.9845	10.25	306	2.26	1.27	2.88	0.05
TALV6	1	9	0.9139	54.70	306	742.62	113.00	3000.00	165008.70
TALV6S	0	7	0.9889*	27.73	306	25.66	10.55	49.14	48.82
TALV6L	0	6	0.9832	9.12	306	2.76	1.87	3.33	0.06
Leaves (Number)									
TNTSL6	4	31	0.8998	30.65	306	5.89	1.00	16.40	3.26
TNTSL6S	2	20	0.9598	13.45	306	2.48	1.22	4.05	0.11
TNTSL6L	1	11	0.9660	15.11	306	0.77	0.18	1.20	0.14
TNLV6	1	6	0.9206	46.37	306	21.68	6.00	72.00	100.49
TNLV6S	0	3	0.9795	21.78	306	4.50	2.52	8.51	0.96
TNLV6L	0	1	0.9915^{NS}	14.74	306	1.27	0.79	1.86	0.03

[1] Shapiro-Wilkes test of normality.
[2] Coefficient of variation.
[3] TLTS5 = total length terminal shoot 2005; TLTS5S = total length terminal shoot 2005 (square root transformed); TLTS5L = total length terminal shoot 2005 (log transformed); TLTS6 = total length terminal shoot 2006; TLTS6S = total length terminal shoot 2006 (square root transformed); TLTS6L = total length terminal shoot 2006 (log transformed); TLAS6 = total length all shoots 2006; TLAS6S = total length all shoots 2006 (square root transformed); TLAS6L = total length all shoots 2006 (log transformed); TLAS56 = total length all shoots 2005 and 2006; TLAS56S = total length all shoots 2005 and 2006 (square root transformed); TLAS56L = total length all shoots 2005 and 2006 (log transformed); TNBR6 = total number branches 2006; TNBR6S = total number branches 2006 (square root transformed); TNBR6L = total number branches 2006 (log transformed); TATSL6 = total area terminal shoot leaves 2006; TATSL6S = total area terminal shoot leaves 2006 (square root transformed); TATSL6L = total area terminal shoot leaves 2006 (log transformed); TALV6 = total area all leaves 2006; TALV6S = total area all leaves 2006 (square root transformed); TALV6L = total area all leaves 2006 (log transformed); TNTSL6 = total number terminal shoot leaves 2006; TNTSL6S = total number terminal shoot leaves 2006 (square root transformed); TNTSL6L = total number terminal shoot leaves 2006 (log transformed); TNLV6 = total number all leaves 2006; TNLV6S = total number all leaves 2006 (square root transformed); TNLV6L = total number all leaves 2006 (log transformed).
[4] Variables in bold type included in flood tolerance index (F.T.I.) calculation
*Significant at $P < 0.05$ level
^{NS} Not significant

of all first flush leaves in 2006 (TALV6L), and total number of all first flush leaves in 2006 (TNLV6L). Flood tolerance index values were then calculated for each family based on these four variables and of these, branch number (TNBR6S) and leaf number (TNLV6L) were most strongly correlated with family flood tolerance index values, based on Spearman's ranked correlations (Table 4-5).

Family rankings for flood tolerance based on F.T.I. values were compared to their corresponding plasticity index for each variable used in the F.T.I. calculations (Table 4-6). In general, there was an inverse relationship in F.T.I. values between families (high value) and plasticity index (low value). The top nine performing families exhibited lower mean plasticity indices across all four variables than the other 18 families. The most plastic traits across all families were total number of branches (TNBR6L) and total number of leaves (TNLV6L), which were also the most strongly correlated traits associated with flood tolerance (Table 4-5).

Several families ranked as either flood tolerant or flood intolerant shared identical mean plasticity index values. For example, family DAL4 ranked second for flood tolerance and shared a mean plasticity index of 0.24 with family SCR2, DAL3, KVL5, and MCN4 with a flood tolerance ranking of 14th, 25th and 27th, respectively. In this case, a closer examination of plasticity index values for each of the four traits that contributed to the family mean plasticity index revealed that the most flood tolerant family, DAL4, had greater shoot length (TLAS56L) across all flooding treatments (e.g. a smaller plasticity index value) than the other four families. DAL4 ranked fourth in plasticity for shoot length, while SCR2, DAL3, KVL5 and MCN4 ranked 17th, 18th, 22nd and 27th, respectively. However, for these same four families, the opposite trend was observed for number of branches produced in response to flooding (TNBR6S). The most flood tolerant of these four families, DAL4,

Table 4-3. Coefficients of determination and the percent contribution to total sums of squares for morphological indices used to assess the flood tolerance of swamp white oak (*Quercus bicolor* Willd.).

		% Contribution to total sums of squares						
Variable	R^2 (d.f.)	Block (2)	Treatment (3)	B x T (6)	Stand (8)	Family(S) (18)	T x S (24)	T x F(S) (54)
Shoot Length (cm)								
TLTS5S[1]	0.4589	2.01	0.45	5.81	1.75	9.55*	6.41	19.40
TLTS5L	0.4573	1.08	0.67	4.91	1.78	0.79*	7.84	19.06
TLTS6S	0.6393	4.13	3.04	30.58	2.05	5.10	6.88	9.47
TLTS6L	0.5955	2.62	1.92	26.24	1.86	6.41*	7.48	10.33
TLAS6S	0.5687	2.77	14.24	10.82	2.00	5.73	5.00	10.48
TLAS6L	0.5304	1.52	10.85	8.34	2.43	7.54*	5.57	11.55
TLASS6S	0.5802	1.28	20.76*	5.89	1.30	7.06*	4.87	12.99
TLAS56L[2]	0.5606	0.77	17.43***	4.45	1.84	8.59***	4.94	13.80
Branches (Number)								
TNBR6S	0.6212	3.11	18.88***	2.92	2.62	8.93***	6.05	14.42
TNBR6L	0.5966	3.06	16.31***	2.68	3.40	9.02***	5.94	14.27
Leaf Area (cm^2)								
TATSL6S	0.6497	5.05	12.22	19.98	2.74	4.75	4.34	10.61
TATSL6L	0.5931	3.64	9.64	15.58	2.12	5.27	5.10	11.42
TALV6S	0.6577	2.08	32.02***	3.42	1.32	5.56*	4.36	8.20
TALV6L	0.5895	1.98	25.64***	3.23	1.68	6.91*	4.46	4.23
Leaves (Number)								
TNTSL6S	0.6310	5.70	4.88	17.27	3.78*	8.05***	7.06	13.23
TNTSL6L	0.5919	4.48	3.61	13.60	3.64*	8.78***	8.11	14.50
TNLV6S	0.5838	2.08	24.64***	0.84	1.01	6.97*	3.68	13.74
TNLV6L	0.5561	2.23	21.68***	0.97	1.38	7.13*	3.39	13.65

*, **, ***, ^{NS} Significant at $P \leq 0.05, 0.01, 0.0001$, or not significant.

[1] TLTS5 = total length terminal shoot 2005; TLTS5S = total length terminal shoot 2005 (square root transformed); TLTS5L = total length terminal shoot 2005 (log transformed); TLTS6 = total length terminal shoot 2006; TLTS6S = total length terminal shoot 2006 (square root transformed); TLTS6L = total length terminal shoot 2006 (log transformed); TLAS6 = total length all shoots 2006; TLAS6S = total length all shoots 2006 (square root transformed); TLAS6L = total length all shoots 2006 (log transformed); TLAS56 = total length all shoots 2005 and 2006; TLAS56S = total length all shoots 2005 and 2006 (square root transformed); TLAS56L = total length all shoots 2005 and 2006 (log transformed); TNBR6 = total number branches 2006; TNBR6S = total number branches 2006 (square root transformed); TNBR6L = total number branches 2006 (log transformed); TATSL6 = total area terminal shoot leaves 2006; TATSL6S = total area terminal shoot leaves 2006 (square root transformed); TATSL6L = total area terminal shoot leaves 2006 (log transformed); TALV6 = total area all leaves 2006; TALV6S = total area all leaves 2006 (square root transformed); TALV6L = total area all leaves 2006 (log transformed); TNTSL6 = total number terminal shoot leaves 2006; TNTSL6S = total number terminal shoot leaves 2006 (square root transformed); TNTSL6L = total number terminal shoot leaves 2006 (log transformed); TNLV6 = total number all leaves 2006; TNLV6S = total number all leaves 2006 (square root transformed); TNLV6L = total number all leaves 2006 (log transformed).

[2] Variables in bold type included in flood tolerance index (F.T.I.) calculation

Table 4-4. Family means for four variables used to assess flood tolerance differences among 27 swamp white oak (*Quercus bicolor* Willd.) seedling families in Missouri.

		Variable[1]			
F.T.I.[2]	Family[3]	TLAS561 Mean	TNBR6S Mean	TALV6L Mean	TNLV6L Mean
80.51	MCN3	1.63 a[4]	1.37 a	2.92 a	1.40 a
77.75	DAL4	1.59 abcd	1.36 ab	2.91 ab	1.40 a
47.09	OF1	1.60 abc	1.34 abc	2.91ab	1.40 a
43.94	MDW1	1.56 abcd	1.35 abc	2.84 abc	1.37 abc
38.34	KVL4	1.55 abcde	1.37 a	2.85 abc	1.39 ab
30.25	MCN1	1.61 ab	1.33 abc	2.85 abc	1.35 abcd
26.30	FKN1	1.53 abcdef	1.32 abc	2.83 abc	1.35 abcd
16.87	KVL3	1.52 abcdef	1.30 abc	2.79 abcd	1.31 abcd
12.39	GBR1	1.51 abcdef	1.28 abc	2.82 abc	1.30 abcd
3.42	MCN2	1.43 def	1.28 abc	2.76 abcd	1.29 abcd
3.39	OF2	1.47 abcdef	1.25 abc	2.82 abc	1.30 abcd
3.36	OF4	1.47 abcdef	1.25 abc	2.81 abc	1.28 abcd
3.00	DAL1	1.58 abcd	1.24 abc	2.77 abcd	1.29 abcd
2.72	SCR2	1.46 abcdef	1.26 abc	2.73 abcd	1.27 abcd
2.49	SCR1	1.46 abcdef	1.25 abc	2.77 abcd	1.26 abcd
1.42	GBR2	1.44 cdef	1.26 abc	2.76 abcd	1.27 abcd
0.94	KVL2	1.48 abcdef	1.23 abc	2.73 abcd	1.24 abcd
0.42	FKN4	1.45 bcdef	1.24 abc	2.67 cd	1.28 abcd
0.41	DAL2	1.46 abcdef	1.23 abc	2.68 cd	1.26 abcd
0.37	KVL1	1.48 abcdef	1.19 c	2.82 abc	1.21 cd
0.22	DAL3	1.46 abcdef	1.20 bc	2.80 abcd	1.22 cd

Table 4-4. (Continued) Family means for four variables used to assess flood tolerance differences among 27 swamp white oak (*Quercus bicolor* Willd.) seedling families in Missouri.

		Variable[1]			
F.T.I.[2]	Family[3]	TLAS561 Mean	TNBR6S Mean	TALV6L Mean	TNLV6L Mean
0.17	OF5	1.53 abcdef	1.26 abc	2.81 abc	1.27 abcd
0.10	GBR3	1.38 ef	1.24 abc	2.71 bcd	1.26 abcd
0.09	MCN5	1.50 abcdef	1.22 abc	2.82 abc	1.23 bcd
0.02	KVL5	1.44 bcdef	1.23 abc	2.69 bcd	1.25 bcd
< 0.01	JVS3	1.48 abcdef	1.19 c	2.69 bcd	1.23 bcd
< 0.01	MCN4	1.38 f	1.18 c	2.61 d	1.20 d

[1] Variables: TLAS56L = total length all shoots in 2005 and 2006 (log transformed); TNBR6S = total number branches in 2006 (square root transformed); TALV6L total leaf area in 2006 (log transformed); TNLV6L = total number leaves in 2006 (log transformed).

[2] F.T.I. = flood tolerance index.

[3] Family name = Stand and tree number within stand.

[4] Family means within a column that do not share a common letter are significantly different at $P < 0.05$.

Table 4-5. Spearman ranked correlation matrix for the four variables used to calculate flood tolerance index (F.T.I.) values for 27 seedling families of swamp white oak (*Quercus bicolor* Willd.) collected in Missouri.

Variable[1]	TNBR6S	TALV6L	TNLV6L	F.T.I.
TLAS56L	0.531	0.725	0.666	0.727
TNBR6S	--	0.613	0.851	0.923
TALV6L	--	--	0.700	0.754
TNLV6L	--	--	--	0.914

[1] Variables: TLAS56L = total length all shoots in 2005 and 2006 (log transformed); TNBR6S = total number branches in 2006 (square root transformed); TALV6L = total leaf area in 2006 (log transformed); TNLV6L = total number of leaves in 2006 (log transformed); F.T.I. = flood tolerance index.

Table 4-6. Comparison of flood tolerance index (F.T.I.) rankings and plasticity index values of 27 swamp oak (*Quercus bicolor* Willd.) families after flooding in Missouri.

F.T.I. Rank	1	2	3	4	5	6	7	8	9	
Family	MCN3	DAL4	OF1	MDW1	KVL4	MCN1	FKN1	KVL3	GBR1	MEAN
					Plasticity Index					
TLAS56L^1	0.16 (1)^2	0.16 (4)	0.13 (3)	0.03 (6)	0.12 (7)	0.20 (2)	0.12 (8)	0.07 (10)	0.21 (11)	0.13
TNBR6S	0.30 (3)	0.39 (1)	0.24 (7)	0.06 (2)	0.29 (6)	0.23 (10)	0.16 (3)	0.16 (5)	0.28 (9)	0.23
TALV6L	0.10 (1)	0.18 (2)	0.13 (2)	0.07 (4)	0.10 (6)	0.13 (5)	0.10 (11)	0.12 (12)	0.12 (8)	0.12
TNLV6L	0.18 (2)	0.24 (3)	0.11 (5)	0.08 (4)	0.17 (1)	0.21 (6)	0.09 (7)	0.12 (8)	0.26 (9)	0.16
MEAN	0.18	0.24	0.15	0.06	0.14	0.19	0.12	0.12	0.22	
F.T.I. Rank	10	11	12	13	14	15	16	17	18	
Family	MCN2	OF2	OF4	DAL1	SCR2	SCR1	GBR2	KVL2	FRK4	MEAN
					Plasticity Index					
TLAS56L	0.29 (24)	0.22 (15)	0.25 (13)	0.15 (5)	0.22 (17)	0.23 (19)	0.15 (23)	0.05 (15)	0.25 (21)	0.20
TNBR6S	0.24 (8)	0.37 (12)	0.28 (14)	0.22 (20)	0.34 (13)	0.39 (11)	0.32 (16)	0.13 (21)	0.33 (15)	0.29
TALV6L	0.09 (18)	0.16 (15)	0.08 (13)	0.11 (19)	0.22 (21)	0.32 (16)	0.16 (17)	0.10 (20)	0.20 (25)	0.13
TNLV6L	0.22 (10)	0.31 (16)	0.17 (14)	0.19 (17)	0.16 (11)	0.20 (14)	0.20 (13)	0.09 (21)	0.22 (18)	0.20
MEAN	0.21	0.26	0.20	0.17	0.24	0.28	0.21	0.09	0.25	

Table 4-6. (continued) Comparison of flood tolerance index (F.T.I.) rankings and plasticity index values of 27 swamp oak (*Quercus bicolor* Willd.) families after flooding in Missouri.

F.T.I. Rank	19	20	21	22	23	24	25	26	27	
Family	DAL2	KVL1	DAL3	OF5	GBR3	MN5	KIVL5	JVS3	MCN4	MEAN
					Plasticity Index					
TLAS56L	0.21 (20)[2]	0.20 (12)	0.21 (18)	0.10 (8)	0.14 (26)	0.12 (25)	0.19 (22)	0.19 (12)	0.22 (27)	0.18
TNBR6S	0.32 (18)	0.33 (17)	0.32 (24)	0.33 (27)	0.15 (19)	0.31 (23)	0.40 (26)	0.32 (25)	0.30 (22)	0.31
TALV6L	0.21 (24)	0.15 (9)	0.17 (14)	0.11 (10)	0.08 (22)	0.19 (7)	0.13 (26)	0.16 (23)	0.17 (27)	0.15
TNLV6L	0.30 (21)	0.22 (25)	0.25 (24)	0.22 (12)	0.14 (19)	0.24 (23)	0.25 (20)	0.25 (26)	0.26 (27)	0.24
MEAN	0.26	0.23	0.24	0.19	0.13	0.22	0.24	0.23	0.24	

[1] Variables: TLAS56L = total length all shoots in 2005 and 2006 (log transformed); TNBR6S = total number branches in 2006 (square root transformed); TALV6L = total leaf area in 2006 (log transformed); TNLV6L = total number of leaves in 2006 (log transformed); F.T.I. = flood tolerance index.

[2] Numbers in parentheses represent the F.T.I. family rankings for each variable within a row.

exhibited a higher level of plasticity (0.39) for this trait in comparison to the other, less flood tolerant families, with the exception of KVL5, which had a comparable plasticity index value of 0.40 and is considered to be flood intolerant. For the remaining two variables, leaf area (TALV6L) and number of leaves (TNLV6L), there were no clear trends detected among these four families in terms shifts in plasticity in response to flooding.

A simple comparison of plasticity index values between the most flood tolerant family, MCN3, and the least flood tolerant family, MCN4, reveals two very different responses to flooding, despite the fact that both families represent two closely adjacent mother trees within the same seed source. MCN3 was less plastic in terms of length of shoots, number of leaves and leaf area, while both families shared an identical plasticity index of 0.30 for number of branches produced. While these data reflect an apparent lack of agreement between flood tolerance and plasticity index values on a family basis, they suggest different recovery mechanisms for specific swamp white oak families in response to flooding.

DISCUSSION

This study demonstrated genetic differences among 27 swamp white oak families in their recovery from flooding, as defined by a flood tolerance index (F.T.I.) (Table 4-4). These index values were calculated using four variables identified by sensitivity analysis. Families that exhibited greater flood tolerance were generally less plastic, which suggests that in this species, flood tolerance can be characterized as a passive, rather than adaptive, response to flooding stress, under our experimental conditions.

This study also demonstrated that time of assessment for evaluating seedling recovery from flooding is important (Table 4-3). For all variables measured, greater differences in flooding response were found in the year following treatment. These results confirm earlier work by Frye and Grosse (1992), in which biomass accumulation was assessed in the year after flooding for 22 tree species in Germany, including three oak species, English oak, sessile oak and pin oak. All species displayed a different recovery pattern in the year following flooding compared to the results obtained at the end of the growing season of the flood. Shoot growth of oaks was retarded in all three species due to an increased frequency in branching, which confirms the utility of including the number of branches (TNBR56L) and shoot length (TLAS56L) variables in our sensitivity analysis. Similar negative impacts on growth of flooded English oak seedlings in the year following flooding were reported by Kuhne and Bartsch (2007). Shoot and total seedling dry weights, leaf number and leaf area decreased between 80 to 90% and shoot length decreased ≈60% in comparison to non-flooded control seedlings. Similar flooding impacts on oak seedling leaf area (TALV6L) and leaf number (TNLV6L) have also been reported (e.g. Anderson and Pezeshki, 1992; Schmull and Thomas, 2000). Other assessments of oak seedling flood tolerance based on height growth increment have been reported at the completion of the growing season in which flooding occurred, rather than during the subsequent "recovery" growing season (Colin-Belgrand et al., 1991; Kabrick et al., 2007).

While the present study focused on growth responses of planted swamp white oak seedlings in the year following flooding, longer term investigations for this species may be useful. Pennington and Walters (2006) reported 2nd and 5th year growth and survival data for swamp white oak seedlings planted adjacent to a series of constructed perched wetlands in Michigan. No differences in mean seedling height were detected at age 2, but heights differed after 5 growing seasons, ranging from 82 cm to 114 cm on the upland and transition planting sites, respectively.

Differences in flooding response among stands of swamp white oak were not detected by analysis of variance in this study. This result was not unexpected since previous genetic analyses using microsatellites in bur oak (*Q. macrocarpa* Michx.), a closely related species, indicated that up to 97% of the variation was expressed within a stand, while only 3% occurred among stands (Craft and Ashley, 2007). Streiff et al. (1998) attributed the lack of stand differences to extensive pollen flow in two European oak species, English oak and sessile oak (members of the same *Quercus* subgenus as swamp white oak). Results from these types of genetic analyses also corroborate observations made in the present study, that for an adaptive trait like flood tolerance, a large degree of intra-stand variation exists in comparison to an essential lack of inter-stand patterns of genetic variation, which never exceeded 4% of the total variation observed.

While there was a lack of significant family(stand) x treatment interactions for the variables used in this study, significant treatment and family(stand) sources of variation were detected for all of the traits included in the Flood Tolerance Index (F.T.I.) calculations (Table 4-3). This suggests that phenotypic plasticity was expressed as a result of flooding, since all accessions performed poorly as a result of flooding, Also, this plasticity was more a passive, rather than adaptive response to flooding stress (Pigliucci and Kolodynska, 2002). While only four variables were included in the calculation of family plasticity index values, it is important to recognize that the best performing families, based on their F.T.I. rankings, exhibited a greater capacity to maintain a stable (less plastic) phenotype across the four flooding treatments. This tendency is defined as homoeostasis by Falconer (1989). A low degree of homeostatic expression can be interpreted to be undesirable since small environmental changes can negatively influence plant performance. However, Nielsen and Jorgenson (2003) reported that similar levels of homeostatic expression can reflect both poor and high levels of adaptability to flooding stress in European beech, which is also a species in the Fagaceae. In the present study, families that expressed a higher degree of homeostasis (lower plasticity) were generally more flood tolerant. This restriction of variation is likely the result of an interaction between a specific underlying trait which may contribute to overall plant fitness, but is less directly tied to fitness in comparison to some other trait (Alpert and Simms, 2002). In the present study, leaf area was the most closely correlated with family flood tolerance index values (Spearman's correlation r = 0.754) than shoot length (r = 0.727) (Table 4-5). Thus, shoot length (TLAS56L) was more plastic than leaf area (TALV6L) across all families in this study, indicating that leaf area plasticity may be more closely linked to flood tolerance than total shoot length plasticity for the swamp white oak seedling families when assessed at the completion of the first flush in the year following flooding

In conclusion, this study demonstrated the presence of genetic variation in response to flooding within swamp white oak which is based at the individual mother tree (or family) level and that no significant gains in flood tolerance can be achieved through the use of seed sources derived specific seed sources (or stands) along a hydrologic gradient. Flood tolerant swamp white oak families were identified in the "recovery" year following flooding by using a flood tolerance index which integrated the total shoot length, total number of branches, total leaf number and leaf area of seedlings. Of these variables, the total number of branches and total leaf number on the first flush in the year following flooding were most highly correlated with flood tolerance index.

CHAPTER 5

CONCLUSIONS

Assessing the flood tolerance of tree species that will be used in future reforestation/afforestation programs on bottomland sites is of critical importance to insure long-term success. The use of odds ratios estimated the numbers of oak seedlings needed to achieve specific survival rates. The value of this evaluation tool, as compared to percent seedling survival, is that odds ratios provided flood tolerance rankings based on survival rates obtained from the first and second growing season following flooding. In addition, odds ratios are appropriate for use in analyzing binomial data that is not normally distributed. The use of odds ratios demonstrated that *Q. bicolor* was the most flood tolerant species of the seven species tested, followed by *Q. palustris* and *Q. macrocarpa*. Seedlings of *Q. shumardii*, *Q. rubra*, *Q. alba* and *Q. muehelenbergii* were less flood tolerant based on survival odds ratios determined at the completion of the first growth flush in the year following flooding (45 weeks post-flood). Within species, significant winter mortality across all three flooding treatments was also observed in both a tolerant (swamp white oak) and intolerant (northern red oak) species in comparison to non-flooded controls. There were no significant differences in survival rates among the three flood treatments in the year following flooding based on odds ratios. While this odds ratio method provides an assessment of post-flood survival at the end of the growing season and after overwintering, longer term studies may be needed to evaluate reforestation efforts over time.

For the 27 swamp white oak families evaluated by sensitivity analysis, survival percentages ranged from 58.6 to 86.2% at 15 weeks post-flood, and 63.8 to 85.3% after 45 weeks. A total of 14 families had winter mortality, while 13 families did not (data not shown). This study also demonstrated that seedling growth measurements, in addition to survival data, are necessary to assess the flood tolerance of swamp white oak seedlings. No significant gains in flood tolerance were achieved through the use of acorns derived from specific seed sources (or stands) along a hydrologic gradient. Flood tolerant swamp white oak families were identified in the "recovery" year following flooding by using a flood tolerance index which integrated the total shoot length, total number of flushing branches, total leaf number and leaf area of seedlings. Of these variables, the total number of flushing branches and total leaf number were most highly correlated with flood tolerance.

Appendix Table A-1. Survival odds ratios for 143 white oak (*Q. alba* L.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	21.32 ***	16.94 ***	17.54 ***	70.8 ***
Odds Ratios at 45 weeks	3F	**1.90** ^{NS}	--	1.26 ^{NS}	1.22 ^{NS}	10.2 ***
	5S	**1.89** ^{NS}	**3.56** ^{NS}	--	1.03 ^{NS}	12.5 ***
	5F	**1.17** ^{NS}	**1.62** ^{NS}	**2.21** ^{NS}	--	12.1 ***
	% survival 45 weeks	54.7 ^{ns}	69.6 ^{ns}	39.0 ^{ns}	58.6 ^{ns}	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05$, 0.01, 0.001, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

Appendix Table A-2. Survival odds ratios for 33 shumard red oak (*Q. shumardii* Buckl.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	20.99 ***	3.50 *	23.33 ***	70.0 ns
Odds Ratios at 45 weeks	3F	**1.67 NS**	--	6.00 *	1.11 NS	10.0 NS
	5S	**2.40 NS**	**4.00 NS**	--	6.67 *	40.0 NS
	5F	**1.67 NS**	**1.00 NS**	**4.00 NS**	--	9.1 *
	% survival 45 weeks	62.5 ns	50.0 ns	80.0 ns	50.0 ns	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05, 0.01, 0.001$, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

Appendix Table A-3. Survival odds ratios for 72 pin oak (*Q. palustris* Muenchh.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	3.78 *	1.89 ^{ns}	1.89 ^{ns}	85.0 ***
Odds ratios at 45 weeks	3 F	**3.56 ***	--	1.99 ^{NS}	1.99 ^{NS}	60.0 ^{NS}
	5S	**10.28 *****	**2.89** ^{NS}	--	1.00 ^{NS}	75.0 *
	5F	**2.67** ^{NS}	**1.33** ^{NS}	**3.86 *****	--	75.0 ***
	% survival 45 weeks	88.9 ***	69.2 *	43.8 ^{ns}	75.0 *	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of *P* ≤ 0.05, 0.01, 0.001, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

Appendix Table A-4. Survival odds ratios for 160 chinkapin oak (*Q. muehlengergii* Engelm.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	8.43 ***	16.67 ***	25.58 ***	84.4 ***
Odds Ratios at 45 weeks	3F	**2.92 ***	--	1.14 ^{NS}	1.64 ^{NS}	15.7 ***
	5S	**7.67 *****	**2.62 ^{NS}**	--	1.44 ^{NS}	14.1 ***
	5F	**3.66 *****	**1.25 ^{NS}**	**2.09 ^{NS}**	--	10.2 ***
	% survival 45 weeks	79.2 ***	56.5 ^{NS}	33.1 ^{NS}	50.9 ^{NS}	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05, 0.01, 0.001$, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

Appendix Table A-5. Survival odds ratios for 78 bur oak (*Q. macrocarpa* Michx.) seedlings subjected to four flooding treatments and assessed at two post-flood dates.

		Odds Ratio - 15 Weeks Post-Flood[1]				
	Treatment[2]	NF	3F	5S	5F	% survival 15 weeks
	NF	--	3.92 *	7.97 ***	8.05 ***	88.2 ***
Odds Ratios at 45 weeks	3F	**3.46** *	--	2.03 $^{\text{NS}}$	2.06 $^{\text{NS}}$	65.7 $^{\text{NS}}$
	5S	**2.47** $^{\text{NS}}$	**1.40** $^{\text{NS}}$	--	1.00 $^{\text{NS}}$	48.5 $^{\text{NS}}$
	5F	**1.40** $^{\text{NS}}$	**2.48** $^{\text{NS}}$	**1.77** $^{\text{NS}}$	--	48.2 $^{\text{NS}}$
	% survival 45 weeks	80.0 ***	53.6 $^{\text{NS}}$	61.7 $^{\text{NS}}$	74.1 $^{\text{NS}}$	

[1] Relative survival rates between two flooding treatments at 15 weeks post-flood is determined by contrasting a species in a given row with an alternate species in the appropriate column. Relative survival rates at 45 weeks post-flood (**bold**) are determined by contrasting a species in a column with an alternate species in a given row in the bottom half of the species matrix. Odds ratios and % survival are non-significant (NS) or significant (*, **, *** of $P \leq 0.05, 0.01, 0.001$, respectively).

[2] Treatments: NF = non-flooded control; 3F = 3 week flood (flowing water); 5S = 5 week flood (stagnant water); 5F = 5 week flood (flowing water).

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VITA

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His research interests include the conservation of endangered plant species, the facilitation of shortleaf pine restoration efforts through genetic improvement, and the application of traditional tree improvement approaches to the development of flood tolerant trees as well as sources of eastern black walnut and Chinese chestnut for improved nut and timber traits.