Floodplain Forest Regeneration Dynamics in the Lower Mississippi River Alluvial Valley

Whitney Anne Kroschel
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FLOODPLAIN FOREST REGENERATION DYNAMICS IN THE LOWER MISSISSIPPI RIVER ALLUVIAL VALLEY

A Dissertation

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

in

The School of Renewable Natural Resources

by
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I believe technical support is no more valuable than moral support. I could not have made it through this experience in one piece without several invaluable friends, including Mary Grace Lemon who I am grateful to have undergone this grind with from start to finish. Other special individuals who have supported me through this time include Marija Zivanovic, Ashley Booth, Erin Johnson Linderman, Cassandra Skaggs, Harry Silvio, Scott Allen, and Rob Conley. I wish I could name all my friends who have been pillars of strength for me in this time, for this list could go on.

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Even though he has no clue, I am very grateful to my dog Pi for being there for me through some of the most challenging periods and for bringing brightness into my world.

Lastly, and most importantly, I am thankful to my parents, Jon and Liz Kroschel, without whom I would not be the person I am to have accomplished this endeavor. They are the foundation of my support system.

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ABSTRACT

Floodplain forest species diversity is driven, in part, by variation in disturbance regime. Flood patterns create heterogeneity in microsite quality from small differences in elevation across a floodplain which, in turn, influence flood timing and duration. Differences in species’ regeneration niches in relation to hydrologic patterns can account for long-term coexistence of various species. In the past century floodplain forests have exhibited a wide range of changes in stand development and species composition as a result of altered hydrology in rivers and floodplains. I evaluated the role of regeneration in floodplain forest systems of the Lower Mississippi River Alluvial Valley to gain insight into the mechanisms behind compositional transitions. Specifically, I focused on how flood timing related to species-specific germination and first-year seedling survival patterns and processes.

Through a controlled greenhouse experiment, I tested the effects of flood timing and duration on first-year seedlings of floodplain forest species. Results showed the effects of complete submergence on first-year seedling survival is affected by the age of the seedling at the time of flooding, and the duration of flooding. Moreover, species displayed specific responses to time of flood onset and flood duration that varied by their post-germination age. The onset of a spring flood event post-germination is therefore likely to have variable effects on woody seedling composition depending on its timing relative to germination. Through examining seedling dynamics at four floodplain locations in the Lower Mississippi River Alluvial Valley (LMAV), I found first-year seedling species composition was significantly influenced by floodplain hydrology through relationships between the timing of flooding and species-specific germination and first-year seedling survival processes. Species generally considered flood-tolerant at maturity tended to demonstrate later germination windows (May and beyond) while many (not all) species considered less-flood tolerant at maturity emerged early in the spring (March-May). Flood duration preceding a seed’s germination window inhibited germination when it fully overlapped with a species’ germination window. Flooding also benefited germination when it receded prior to the close of species’ germination windows, likely through improved soil moisture availability, but possibly through other mechanisms such as nutrient supplementation. Additionally, post-germination flood timing significantly influenced seedling composition through the event of a second flood which induced seedling mortality. Spatial and temporal variation in the timing of flood recession would diversify species’ opportunities to benefit from flooding in the LMAV because of the distinct emergence windows demonstrated by species in this study. This would ultimately lead to diversification in seedling species composition in both space and time. A temporally and spatially dynamic annual flood regime would likely promote greater diversity in seedling species composition through differentiation in species’ germination and seedling survival processes.
CHAPTER 1. GENERAL INTRODUCTION

Regeneration is a well-documented limiting process of forest stand development and species composition worldwide (e.g., Streng et al. 1989, Ribbens et al. 1994, Clark et al. 1998, Hubbell et al. 1999, Hooper et al. 2004, Caron et al. 2015, Dodson et al. 2014, Prevosto et al. 2015). Yet historically, research has explored other factors to explain species-richness (e.g., phenotypic variation, environmental fluctuations, competitive ability) without necessarily considering the role of regeneration (Grubb 1977). Consequently, much is known about later life processes (e.g., survival, growth, and mortality) to explain stand dynamics (Oliver et al. 2005, Bergeron 2000, Kubota et al. 2004), forest resilience (Hansen et al. 2003, Thompson et al. 2009, Reyer et al. 2015), and forest succession (van der Valk 1981, Saldarriaga et al. 1988, Guariguata and Ostertag 2000), which collectively influence forest species composition (Grime 1977, Grubb 1977, Bastias et al. 2019, Guo et al. 2020). Still, much remains unknown about the role of the regeneration process due to the complex and relatively sensitive nature of the fundamental regeneration mechanisms controlling the outcome of forest species composition. All life stages and associated processes are critical for understanding forest development and species composition, but here I emphasize the importance of mechanisms driving regeneration and how these may influence forest stand composition.

Grubb (1977) first introduced the concept of the regeneration niche, which is the high chance of an adult individual being replaced by another adult of the same species. Herein, Grubb exposed the relative complexity of the mechanisms required for determining the co-existence of numerous species within a community. Moreover, the need was recognized for more focus on regeneration and its contribution to understanding the complete niche concept as well as species composition because the regeneration niche is more restricted than the habitat niche.

Regeneration – the formation of new individuals – can be disassembled into the stages of seed production, dispersal, germination, establishment, and survival; each one a separate and distinct process.

A better understanding of the regeneration role in maintaining current species composition is especially needed in floodplain forests. Characterized by frequent seasonal flooding, floodplain forests are relatively difficult to study due to dynamic hydrologic and geomorphic mechanisms that confound an already complex regeneration process. Much of what we know pertains to seedling flood tolerance and survival from the establishment stage and beyond (e.g., Boerner and Brinkman 1996, Battaglia et al. 1999, McCarthy and Evans 2000, Denslow and Battaglia 2002, Gee 2012). Less focus has been applied to the initial regeneration stages and their combined impact (Sharitz and Lee 1985, Streng et al. 1989, Jones et al. 1994, Sarneel et al. 2014).

Some clarity of floodplain forest composition has been gleaned from systems in which a certain variable can be isolated or eliminated, by doing so, simplifying the overall processes. For instance, among floodplains worldwide the “depth to water table” variable has been documented as directly or indirectly exercising a significant role on tree species survival (Busch and Smith 1995, Shafroth et al. 2000, Rood et al. 2003, Cunningham et al. 2011). In Australia, forest dieback of *Eucalyptus* sp. was examined in relation to water table levels along the Murray River;
it was discovered that stand mortality was linked to associated groundwater declines (Cunningham et al. 2011). In the western United States, *Populus fremontii/Salix exigua* communities were restored along the Truckee River after river discharge was increased from an upstream impoundment to support regeneration conditions (Rood et al. 2003). However, in floodplains where groundwater and surface water are inherently linked, the dynamics of the hydrology and geomorphology complicate analytical attempts to isolate important variables for species composition study, especially as they pertain to regeneration. This complexity is especially evident in floodplain forests of the southeastern United States.

Since the early 1900s modifications to rivers for flood control and navigation purposes have dramatically altered the natural hydrologic and geomorphic processes of most floodplains in the Southeast (Dynesius and Nilsson 1994, Bayley 1995, Gore and Shields 1995, Biedenharn and Watson 1997, Pinter et al. 2006, Hudson et al. 2008). Extensive channel engineering throughout the 20th Century of the Mississippi River and its major tributaries has altered channel flow behavior by means of meander bend cutoffs and channel entrenchment (Pinter et al. 2006, Hudson et al. 2008). Changes in flood behavior can cumulatively be attributed to channel adjustments, precipitation shifts, land-use changes, dam and levee construction, and channel incision. Simultaneously, river floodplains may experience changes in flood water regimes, ground water levels, erosion patterns, and sedimentation processes (Gore and Shields 1995, Pinter et al. 2006, Hudson et al. 2008). It is then reasonable that the resulting lag effects on floodplain forest species composition is a challenging problem to understand because one major event may take several years to reveal its effects in the forest community (McCarthy and Evans 2000, Faust 2006, Gee 2012, Jacobson and Faust 2014). There is evidence that floodplain forests in Louisiana are shifting from shade-intolerant *Quercus*-dominated forest to shade-tolerant communities of *Celtis/Ulam/Fraxinus* species (Gee 2012, LDWF pers. comm. 2015); the former community tends to include more flood-tolerant species relative to the latter (Bedinger 1971, McKnight et al. 1980). Transitions to more shade-tolerant communities create difficulty for shade-intolerant species (*Quercus*) to regenerate. In addition to historic and current hydrologic modifications, impending future changes associated with drought and water management must be considered when evaluating floodplain forest species composition.

Understanding fundamental patterns and process of forest regeneration as they relate to floodplain dynamics is necessary for developing successful management and monitoring strategies (King and Keim 2019). Ultimately, if we can understand mechanisms contributing to compositional change, we can potentially predict the status of floodplain forests years from now.

This research investigated the regeneration process of trees species in the context of floodplains of the Lower Mississippi River Alluvial Valley (LMAV). I focused on species-specific responses to variations in flood hydroperiod (timing, frequency, duration, depth) in an effort to highlight different regeneration strategies among species that will aid in ecological understanding of floodplain regeneration dynamics in the LMAV and beyond. I hypothesized that species-specific differences in germination and survival within seedlings’ first-year may influence early floodplain forest species composition, and may therefore influence long-term forest community composition.

Questions/objectives for each chapter are described below:
Chapter 2: Tree Regeneration by seed in bottomland hardwood forests: a review.

Objective: To synthesize existing literature on bottomland hardwood forest regeneration by seed to identify the mechanisms by which regeneration processes, as affected by abiotic and biotic variables, may alter BLH species composition.

Chapter 3: Floodplain forest tree seedling response to variation in flood timing and duration.

Objective: To determine if the effects of complete submergence on seedling survival varies by species, age of seedling, and flood duration.

Chapter 4: First-year tree seedling dynamics in floodplain forests of the Lower Mississippi River Alluvial Valley.

Questions: (1) What is the effect of preceding total flood days on seedling emergence? (2) What is the relationship between seedling emergence and preceding water levels, including both groundwater and surface water? (3) Does the timing of flood recession demonstrate an effect on seedling emergence? (4) Does light availability affect seedling emergence? (5) What is the effect of post-germination flooding on first-year seedling mortality?

Early filters on seedling dynamics will yield insight into the potential changes hydrologic modifications exert on regeneration dynamics. These effects can be expected to vary by species, but the differences among species and the extent of their variation remain unknown. Identifying these early patterns and process at the species-level within this highly-modified region of Southeastern floodplain forests will aid in improving understanding and management of these ecosystems long-term.
CHAPTER 2. TREE REGENERATION BY SEED IN BOTTOMLAND HARDWOOD FORESTS: A REVIEW

Introduction

Bottomland hardwood forests (BLH) are found in temperate, humid regions of the southeastern United States primarily on alluvial floodplains adjacent to rivers. Historic BLH were a product of the natural hydrologic and geomorphic processes associated with their adjacent rivers. Over time, repeated flooding and erosional and depositional events created a dynamic landscape that supported extensive floral and faunal diversity (Allen et al. 2001, Hodges 1997, Wharton et al. 1982). BLH are most extensive in the Lower Mississippi Alluvial Valley (LMAV) where about 10 million ha of BLH originally existed (Hefner and Brown 1985, National Research Council 1982). With the development of agriculture within and around the LMAV, approximately 80% of BLH area was cleared for field crops (MacDonald et al. 1979, US Department of the Interior 1988). Similarly, East Texas lost over 60% of historic BLH ecosystems but still maintains ~664,860 ha along major rivers and tributaries such as the Neches, Trinity, and Sabine rivers (Allen 1997, Elliott et al. 2014, Frye 1987).

In addition to direct conversion, BLH forests have been affected by anthropogenic alterations to the hydrology of southeastern rivers and floodplains. Since the late 1800s, modifications to rivers for flood control and navigation purposes have dramatically altered the natural hydrologic and geomorphic processes of most BLH floodplains (Allen et al. 2001, Biedenharn and Watson 1997, Dynesius and Nilsson 1994, Hudson et al. 2008, Pinter et al. 2006, Stanturf et al. 2001, Tockner and Stanford 2002). Particularly in large rivers, e.g., the Mississippi and Arkansas rivers, many floodplains have been disconnected from their associated channels by levee establishment and river channelization. This disconnection between channels and floodplains has eliminated regular flooding events which are important for shaping the structure and function of these ecosystems (Gore and Shields 1995, Messina and Connor 1998, Tockner and Stanford 2002, Wharton et al. 1982). Flooding acts as a disturbance agent, seed dispersal vector, soil moisture source, and generator of geomorphic features (Wharton et al. 1982). When flooding is altered, BLH forests take on different characteristics, such as drier soils, denser understories, and less flood-tolerant tree species (Gee 2012, Hanberry et al. 2012).

Understanding how modifications to BLH systems have affected tree species composition is particularly difficult because the vegetation is strongly controlled by the hydrology and geomorphology, and each process is intricately connected. Moreover, the lag time between cause and effect complicate understanding: it may take decades for the impacts of major events on

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Recent research and anecdotal evidence suggests many BLH are shifting from more flood-tolerant, shade-intolerant communities (e.g., overcup oak/water hickory) to less flood-tolerant, shade-tolerant communities (e.g., sugarberry/American elm/green ash; willow oak/water oak/American elm forests) (Darst and Light 2008, Alldredge and Moore 2014, Hanberry et al. 2012, Gee et al. 2014). These patterns suggest that conditions under which historic BLH stands developed (Shelford 1954) have been altered to the extent that they can no longer maintain their former levels of species composition (Lockhart et al. 2010).

The regeneration process is critical for maintaining species composition and may be the ultimate cause for transitions in species assemblages. Regeneration is defined as the replacement of a mature individual by an individual of the same species (Grubb 1977, Poorter 2007). This process involves multiple stages which include seed production, seed dispersal, seedling emergence (germination), seedling establishment, and survival (Fig. 2.1). Sprouting is another form of regeneration that has proven useful in forest management, yet it remains contingent upon the success of prior establishment by the individual producing the sprout (Stanturf and Meadows 1994). Regeneration depends upon both internal and external controls, i.e., innate physiological and autecological mechanisms as well as abiotic, environmental factors including climate, disturbances, and interactions with other organisms (Price et al. 2001). Studies on the importance of regeneration, specifically seedling establishment, while essential, tend to be tedious, time consuming, and the time needed to develop an understanding of the temporally variable processes exceeds that of traditional ecological studies (Clark et al. 1999a). Specifically in BLH, there is a general lack of understanding regarding the regeneration process because of the difficulty in studying a highly variable ecosystem characterized by frequent seasonal flooding that varies within and among years (Wharton et al. 1982). Much of what is known about BLH regeneration pertains to physiological and absolute (i.e., how long a seedling can withstand continuous flooding) flood tolerance of seedlings and their survival from the establishment stage and beyond (e.g., Battaglia et al. 1999, Battaglia and Sharitz 2006, Denslow and Battaglia 2002, Elderd 2003, Hosner 1958, Jones et al. 1989, McCarthy and Evans 2000, McDermott 1954). Less focus has been applied to the initial regeneration stages and their combined effects (Battaglia et al. 2000, Jones et al. 1994, King 1995, Sharitz and Lee 1985, Streng et al. 1989, Sarneel et al. 2014).

Here I focus on regeneration in BLH where a history of natural and anthropogenic disturbances has synergistically produced a variegated system of floodplains, each under its own suite of environmental influences that have caused a range of dynamic complications. In this study, I review and synthesize existing literature on BLH regeneration by seed to identify the mechanisms by which regeneration processes, as affected by abiotic and biotic variables, may alter BLH species composition.
Figure 2.1. The stages of the regeneration process and major influential variables. Adapted from Price et al. 2001.

**Seed production**

Relatively few studies have evaluated seed production in BLH. Those that did confirmed findings from previous studies in other ecosystems which showed that heavier seeded species (e.g., *Quercus* spp.) produce fewer, larger seeds and light-seeded species (e.g., *Platanus occidentalis*) produced relatively many small seeds (Battaglia et al. 2008, Harper 1977, Jones et al. 1994, Streng et al. 1989). Streng et al. (1989) collected seedfall data for three fruiting seasons and calculated a much higher between-year variation in heavy-seeded species compared to light-seeded species.

Additional factors such as seed viability and/or herbivory can restrict recruitment, regardless of seed abundance. In a study of baldcypress (*Taxodium distichum*)-water tupelo (*Nyssa aquatica*) seed production, Sharitz and Lee (1985) determined that total seed production was adequate for successful regeneration, but that low seed viability, as well as insect parasitism and frugivory, were limiting factors in successful species recruitment. Jones et al. (1994) noted substantial disturbance to the forest floor (>25%) from feral pig rooting. Other research has demonstrated a strong preference of hogs for both hard and soft mast, as well as for the soft tissue of fresh herbs and seedlings (Wood and Roark 1980). The fruit of heavy-seeded species (e.g., *Quercus* spp., *Nyssa* spp., and *Carya* spp.) are so favored by wild hogs that the presence of hogs in a BLH stand may influence future overstory composition (Siemann et al. 2009). The
effect of seed herbivory from other species is less clear, but white-tailed deer (*Odocoileus virginianus*) are reported to browse on BLH seedlings (Castleberry et al. 1999, 2000). More investigation is needed to determine which frugivores, herbivores, and pests can influence certain species’ seed production and the extent of those effects.

**Seed dispersal**

Upon successful production of viable seeds, mature seeds must be dispersed to suitable regeneration sites within the environment. Dispersal depends on several factors including the adult tree fecundity, presence of dispersal vectors (animal, wind, water), phenology (late summer, fall, or spring), and species seed type (e.g., drupe, acorn, samara) (Boedeltje et al. 2004, Clark et al. 1998, 1999a, 1999b; Grubb 1977, Howe and Smallwood 1982, Matlack 1994, McEuen and Curran 2004, Russo et al. 2006). Several studies have addressed dispersal of various BLH species. In BLH ecosystems, animals, wind, gravity, and water are the major dispersal vectors for seeds (King and Allen 1996, McCarthy and Evans 2000, Reid et al. 2014, Schneider and Sharitz 1988, Sharitz and Lee 1985, Streng et al. 1989). Hard mast species such as oaks (*Quercus* spp.) and hickories (*Carya* spp.) are often desirable BLH species for wildlife (Stanturf et al. 2000), but they are poorly dispersed relative to wind-dispersed species such as sycamore (*Platanus occidentalis*) or elm (*Ulmus americana*) (Battaglia et al. 2008, Cosgriff and Brown 2004, McCarthy and Evans 2000, Streng et al. 1989). Hydrochory, seed dispersal via water, is an important means of dispersal for floodplain species (Reid et al. 2014, Schneider and Sharitz 1988) and is particularly important for bottomland oaks. For instance, overcup oak (*Quercus lyrata*) is capable of floating while viable (McCarthy and Evans 2000). Floodwater currents promote hydrochory functions by rolling or pushing seeds along the floodplain floor (McCarthy and Evans 2000, Schneider and Sharitz 1988). Seed transport by animals (e.g., blue jays, gray squirrels) is another important dispersal vector (McCoy et al. 2004) but is difficult to measure (Darley-Hill and Johnson 1981), which would potentially underestimate the dispersal distance of some of the heavier-seeded species that have relatively poor dispersal otherwise (Battaglia et al. 2008, Streng et al. 1989).

Dispersal vectors could influence BLH regeneration, even in the presence of a regular flooding regime (Battaglia et al. 1995). In a study of dispersal patterns in a 20-year-old abandoned agricultural field subject to natural seed rain in northeast Louisiana, Battaglia et al. (2008) determined that dispersal was not a limiting factor in the regeneration process for the light-seeded American elm or cedar elm (*Ulmus crassifolia*), both wind-dispersed, and the bird-dispersed sugarberry (*Celtis laevigata*). In the same study, the heavy seeded oak and hickory species were severely dispersal limited, with propagules absent from the site despite the presence of mature trees on the bordering levees. In an earlier study at the same site, Battaglia et al. (2002) documented that the six dominant tree species were all primarily dispersed by wind or birds with the exception of persimmon (*Diospyros virginiana*).

It is unclear how the altered hydrology of many floodplains has affected the efficiency of the various dispersal vectors within BLH communities. With the reduction or elimination of flooding in various locations, we would expect dispersal via hydrochory to become obsolete, which in
turn, may negatively influence dispersal of heavy-seeded species. Whether or not this has influenced regeneration and subsequent species composition remains unknown. The dynamics of animal-dispersed seeds is also unclear with regards to hydrologic modifications and requires further investigation.

**Germination**

Germination is primarily dependent on seed viability, soil moisture, soil temperature, ambient air temperature, and light availability (e.g., Evans and Etherington 1990, Holl 1999, McLaren and McDonald 2003, Sarneel et al. 2014). Within a forest ecosystem, microsites of varying quality create a mosaic of conditions in which different species may germinate depending on their tolerance to their specific location (Grubb 1977). The concept of “windows of opportunity” is important for consideration of germination success. This may refer to small disturbance events that create favorable germination conditions (Eriksson and Froborg 1996); or it could apply to species-specific germination windows, i.e., phenological differences in emergence timing (Rathcke and Lacey 1985, Sarneel et al. 2014, Streng et al. 1989). Within a single growing season, dynamic environmental conditions such as flood frequency may regulate germination success (Toner and Keddy 1997).

Seed viability in BLH species varies across the floodplain because of the influence of abiotic factors as well as natural intrinsic variation by species (Goodson et al. 2003). The percentage of viable seeds can range from 70-80 in sweetgum (*Liquidambar styraciflua*) to 35-45 in willow oak (*Quercus phellos*) (Bonner and Gammage 1967). The degree to which flooding affects seed viability in BLH is uncertain because there has been limited research. A few studies have examined germination success of select BLH species following various periods of complete inundation. Overcup oak can survive and even benefit from periods of prolonged flooding (Cosgriff and Brown 2004, Pierce and King 2007), whereas other oak species (swamp chestnut oak, *Quercus michauxii* and Nuttall oak, *Quercus texana*) are negatively affected by increased flooding (Briscoe 1961, Pierce and King 2007). In a baldcypress-water tupelo swamp Schneider and Sharitz (1986) reported a high proportion of nonviable baldcypress and water tupelo seeds which they attributed to naturally low viability and persistent flooding. Interestingly, one study documented the viability of sugarberry lasting up to five years in floodplain soils (Meadows et al. 2006). More research is yet needed to discern the inundation effects (or lack thereof) on seed viability and germination potential of different BLH species.

Other factors involved in the germination process such as soil conditions, temperature, and light have not been thoroughly evaluated in BLH systems. Battaglia et al. (2000) found light to positively affect emergence of swamp chestnut oak and sweetgum, except for when sweetgum was in full sunlight. Emergence was consistently lower in shade conditions (Battaglia et al. 2000). The mechanisms behind germination of BLH species remains a topic in need of substantial further research.
Establishment

Absolute tolerance to flood events of mature trees may not be as important as first-year germinants’ tolerance to flood events. In general, the species-specific time of germination influences the probability of successful seedling establishment. Seeds that germinate earlier in the season tend to have a lower chance of survival than those that germinate later, but the ones that do survive have the advantage of a longer growing season (Baskin and Baskin 1972, Gross 1984, Rathcke and Lacey 1985, Streng et al. 1989). Factors such as light availability and microtopography may also be regulators of germination success (Battaglia et al. 2000, Battaglia and Sharitz 2006, King and Allen 1996). Because BLH species are adapted to such a variable environment, it is possible that the timing of regeneration events, such as germination, are less sensitive to seasonal microsite cues and are more strongly controlled by intrinsic phenological patterns which developed over long time spans and are specific to each species, i.e., the germination “windows of opportunity” discussed in the previous section. Species-specific relationships between germination conditions and germination timing need to be evaluated in more detail if we are to better define the window of opportunity per species.

Strategies for tree species in relatively less hydrologically altered systems include high seed set (e.g., Ulmus spp.) with high seed (or seedling) mortality, and less frequent and abundant seed production with high seed (or seedling) survivorship (e.g., Quercus spp.) (Rathcke and Lacey 1985). The high natural diversity of BLH indicates that both reproductive strategies have succeeded in the presence of regular flooding events. Research by Streng et al. (1989) showed that BLH species emerged at different points during the growing seasons, the dates of which were significantly correlated with seed mass. Their data illustrated the use of different seasonal windows of opportunity per species, as well as the trend for lighter-seeded species to emerge before heavier seeded species (Streng et al. 1989).

If species are strongly linked to a temporal schedule as Streng et al. (1989) hypothesized, then the establishment stage becomes crucial for determining the success of newly emerged seedlings. Establishment is here defined as the survival of an individual from emergence through the first three growing seasons (Cooper et al. 1999). Successful establishment may determine a particular tree’s long-term role in the community, in that individuals with high initial growth after establishment have a better chance of reaching the canopy (Dekker et al. 2009). Similar to germination, this process is dependent on microsite quality variables such as soil moisture, soil temperature, ambient air temperature, light availability, soil nutrient content, and species-specific growth rate (Cooper et al. 1999, Grubb 1977). Much of the current regeneration literature has focused on this stage due to the vulnerability and high mortality rates of seedlings in the first few growing seasons (e.g., Boerner and Brinkman 1996, Gray and Spies 1997, Jones et al. 1994, Molofsky and Augspurger 1992, McDermott 1954, Sack 2004, Streng et al. 1989).

Few studies on BLH seedlings have followed individuals long enough to measure successful establishment (Jones et al. 1994, Streng et al. 1989), however, data collected even within the first season of growth could be valuable to understand limitations in recruitment. McDermott (1954) tested the effects of extended soil saturation on six BLH species, including alder (Alnus rugosa), sycamore, river birch (Betula nigra), American elm, winged elm (Ulmus alata), and red maple...
(Acer rubrum). He found that all of them recovered either rapidly or moderately after 32 days of continuous soil saturation. Hosner (1958) tested survival rates of a different variety of six BLH species – eastern cottonwood (Populus deltoides), boxelder (Acer negundo), black willow (Salix nigra), green ash (Fraxinus pennsylvanica), sweetgum, and silver maple (Acer saccharinum). With the exception of silver maple, all species survived at least eight days of submersion. Jones et al. (1989) also tested effects of flooding on seedlings of light-seeded species and found little to no reduced growth in waterlogged conditions. In all of the above cases light-seeded and moderately light-seeded species were able to survive and/or recover after substantial flood stress, despite some signs of reduced growth. One caveat to note is that each of these studies evaluated seedlings with at least one fully expanded leaf or a minimum of 7.6 cm height (Hosner 1958, Jones et al. 1989, McDermott 1954). The effects from flooding may be different if tested on newly emerged seedlings.

Concerning heavier-seeded species, Battaglia et al. (2000) examined mortality rates of newly emerged seedlings of swamp chestnut oak and determined mortality was affected primarily by water table levels. One reason for this is that flood stress reduces the photosynthetic capacity of seedlings (Pezeshki and Anderson 1997). Completely submerged seedlings tend to have lower survival rates than those that experience little or no flooding (Jones et al. 1989). When compared to light-seeded species in a natural BLH habitat, Streng et al. (1989) found seedlings of heavier-seeded species to have higher survivorship compared to lighter-seeded species; however this effect was countered by the greater abundance of lighter-seeded species which increased the chances of at least some of them surviving through the first growing season. The natural regeneration field-based studies conducted by Streng et al. (1989) and Jones et al. (1994) produced different results regarding flood-effects on seedling densities. Where the former study found that flooding significantly reduced the densities of light-seeded species, the latter determined that flooding had no effect on the density of light-seeded species. In both studies, heavy-seeded species were less affected by flooding and the probability of seedling survival of all species significantly increased after the first growing season and continued to do so during the first few years after germination.

Establishment is also dependent on seed type and how a seed is influenced by its specific location on the floodplain. Regular disruption from flood events may reduce the abundance of light-seeded species, producing a more comparable regeneration success rate with that of heavy-seeded species (Streng et al. 1989). However, if regular disturbance events (i.e., flooding) are eliminated or significantly reduced where they would otherwise limit the regeneration of the light-seeded species, the trajectory of succession in forest ecosystems could change in favor of the light-seeded species (Hobbs and Huenneke 1992). Over time, heavy-seeded species could become outcompeted by the more abundant, light-seeded species (Gee et al. 2014). Several studies have indicated an increased dominance by light-seeded species (Gee et al. 2014, Hanberry et al. 2012, Schneider and Sharitz 1986, Streng et al. 1989) and altered hydrologic processes may be at least partially responsible.

Light availability may also be a limiting factor on seedling establishment, though research suggests not to the same extent as flooding. Like the effects of flooding, the effects from light seem to vary by seed type. Because light-seeded species emerge earlier in the growing season...
(mid-Feb. to mid-April), light availability is greater due to the canopy not having fully expanded (Streng et al. 1989). Conversely, heavy-seeded species emerge later but their survivorship depends primarily on seed endosperm which can persist for up to one year (Grime and Jeffrey 1965, Sork 1987). This energy reserve in heavier seeds may explain their relatively high survivorship despite the shorter growing season within the first year, but light may become an important factor in subsequent establishment years. Battaglia et al. (2000) found significant interactions between light availability and water table level, driven by reduced establishment and survival in low light and high water table treatments. In contrast, other evidence did not find light to be a limiting factor through the establishment stage of regeneration, though its importance for survival increases beyond this stage (McCarthy and Evans 2000).

### Survival

The survival stage is the period from successful establishment (>3 years) and thereafter until mortality. In forest systems in general, as an individual tree ages, significant variables from those mentioned in the establishment stage (soil moisture, temperature, light availability, and growth rate) remain important, but some variables such as water table level, precipitation, and competition begin to play a larger role in the survival process (Grime 1977, Grubb 1977) which in turn, may influence trade-off strategies (e.g., Battaglia and Sharitz 2006, Beckage and Clark 2003, Oki et al. 2013, Sterck et al. 2006). Research focus on this life stage has become increasingly prominent with regard to climate change, drought risk, and the potential implications for stand management. Climate change predictions for North America include greater drought severity in the next several decades (Cook et al. 2015), including longer drought duration, higher heat severity, and greater drought frequency which may cause increased tree mortality rates and rapid die-off events (Allen et al. 2010, Dale et al. 2001, Iverson and Prasad 1998).

In BLH, as seedlings develop and transition into saplings and then mature individuals, the influence of flooding seems to decline as the importance of light increases (Battaglia and Sharitz 2006, Hall and Harcombe 2001, King and Allen 1996, McCarthy and Evans 2000, Oki et al. 2013). Theoretically every species has an adapted tolerance to a segment of the light spectrum because physiological attributes for one extreme are usually incompatible with those of the other extreme (Vallardares and Niinemets 2008). Thus, for optimal performance, species are generally recognized as shade-tolerant or shade-intolerant, but not both (Hall and Harcombe 1998); however, ontogenetic niche shifts may contribute to variability within species (Eriksson 2002, Gabler and Siemann 2012, Nakazawa 2015). There is evidence that shade tolerance and intolerance has effects on survival success among BLH species. Shade-tolerant species grew faster than shade-intolerant species in low light and shade-intolerant species grew faster than shade-tolerant species in high light in a southeast Texas floodplain (Lin et al. 2004). These results were consistent across both wet and dry sites indicating that slight or moderate flooding did not limit survival. Only when flooding was severe did it influence sapling survival in that shade-tolerant saplings experienced higher mortality (Lin et al. 2004). Another eastern Texas study suggested that canopy gaps, in combination with climatic variability (i.e., drought and
flood events), produced the most favorable conditions for species diversity, and flooding tended
to have a synchronous effect on all species at the sapling age (Hall and Harcombe 2001).
Battaglia and Sharitz (2006) found no difference between saplings of species and their relative
distance to the water table, however, when light was taken into consideration, shade-tolerant
species were generally found in drier areas and less shade-tolerant species occurred in more
open, wetter areas – supporting a flood/shade tradeoff strategy. When flooding is also removed
or reduced as a stressor, light availability may become more of a limiting factor for some BLH
species. Gee et al. (2014) documented a significant increase in the relatively shade-tolerant
sugarberry compared to the less shade-tolerant overcup oak following the construction of a ring
levee around a BLH site that had formerly been exposed to flooding. Removal of flooding can
also increase stem densities (Hanberry et al. 2012), presumably reducing light availability as
well.

Canopy gaps are also suspected to have a constructive role in controlling the success of
young trees because they release less shade-tolerant species, such as oaks (Allen et al. 2001)
from overstory competition (King and Allen 1996, Oliver et al. 2005) and promote species
greater survivorship of saplings growing in higher light conditions than those in shaded
conditions. Similar to Battaglia et al. (2000), their study found that the combined effects of
shading and flooding reduced the survival rate of overcup oak saplings, and saplings in shallow
flooded areas had a better chance of survival than ones in deeply flooded areas (McCarthy and
Evans 2000). Thus, sites that are open and wet may provide a better opportunity for bottomland
oaks to succeed, whereas drier sites that are shaded or open may allow other competitor species
such as sugarberry to perform better than oaks. The effect of canopy gaps on BLH composition
was examined by King and Antrobus (2005); they found that small-scale canopy gaps (i.e., gaps
created from the loss of a single tree) may not create sufficiently large openings with adequate
light to facilitate canopy replacement by shade-intolerant species. Without large-scale
disturbances, such as timber harvests or storm damage, floodplain forests will likely progress to
more shade-tolerant plant communities (King and Antrobus 2005).

Species Composition

Evaluating the role of regeneration in BLH systems may yield important insight into the
mechanisms behind compositional transitions. Studies such as Streng et al. (1989) and Jones et
al. (1994) demonstrate both the complexity and sensitivity of the regeneration process and how
easily recruitment can be influenced within the first few growing seasons. This critical period of
development is fundamentally important for understanding the current state of BLH systems.
Presently, BLH systems vary widely in hydrologic and geomorphic characteristics which
subsequently affect the associated vegetation. For instance, in west Tennessee the effects from
channelization have altered sedimentation deposition such that species composition has
transitioned to a more disturbance-tolerant community (Oswalt and King 2005). In eastern Texas
soil moisture is suspected to be a limiting factor controlling the western ranges of several BLH
species such that the presence or absence of certain species is more closely associated with the
availability of groundwater than with climate or precipitation patterns (Shankman et al. 2012). Several studies have demonstrated a relationship between reduced flooding and a shift from hydric to more mesic communities: Following the construction of a major dam in eastern Texas, downstream bottomland forest species displayed evidence of transitioning to upland species (Alldredge and Moore 2014). In some BLH of Louisiana and Arkansas, the sudden increase in understory sugarberry since the mid-1900s is suspected to have been caused by a rapid decline in flood frequency (Gee 2012, Gee et al. 2014). In southwestern Kentucky both mature and young stands appear to be moving towards more mesic species compositions as a result of human-altered hydrology (Shear et al. 2006); a similar pattern has also been documented in northeastern Arkansas (King and Antrobus 2005). By tracing some of these compositional changes back to stages in the regeneration process, further research could reveal the fundamental components of regeneration success as well as regeneration limitations.

Succession in BLH may also contribute to changes in species composition, but it is not the principal instigator of the transitions toward less flood tolerant communities in many hydrologically altered systems. The primary reason for this is because the progression from an overcup oak-water hickory type to an ash-elm-sugarberry type requires depositional processes to raise the floodplain elevation high enough to support the less flood-tolerant species (Hodges 1997, Lockhart 2010). In many areas with observed species composition changes, there have been no excessive depositional forces present since the hydrologic modifications (Shear et al. 2006, Alldredge and Moore 2014, Gee 2012, Gee et al. 2014). With little to no deposition, BLH stands on floodplain flats will move towards an overcup oak-water hickory type which may endure for hundreds of years (Hodges 1997). If deposition processes are present, BLH stands can transition towards an elm-ash-sugarberry type which may also persist for centuries, but the final climax type is an oak-hickory forest which is estimated to take a minimum of 600 years to develop (Shelford 1954, Hodges 1997, Lockhart et al. 2010). The rate at which hydric BLHs have been transitioning to mesic stands such as ash-elm-sugarberry exceeds that which is predicted for natural BLH succession (Shelford 1954, Hodges 1997). With the lack of deposition and the reduction of flooding in many BLH sites, it is doubtful that species composition changes at these sites are unrelated to human-altered floodplain hydrology.

As with most ecological processes, multiple variables are responsible for the BLH species assemblages recognized today. Hence, flooding on its own is not entirely responsible for maintaining BLH communities in their natural conditions. Geomorphic processes, such as the types and rates of sedimentation, also influence regeneration processes and tree species composition (Hupp and Osterkamp 1996, Oswalt and King 2005, Pierce and King 2007). Through manipulation of soil characteristics, flood regimes affect site composition by influencing soil drainage, aeration, and soil redox potential, among other attributes (Kupfer et al. 2010). Drought is also expected to increase in the future and the effects of drought may be intensified due to altered surface and subsurface hydrology affecting soil moisture and hence, seedling survival (Markesteijn and Poorter 2009). In areas such as east Texas drought has become a more prominent event in BLH forests in recent years and may extend its effects eastward in the presence of climate change (Martinez-Vilalta et al. 2012, Pederson et al. 2012). Although these disturbances are largely outside of this review, a process-based understanding of
regeneration will facilitate our broader understanding of the effects of drought and sedimentation processes on future forest composition.

Other past and present disturbances such as wind storms, parasitism/herbivory, and fire must also be considered. Light availability, precipitation, soil nutrients, soil texture, and canopy gap size are also regulators in species site colonization and survival (Robertson and Augspurger 1999). A common issue in BLH with reduced or eliminated flooding is the colonization of many shade-tolerant species (King and Antrobus 2001, 2005; Hanberry et al. 2012). Without select harvesting, thinning, or other regular canopy disturbances shade-tolerant trees can thrive in high densities within the understories, shading out competitors that require full sunlight (e.g., oaks) (King and Antrobus 2005, Hanberry et al. 2012). Evidence suggests that flooding alone cannot always maintain shade-intolerant tree species and the presence of large gaps is also necessary to promote their regeneration (King and Antrobus 2001; 2005). In much of the range of BLH, large canopy gaps can easily be produced by hurricanes which can cause extensive wind damage and shift succession to a different state (Battaglia et al. 1999). Large-scale disturbances such as channel migration can affect forest edge composition and structure; migration rates on annual-decadal scales support lower tree density, basal area, and richness in contrast to decadal-centennial migration rates which allow for greater density, basal area, and richness (Meitzen 2009). Collectively, all of the variables that contribute to the structure, composition, and function of BLH stands are important in time and space, but flooding is the primary disturbance that played the greatest role in developing BLH ecosystems.

Conclusion

Within the past century BLH have exhibited a wide range of changes in stand development and species composition as a result of altered hydrology in rivers and floodplains. Evaluating the role of regeneration in BLH systems may yield important insight into the mechanisms behind compositional transitions. Research to date has revealed important trends between abiotic and biotic processes that promote and inhibit successful regeneration of BLH species, but much remains in need of further investigation. The influence of herbivory, frugivory, and pests on seed production is not fully understood among species; those species more heavily targeted could become less prevalent in the future canopy. Wind and bird-dispersed species seem to have an advantage reaching favorable regeneration sites compared to gravity and water-dispersed species, but how these vectors have been affected in floodplains with altered hydrology is not directly known. We also have yet to identify the mechanisms behind germination windows of opportunity among species and what drives the timing of seedling emergence. Although I have made progress discovering promoters and inhibitors of seedling establishment, more long term studies are necessary to detect successful seedling establishment and how it relates to germination timing, seed type, light availability, location on the floodplain, and canopy gaps. The high complexity involved in recruitment as well as the vulnerability of species at that age in development provides many open avenues for further research in this area.
CHAPTER 3. FLOODPLAIN FOREST TREE SEEDLING RESPONSE TO VARIATION IN FLOOD TIMING AND DURATION

Introduction

Floodplain forest species diversity is driven, in part, by variation in disturbance regime (Connell 1978, Parolin 2012). Flood patterns create heterogeneity in microsite quality from small differences in elevation across a floodplain which, in turn, influence flood timing and duration (Titus 1990, Hodges 1997). Over time, these various microsite conditions have contributed to niche partitioning among tree species which has ultimately influenced floodplain forest species assemblage through space and time. In particular, differences in species’ regeneration niches can account for long-term coexistence of various species (Grubb 1977).

The regeneration process is a sensitive period in floodplain tree species’ life cycles and can strongly affect tree community composition. Within this process, the seedling stage is one of the most vulnerable periods of a tree’s life (Kitajima and Fenner 2000). A suite of factors influences seedling emergence, establishment, growth, and survival with the potential of shaping tree species composition long-term. Different strategies among floodplain tree species enhance seedling survival in floodplain systems. Strategies reflect species’ adaptations to their distinctive regeneration niche, increasing the chance of an individual replacing a mature member of its own species (Grubb 1977). Heavier-seeded species (e.g., Quercus spp.) generally produce fewer, larger seeds, and light-seeded species (e.g., Ulmus americana) produce relatively many small seeds (Harper 1977, Streng et al. 1989, Jones et al. 1994, Schone and Jentsch 2007, Battaglia et al. 2008). Heavy-seeded species generate more robust seedlings with greater energy reserves whereas light-seeded species yield small seedlings that are relatively more abundant. Compared to small seedlings of light-seeded species, a larger seedling with more energy reserves may be less vulnerable to disturbance (e.g., flooding) at the individual level (Parolin 2012). But at the cohort level, many small seedlings may be less sensitive to disturbance relative to fewer heavy-seeded species.

In addition to seedling size and abundance, there is evidence of emergence phenology affecting first-year seedling survival. Seeds that germinate earlier in the season are more vulnerable to disturbance, but if an early germinant seedling survives the disturbance event, it has the advantage of a longer growing season (Baskin and Baskin 1972, Gross 1984, Rathcke and Lacey 1985, Streng et al. 1989). There is further evidence that time of seedling emergence among floodplain species is predictable, with light-seeded species emerging earlier in the growing season compared to heavy-seeded species (Streng et al. 1989). Annual spring floods in floodplain forests may therefore differentially affect species’ emergence depending on extent of temporal and spatial overlap between emergence and flooding. In Amazonian floodplain forests, which support over 1000 species of flood tolerant trees, species exhibit a wide range of regeneration adaptations to variations in flood intensity (Parolin 2012). In temperate floodplain forests, many light-seeded seedlings tolerate brief periods of inundation (McDermott 1954; Hosner 1958, 1960; Jones et al. 1989), but little work has been done on heavy-seeded species.
In general, research on tree regeneration has often focused on the establishment stage, which includes individuals ≥ 1 year of age (Boerner and Brinkman 1996, Gray and Spies 1997, Molofsky and Augspurger 1992), but much remains to be learned about first-year seedlings. First-year seedling probability of surviving flooding can be significantly less than second-year seedlings (Streng et al. 1989, Jones et al. 1994). Along the Rhine River in Europe, survival of first year woody seedlings was closely tied to seedling height and flood duration (Deiller et al. 2003). In Amazonian floodplains, the tolerance to complete submergence of new tree seedlings varies from a few days to several weeks (Parolin et al. 2004). Some light-seeded temperate species (e.g., *Celtis laevigata*) tolerate complete inundation (Hosner 1958, 1960). Jones et al. (1989) revealed the high vulnerability of newly emerged seedlings to short-duration floods (3-4 days of complete inundation) from testing *Acer rubrum, Betula nigra, Platanus occidentalis, Quercus pagoda,* and *U. americana.* The same study also tested these species under waterlogged soil conditions and found high survival among all species, further indicating that flood depth could also have a significant effect on survival. Much is still to be learned about seedling tolerance of more heavy-seeded species in completely submerged conditions. Identifying these species-specific responses to variations in flood timing, depth, and duration within the regeneration process is increasingly important in the context of altered floodplain hydrology.

Changes in flood behavior in the past century in North American can cumulatively be attributed to channel adjustments, precipitation shifts, land-use changes, dam and levee construction, and channel incision (Pinter et al. 2006, Hudson et al. 2008). As a result, river floodplains have experienced changes in flood water regimes, ground water levels, erosion patterns, and sedimentation processes (Gore and Shields 1995, Stanturf et al. 2001, Pinter et al. 2006, Hudson et al. 2008). Many studies have demonstrated a relationship between reduced flooding and a shift from hydric to more mesic communities (Shear et al. 2006, Alldredge and Moore 2014, Hanberry et al. 2012). Research also suggests that the sudden increase of *C. laevigata* in the understory since the mid-1900s in some bottomland forests in Louisiana is due to a rapid decline in flood frequency (Gee 2012, Gee et al. 2014) and alteration of the light environment (Oliver et al. 2005) which may also be linked to reduced flooding leading to increased stem densities (Hanberry et al. 2012; King and Keim 2019). In southwestern Kentucky, both mature and young stands appear to be moving from hydric towards more mesic species composition as a result of human-altered hydrology (Shear et al. 2006); King and Antrobus (2005) documented a similar pattern in northeastern Arkansas. These patterns are not just confined to North America; many temperate floodplains in Europe are experiencing diminished regeneration of *Quercus* spp. linked to drier floodplain conditions (Stojanović, et al. 2015).

The purpose of this study was to identify differences in flood tolerance among species within the regeneration process. I conducted a controlled greenhouse experiment using both light- and heavy-seeded species from the Lower Mississippi River Alluvial Valley that ranged in flood and shade tolerance levels (Table 3.1). Specifically, I evaluated how the effects of complete submergence on seedlings varied by 1) species; 2) seedling age; and 3) flood duration. I hypothesized that: 1) mortality would increase the earlier a flood event occurs after emergence; and 2) longer flood duration would have greater negative effects on light-seeded species’ survival relative to heavy-seeded species.
Table 3.1. The flood and shade tolerance classifications, and seed mass, of six floodplain forest species from the Lower Mississippi River Alluvial Valley (McKnight et al. 1980).

<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>Flood tolerance</th>
<th>Shade tolerance</th>
<th>Seed mass (g)(^a)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Celtis laevigata</em> (sugarberry)</td>
<td>moderately tolerant</td>
<td>very tolerant</td>
<td>0.065(^b)</td>
</tr>
<tr>
<td><em>Fraxinus pennsylvanica</em> (green ash)</td>
<td>moderate</td>
<td>intermediate</td>
<td>0.025</td>
</tr>
<tr>
<td><em>Quercus lyrata</em> (overcup oak)</td>
<td>moderate</td>
<td>intolerant</td>
<td>6.048</td>
</tr>
<tr>
<td><em>Quercus phellos</em> (willow oak)</td>
<td>moderate – weak</td>
<td>intolerant</td>
<td>1.152</td>
</tr>
<tr>
<td><em>Quercus texana</em> (Nuttall oak)</td>
<td>moderate</td>
<td>intolerant</td>
<td>5.040</td>
</tr>
<tr>
<td><em>Ulmus americana</em> (American elm)</td>
<td>moderate – weak</td>
<td>tolerant</td>
<td>0.006</td>
</tr>
</tbody>
</table>

\(^a\) Mean seed mass based on seeds supplied from Louisiana Forest Seed Co. (2017).
\(^b\) Mass represents only the nulet of the seed, not the full drupe.

Methods

This experiment was conducted at a greenhouse facility at Louisiana State University Agricultural Center (LSU) during spring-summer 2017 and 2018. To test seedling response to variation in flood timing and duration, the experiment was a split-plot design with flood duration serving as the main plot treatment and flood timing was the sub-plot treatment. Flood duration treatments were non-flooded control, 5 days, 15 days, and 25 days. To simulate flood timing, seedlings were grown to 3-weeks, 6-weeks, or 9-weeks post-germination before testing to represent the onset of early, mid, or late spring flooding (Table 3.2).

I tested three lighter-seeded species: *U. americana*, *C. laevigata*, and *F. pennsylvanica*; and three heavy-seeded species: *Quercus lyrata*, *Quercus texana*, and *Quercus phellos*. These species vary in flood tolerance, shade tolerance, and seed size (Table 3.1). This assemblage was selected because many formerly *Quercus*-dominated floodplain sites have been transitioning into *Celtis/ Fraxinus/Ulmus* spp. communities (Tremolieres et al. 1998, Oliver et al. 2005, Haase and Glaser 2009, Gee et al. 2014). *Ulmus americana*, *C. laevigata*, and *Q. texana* were tested in 2017 and *C. laevigata*, *F. pennsylvanica*, *Q. lyrata*, and *Q. phellos* were tested in 2018. *Celtis laevigata* was used in both years to verify experiment precision and consistency.

Seeds were obtained from Louisiana Forest Seed Co. in early spring of each year and stored at 4°C until the experiment began in early March of each year. In an indoor greenhouse, seedlings were germinated in flats of conventional potting soil. Within 1-5 days of emergence, seedlings were transplanted to individual pots filled with sterilized mineral silt sediment and fertilized with 6 g of Osmocote 14-14-14 slow release fertilizer. Seedlings were transplanted with the potting soil directly around their roots to avoid root damage and limit disturbance to the root system.
Table 3.2. Greenhouse experiment design to test the effects of flood timing and flood duration on first-year seedlings of bottomland hardwood forest species. This design was implemented for each species.

<table>
<thead>
<tr>
<th>Flood Duration</th>
<th>5 d</th>
<th>15 d</th>
<th>25 d</th>
</tr>
</thead>
<tbody>
<tr>
<td>Flood</td>
<td>3-week</td>
<td>3-week</td>
<td>3-week</td>
</tr>
<tr>
<td>Timing</td>
<td>6-week</td>
<td>6-week</td>
<td>6-week</td>
</tr>
<tr>
<td>Control</td>
<td>Non-flooded</td>
<td>Non-flooded</td>
<td>Non-flooded</td>
</tr>
</tbody>
</table>

After transplanting, seedlings were grown inside the greenhouse until treatment initiation. Seedlings were watered daily and pots were rotated weekly to reduce placement bias within the greenhouse. Seedlings were randomly assigned a treatment initiation date based on emergence date; once they reached their designated age, they were randomly assigned to a treatment. Seedlings were flooded to complete submergence in outdoor plastic, white, translucent tanks (1 x 1 x 0.75 m). We implemented complete submergence because bottomland seedlings have demonstrated tolerance to saturated soils (McDermott 1954, Jones et al. 1989). Tank assignment was random among treatments groups. Tanks were filled with tap water upon treatment initiation and once a treatment began, water was only added if evaporation risked exposing seedling leaves or stems. Control groups were placed in identical un-flooded tanks and watered daily. Each treatment group consisted of an average of 16 individual seedlings except for the 15-day, 9-week green ash treatment which was omitted due to lack of available seedlings. Seedlings were exposed to 100% ambient light conditions during both outdoor and indoor periods of the experiment to avoid shade-stress (Battaglia et al. 2000, Lin et al. 2004, Battaglia and Sharitz 2006, Mann et al. 2008). Dissolved oxygen and water temperature were measured in each tank throughout the treatments. After treatment conclusion, seedlings were removed from tanks and placed inside the greenhouse where they were watered daily and rotated weekly.

Seedling morphological measurements were made immediately before and within 24 hours after treatments, including the control groups; this included stem height, number of true leaves, and stem diameter at either 4 cm (Quercus spp.) or 2 cm (U. americana, F. pennsylvanica, C. laevigata) above the soil surface. I monitored post-treatment seedling survival for 30 days after treatment completion. Seedlings were marked as dead if the stem was fully devoid of fleshy, green-colored tissue.

Analysis

I used logistic regression to analyze differences ($\alpha < 0.05$) in effects of flood duration on each species. Survival was modeled using main and interactive effects of flood treatment and seedling age. Model performance was ranked using Akaike’s information criterion, and model fit was evaluated using McFadden’s and Nagelkerke pseudo R\(^2\) which compares a model without predictors to a model including all predictors (Hu et al. 2006, Smith and McKenna 2013). Among age-groups, post-hoc pairwise differences in the effects of flood treatments were
determined by Z-tests on two proportions that were Bonferroni corrected. Three-week seedling survival probability was modeled based on cumulative days submerged and results were assessed using a -2-log likelihood method. Model fit was based on the change in deviance between the model and the null model (no variables included), and a change in deviance greater than the critical Chi square (α < 0.05) determined whether the modeled relationship was significant. To assess the effects of submergence on seedling morphology, analysis of variance (ANOVA) was run for all species treatments and age groups separately to evaluate stem height, stem diameter, and number of leaves compared to control groups. Tukey’s HSD tests were run when significant differences were found (α < 0.05). All analyses were performed in R (The R Group, 2020).

Results

Seedling Morphology

I evaluated the effects of food duration and timing on seedling survival on a total of 1432 seedlings (Table 3.3). There was no effect of year (2017 vs 2018) on C. laevigata survival across all treatments (p > 0.05), nor was there interaction between dissolved oxygen and survival or water temperature and survival (p > 0.05).

Table 3.3. The cumulative number of seedlings tested by age group, and the total, of six bottomland hardwood species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of seedlings tested</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>3 weeks</td>
</tr>
<tr>
<td>Celtis laevigata</td>
<td>155</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>80</td>
</tr>
<tr>
<td>Quercus lyrata</td>
<td>120</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>42</td>
</tr>
<tr>
<td>Quercus texana</td>
<td>59</td>
</tr>
<tr>
<td>Ulmus americana</td>
<td>43</td>
</tr>
</tbody>
</table>
Table 3.4. Mean values of the three light-seeded species' morphological measurements (±SE) for each age group pre-treatment and the mean differences (±SE) between pre- and post-treatment morphology of the experimental groups and the control groups. Each treatment group was compared to a non-flooded control group that was measured at the same time as the treatment group before and after flooding. Significant differences (p < 0.05) between changes in morphology of each treatment group and its control group are identified by (*).

<table>
<thead>
<tr>
<th>Species</th>
<th>Age  (weeks)</th>
<th>Stem Height (cm) Pre-treatment</th>
<th>Stem Diameter (mm) Pre-treatment</th>
<th>No. Leaves Pre-treatment</th>
<th>No. Days Submerged</th>
<th>Change in Stem Height (cm) Control Groups</th>
<th>Change in Stem Diameter (mm) Control Groups</th>
<th>Change in No. Leaves Experimental Groups</th>
<th>Change in No. Leaves Control Groups</th>
<th>Proportion Survived (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Celtis laevigata</td>
<td>3</td>
<td>8.48 (0.25)</td>
<td>1.13 (0.02)</td>
<td>7.2 (0.22)</td>
<td>5</td>
<td>-0.02 (0.04)</td>
<td>1.02 (0.40)</td>
<td>-0.10 (0.03)</td>
<td>0.08 (0.09)</td>
<td>3.5* (0.9)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>20.3 (0.64)</td>
<td>1.91 (0.05)</td>
<td>7.9 (0.76)</td>
<td>15</td>
<td>-0.74* (0.37)</td>
<td>3.15 (0.45)</td>
<td>0.0 (0.0)</td>
<td>0.0 (0.07)</td>
<td>-8.4* (1.6)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>35.2 (1.20)</td>
<td>3.05 (0.09)</td>
<td>44.5 (2.96)</td>
<td>25</td>
<td>0.00* (0.76)</td>
<td>2.2 (0.18)</td>
<td>-0.02 (0.03)</td>
<td>0.17 (0.11)</td>
<td>-2.7 (0.7)</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>3</td>
<td>6.10 (0.28)</td>
<td>1.20 (0.03)</td>
<td>5.9 (0.17)</td>
<td>5</td>
<td>-5.10* (1.89)</td>
<td>8.83 (0.86)</td>
<td>-0.04* (0.03)</td>
<td>1.08 (0.15)</td>
<td>-16.5* (2.5)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>10.0 (0.44)</td>
<td>1.98 (0.11)</td>
<td>10.6 (0.26)</td>
<td>15</td>
<td>-0.09 (0.07)</td>
<td>1.28 (0.26)</td>
<td>-0.03 (0.01)</td>
<td>0.17 (0.09)</td>
<td>-21.0 (4.6)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>11.5 (0.75)</td>
<td>1.82 (0.12)</td>
<td>11.5 (0.65)</td>
<td>25</td>
<td>-0.33* (1.06)</td>
<td>3.65 (0.03)</td>
<td>-0.05* (0.12)</td>
<td>0.55 (0.6)</td>
<td>-42.3* (5.6)</td>
</tr>
<tr>
<td>Ulmus americana</td>
<td>3</td>
<td>6.29 (0.32)</td>
<td>1.00 (0.00)</td>
<td>7.14 (0.22)</td>
<td>5</td>
<td>0.00* (0.03)</td>
<td>1.50 (0.20)</td>
<td>0.0 (0.00)</td>
<td>0.0 (0.06)</td>
<td>-0.3 (0.08)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>18.2 (0.94)</td>
<td>1.76 (0.07)</td>
<td>14.6 (0.58)</td>
<td>15</td>
<td>-0.31* (0.55)</td>
<td>6.17 (1.12)</td>
<td>-0.13* (0.12)</td>
<td>1.93 (0.21)</td>
<td>-9.0* (0.6)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>42.2 (1.88)</td>
<td>3.27 (0.11)</td>
<td>36.2 (2.61)</td>
<td>25</td>
<td>0.00* (0.93)</td>
<td>2.08 (0.02)</td>
<td>-0.05* (0.09)</td>
<td>0.05 (0.09)</td>
<td>-9.8* (1.5)</td>
</tr>
</tbody>
</table>


Table 3.5. Mean values of the three heavy-seeded species’ morphological measurements (±SE) for each age group pre-treatment and the mean differences (±SE) between pre- and post-treatment morphology of the experimental groups and the control groups. Each treatment group was compared to a non-flooded control group that was measured at the same time as the treatment group before and after flooding. Significant differences (p < 0.05) between changes in morphology of each treatment group and its control group are identified by (*).

<table>
<thead>
<tr>
<th>Species</th>
<th>Age (weeks)</th>
<th>Stem Height (cm) Pre-treatment</th>
<th>Stem Diameter (mm) Pre-treatment</th>
<th>No. Leaves Pre-treatment</th>
<th>No. Days Submerged</th>
<th>Change in Stem Height (cm) Experimental Groups</th>
<th>Change in Stem Height (cm) Control Groups</th>
<th>Change in Stem Diameter (mm) Experimental Groups</th>
<th>Change in Stem Diameter (mm) Control Groups</th>
<th>Change in No. Leaves Experimental Groups</th>
<th>Change in No. Leaves Control Groups</th>
<th>Proportion Survived (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Quercus lyrata</td>
<td>3</td>
<td>14.9 (0.41)</td>
<td>1.84 (0.05)</td>
<td>10.6 (0.40)</td>
<td>5</td>
<td>-0.62 (0.25)</td>
<td>0.21 (0.01)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.75 (0.01)</td>
<td>0.75 (0.01)</td>
<td>0.01 (0.01)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>16.9 (0.62)</td>
<td>2.05 (0.08)</td>
<td>11.6 (0.47)</td>
<td>5</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>19.5 (0.50)</td>
<td>2.42 (0.07)</td>
<td>11.7 (0.50)</td>
<td>5</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>3</td>
<td>12.6 (0.43)</td>
<td>1.59 (0.06)</td>
<td>15.9 (0.67)</td>
<td>5</td>
<td>-0.15 (0.19)</td>
<td>0.30 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.70 (0.05)</td>
<td>0.70 (0.05)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>12.0 (0.29)</td>
<td>1.49 (0.04)</td>
<td>12.8 (0.75)</td>
<td>5</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>18.3 (0.71)</td>
<td>2.02 (0.05)</td>
<td>18.9 (1.09)</td>
<td>5</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td>Quercus texana</td>
<td>3</td>
<td>21.1 (0.85)</td>
<td>2.38 (0.09)</td>
<td>10.8 (0.74)</td>
<td>5</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>30.1 (1.18)</td>
<td>3.62 (0.10)</td>
<td>20.0 (0.93)</td>
<td>5</td>
<td>-0.13 (0.06)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
<tr>
<td></td>
<td>25</td>
<td>40.0 (0.97)</td>
<td>4.85 (0.08)</td>
<td>26.9 (1.15)</td>
<td>5</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.00 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.50 (0.00)</td>
<td>0.00 (0.00)</td>
</tr>
</tbody>
</table>
Seedling height varied among both species and age groups, with *Quercus* species displaying the greatest mean height among species at age 3-weeks (\( \bar{x} \geq 12.6 \text{ cm}; n = 173 \)) compared to the other three species (\( \bar{x} < 8.5 \text{ cm}; n = 185 \)) (Tables 3.4 and 3.5). This pattern changed among the 9-week-old seedlings in that *U. americana* (\( \bar{x} = 42.2 \text{ cm}; n = 64 \)), followed by *Q. texana* (\( \bar{x} = 40.0 \text{ cm}; n = 75 \)), and *C. laevigata* (\( \bar{x} = 35.2 \text{ cm}; n = 120 \)) developed the tallest seedlings. Although stem diameter was measured at 4 cm above the soil surface in oaks, and 2 cm above the soils surface in the other three species, the mean stem diameters of the 3-week seedlings were greatest among the *Quercus* species (\( \bar{x} \geq 1.59 \text{ mm} \)). The 9-week species with the largest stem diameter s were *Q. texana* (\( \bar{x} = 4.85 \text{ mm}; n = 75 \)), *U. americana* (\( \bar{x} = 3.27 \text{ mm}; n = 64 \)), and *C. laevigata* (\( \bar{x} = 3.05 \text{ mm}; n = 120 \)). All three *Quercus* species had the greatest average number of leaves at 3-weeks compared to the other species (\( \bar{x} \geq 10; n = 173 \)); the 9-week-old species with the greatest number of leaves was *C. laevigata* (\( \bar{x} = 44.5; n = 120 \)) followed by *U. americana* (\( \bar{x} = 36.2; n = 64 \)).

Among the light-seeded species, the 25-day treatment produced the greatest loss of living stem and leaf quantity (Table 3.4). Leaf loss was the most consistent morphological change after the 15-day and 25-day treatments. Among the *Quercus* species, less change relative to the light-seeded species was observed compared to the controls (Table 3.5). Significant morphological differences (\( p < 0.05 \)) among treatment and controls were primarily observed in the 25-day treatment group. Across all species, little variation occurred in stem diameters before and after treatments. Small changes in the location of the soil surface relative to the stem after treatments were common among individuals, even with careful placement and removal of pots into and out of the tanks. After the 25-day treatments the soil surface was relatively fluid until the water completely drained, causing uncertainty in the replication of diameter measurements after treatment. With that caveat in mind, when compared to the controls, the only differences in stem diameter occurred in groups submerged for 25 days (\( p < 0.05 \)).

**Survival**

The 3-week-old seedlings demonstrated the greatest negative response to flood duration compared to seedlings at ages 6- and 9-weeks (Fig. 3.1) based on the pairwise differences in the effects of flood treatments. *Ulmus americana*, *F. pennsylvanica*, and *C. laevigata* had reduced survival after the 15- and 25-day treatments (\( p < 0.05 \)); the former two species did not have any 3-week-old seedlings survive the 15- or 25-day treatments. *Celtis laevigata* displayed 25% and 3% survival after 15-day and 25-day treatments, respectively (\( p < 0.05 \)). Among 6-week-old seedlings, *C. laevigata* and *U. americana* showed reduced survival after the 15- and 25-day treatments (\( p < 0.05 \)), and *F. pennsylvanica* declined in survival after the 25-day treatment (\( p < 0.05 \); Fig. 3.2). *Ulmus americana* showed the greatest sensitivity to flooding among seedlings at 9-weeks of age, with both the 15- and 25-day treatments resulting in less than 50% survival (\( p < 0.05 \); Fig. 3.3). *Celtis laevigata* survival dropped below 80% (\( p < 0.05 \)), but *F. pennsylvanica* showed no significant reduction in survival after 25-days of submergence (\( p < 0.05 \)).

*Quercus texana* demonstrated the greatest survival rates after the 15-day (92%) and 25-day treatments (64%) for 3-week-old seedlings (\( p < 0.05 \); Fig. 3.1). Among the *Quercus* spp. of this age group, only the 25-day treatment resulted in a decline in survival from the controls (\( p <
For 6-week-old seedlings, *Q. texana* displayed the greatest overall survival, with 74% survival after 25 days submergence which did not differ (p > 0.05) from the controls (Fig. 3.2). Among the other two *Quercus* species however, the 15- and 25-day treatments significantly decreased seedling survival relative to the controls (p <0.05; Fig. 3.2). Of the 9-week-old seedlings, only *Q. phellos* showed sensitivity to the flood treatments, with 43% survival after 25-days submerged (p < 0.05; Fig. 3.3). The other two *Quercus* species showed no difference in survival after the treatments relative to the controls (p > 0.05).

Five days of submergence did not affect survival of any species of any age group. Survival after 15-days of flooding varied from complete mortality of 3-week-old *U. americana* to 92% survival of *Q. texana* (Fig. 3.1). After 25 days of flooding survival ranged from complete mortality of *F. pennsylvanica* and *U. americana* to 64% survival of *Q. texana* (Fig. 3.1). Among 6-week-old seedlings, the 25-day treatment reduced survival of all species except *Q. texana* (p < 0.05; Fig. 3.2). Only the 25-day treatment affected survival of 9-week-old seedlings, and only for *C. laevigata, U. americana,* and *Q. phellos* (p < 0.05; Fig. 3.3). The other two shorter-duration treatments on the 9-week-old seedlings had minimal influence on survival.

![Graph](image)

**Figure 3.1.** Survival of seedlings at 3-weeks post-emergence after complete submergence in one of three treatments and a control. Bars indicated by the same letters are not significantly different (p < 0.05); tests of significance were restricted to groups within species. The non-flooded control group is represented by “0” days submerged. Species Codes: CELA = *Celtis laevigata*, FRPE = *Fraxinus pennsylvanica*, QULY = *Quercus lyrata*, QUPH = *Quercus phellos*, QUTE = *Quercus texana*, ULAM = *Ulmus americana*. 

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Figure 3.2. Survival of seedlings at 6-weeks post-emergence after complete submergence in one of three treatments and a control. Bars indicated by the same letters are not significantly different ($p < 0.05$); tests of significance were restricted to groups within species. The non-flooded control group is represented by “0” days submerged. Species Codes: CELA = Celtis laevigata, FRPE = Fraxinus pennsylvanica, QULY = Quercus lyrata, QUPH = Quercus phellos, QUTE = Quercus texana, ULAM = Ulmus americana.

Figure 3.3. Survival of seedlings at 9-weeks post-emergence after complete submergence in one of three treatments and a control. Bars indicated by the same letters are not significantly different ($p < 0.05$); tests of significance were restricted to groups within species. The non-flooded control
group is represented by “0” days submerged. Species Codes: CELA = *Celtis laevigata*, FRPE = *Fraxinus pennsylvanica*, QULY = *Quercus lyrata*, QUPH = *Quercus phellos*, QUTE = *Quercus texana*, ULAM = *Ulmus americana*.

Flood treatment was a significant predictor of seedling survival among all species (Table 3.6). The interaction of treatment and seedling age produced the best fit model for *C. laevigata* (p < 0.05), *F. pennsylvanica* (p < 0.001), and *Q. lyrata* (p < 0.05). *Quercus phellos*, *Q. texana*, and *U. americana* survival was best explained by both treatment and age, however, only treatment was significant in the models (p < 0.001). The effects of age on survival was significant for *C. laevigata* (p < 0.001), *F. pennsylvanica* (p < 0.001), and *Q. lyrata* (p < 0.05), but not for the other species.

The 3-week-old seedling survival probability was based on cumulative days submerged and was significant for all species (Chi sq. < 0.01; Fig. 3.4). The 50% survival estimate occurred the earliest after flooding onset in *U. americana* (~8 days) followed by *C. laevigata* and *F. pennsylvanica*. The *Quercus* spp. 50% survival estimate occurred after ~17 days in *Q. phellos* and even later in both *Q. lyrata* and *Q. texana*.

### Table 3.6. The three best models ranked in descending order by Akaike’s information criterion corrected for a small sample size (AIC<sub>c</sub>); (+ns) variable included and not significant, (+) variable included and significant, (−) variable not included.

<table>
<thead>
<tr>
<th>Species</th>
<th>Age</th>
<th>Treatment</th>
<th>Age*Treatment</th>
<th>AIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>ΔAIC&lt;sub&gt;c&lt;/sub&gt;</th>
<th>McFadden’s R&lt;sup&gt;2&lt;/sup&gt;</th>
<th>Nagelkerke R&lt;sup&gt;2&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Celtis laevigata</em></td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>215.11</td>
<td>0.00</td>
<td>0.586</td>
<td>0.712</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>222.09</td>
<td>-6.98</td>
<td>0.568</td>
<td>0.696</td>
</tr>
<tr>
<td></td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>323.12</td>
<td>-108.01</td>
<td>0.362</td>
<td>0.492</td>
</tr>
<tr>
<td><em>Fraxinus pennsylvanica</em></td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>104.85</td>
<td>0.00</td>
<td>0.542</td>
<td>0.683</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>122.14</td>
<td>-17.29</td>
<td>0.449</td>
<td>0.595</td>
</tr>
<tr>
<td></td>
<td>−</td>
<td>+</td>
<td>−</td>
<td>153.50</td>
<td>-48.65</td>
<td>0.291</td>
<td>0.420</td>
</tr>
<tr>
<td><em>Quercus lyrata</em></td>
<td>−</td>
<td>−</td>
<td>+</td>
<td>191.93</td>
<td>0.00</td>
<td>0.234</td>
<td>0.346</td>
</tr>
<tr>
<td></td>
<td>+</td>
<td>+</td>
<td>−</td>
<td>197.60</td>
<td>-5.67</td>
<td>0.208</td>
<td>0.305</td>
</tr>
<tr>
<td></td>
<td>−</td>
<td>+</td>
<td>−</td>
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<tr>
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<td>−</td>
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<tr>
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<td>132.97</td>
<td>-4.28</td>
<td>0.368</td>
<td>0.504</td>
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</tbody>
</table>
Figure 3.4. Logistic regression model for the 3-week-old seedling survival probability versus number of days submerged. Species Codes: CELA = Celtis laevigata (Chi sq. < 0.01), FRPE = Fraxinus pennsylvanica (Chi sq. < 0.01), QULY = Quercus lyrata (Chi sq. < 0.01), QUPH = Quercus phellos (Chi sq. < 0.01), QUTE = Quercus texana (Chi sq. < 0.01), ULAM = Ulmus Americana (Chi sq. < 0.01).

Discussion

The results of this study indicate that complete submergence on first-year seedling survival of bottomland tree species is influenced by the age of the seedling at the time of flooding, and the duration of flooding. I found an increase in survival probability with an increase in age, which supported my first hypothesis that the earlier a flood event occurs after emergence, the greater occurrence of mortality among seedlings. All species in our study demonstrated a higher sensitivity to flooding at three weeks of age compared to six and nine weeks of age, indicating substantial changes in seedling resilience within the first few months after emergence. The onset of a spring flood event post-germination can therefore have variable effects on woody seedling composition depending on its timing relative to germination. My results also revealed that increased flood duration adversely affected floodplain tree seedling survival at all ages, with 3-week-old seedlings demonstrating the greatest mortality. These results
agreed with my second hypothesis that longer flood duration would have greater negative effects on light-seeded species’ survival relative to heavy-seeded species, but this was only supported by the 3-week age group. These results provide evidence that the three lighter-seeded species are more vulnerable to flood disturbance within their first few weeks of seedling life compared to heavy-seeded species, but this disparity is time-limited; the survival results of the older seedlings groups did not separate out by seed size. These effects demonstrate how variation in surface flooding regime, along with heterogeneity in floodplain microtopography, could influence first-year seedling composition via differences in flood duration. A temporally and spatially dynamic annual flood regime would likely promote greater diversity in floodplain seedling species composition relative to a floodplain with stable hydrologic conditions.

Flood timing

Spring flooding can influence first-year woody seedling survival in floodplain forests, but variability in the timing of flood onset relative to seedling emergence may produce widely varying results in seedling composition. The general increasing tolerance to submergence from the 3-week-old seedlings to 6-week-old and then 9-week-old seedlings, across species, indicated substantial changes in seedling resilience within the first few months after germination. A greater age represents more time to develop root systems, increase height, and particularly in the case of the small-seeded species – acquire energy resources, which is reflected in the seedling morphological results with older seedlings displaying greater heights, stem diameters, and leaf quantity compared to younger seedlings (Tables 3.4 and 3.5). In floodplain forests, the advantage of early emergence is in the elongation of the growing season (Baskin and Baskin 1972, Gross 1984, Jones et al. 1997), providing the seedling with a head start over later germinants (Streng et al. 1989, Jones et al. 1994). However, depending on an individual seedling’s position within a floodplain, the chance of a flood disturbance may increase with an earlier emergence date (Streng et al. 1989). The results presented here are specifically relevant in the event of a second flood during the growing season. Toner and Keddy (1997) determined the time between the end of the first flood and the onset of a second flood controlled whether floodplain vegetation developed into woody or herbaceous species. A greater time interval prior to the second flood increased the probability of woody species occurrence because seedlings had more time to develop and/or recover after the first flood. My results and those of Streng et al. (1989) suggest that the timing of a second flood and/or a late season flood onset relative to germination time of individual species can affect the seedling composition of woody species. Due to asynchronous germination times (Streng et al. 1989, chapter 4), the probability of a seedling experiencing a first or second flood varies among species even at the same location in the floodplain.

The amelioration of the effect of submergence with increasing age across species is similar to other floodplain species’ adaptations. In Amazonian floodplain forests many tree species demonstrate rapid growth (e.g., 1-4 m in eight months) following germination, an adaptation which increases their chances of survival by reducing the likelihood of complete submergence (Parolin 2012). An experiment involving similar genera to this study from trees along the Rhine River in Europe found high survival among one-year old seedlings after three months of partial submergence (5 cm); this was significantly greater than survival of the same
species after complete submergence (Siebel et al. 1998). The results of this experiment further support that seedling development affects an individual’s chance of survival in the event of a post-germination flood, with older seedlings more likely to recover from a flood disturbance.

Notably, the Quercus species performed equal to or better than the other three species across all flood durations within the 3-week age group. This pattern provides evidence that some heavy-seeded floodplain forest species demonstrate greater capacity to overcome flood stress at an early age. This ability is likely due to the significant amount of energy stored in acorn cotyledons which contributes to the development of a relatively robust seedling (Johnson et al. 2009). Moreover, survival among the six species at 3-weeks post-germination roughly correlates to seed mass (Table 1; USFS 1974, Johnson et al. 2009), with the lighter-seeded C. laevigata and F. pennsylvanica demonstrating 43% and 49% cumulative seedling survival, and the light-seeded U. americana with 30% survival. It is possible that the hypogeal germination of Quercus species may have affected our survival rates because seedlings were transplanted shortly after emergence. Hypogeal germination supports seedling resilience by allowing the plant to gain additional nutrients before stem elongation (Johnson et al. 2009). However, we monitored seeds regularly during the germination phase and noted that emergence of the radicle in acorns tended to lead epicotyl emergence by only 1-3 days. Among the 9-week-old seedlings, no group experienced less than 42% survival. This may be because the morphology of seedlings among species was more equal by this age as a result of the lighter-seeded species’ greater growth rates (Gross 1984). The variation in seed/seedling size and survival rates reflects evolved strategies of woody floodplain species (Streng et al. 1989, Jones et al. 1994). This disparity in seedling survival among species within the first few months post-germination highlights the potential of dynamic disturbance patterns to not only reset and maintain succession, but to create windows of opportunity favoring multiple regeneration strategies.

**Flood duration**

We implemented complete seedling submergence in all flood treatments and found greater flood duration adversely affected floodplain forest tree seedling survival at all ages, with 3-week seedlings demonstrating the greatest mortality. Our shortest flood treatment of five days resulted in >90% survival for all age groups of all species. Previous studies have examined seedling response to flooding and found similar response to short duration inundation (Hosner 1958, 1960, Jones et al. 1989). After the 15-day treatment, the 3-week-old light-seeded species displayed lower survival compared to the Quercus species. In this age group, the same discrepancy was present between light- and heavy-seeded species after the 25-day treatment. These results agreed with my expectation that longer flood duration would have greater negative effects on light-seeded species’ survival relative to heavy-seeded species, but this was only supported by the 3-week-old age group. These results indicate the three lighter-seeded species are more vulnerable to flood disturbance within their first few weeks of seedling life compared to heavy-seeded species. Hosner (1958) tested survival of submergence of several first-year light-seeded floodplain tree species and documented 100% mortality of all species except Salix nigra after 32 days. In a study along the Rhine River, 28 days of complete submergence of one-year-old tree seedlings resulted in morphological damage (Siebel et al. 1998). Additionally, the effects
of complete inundation can differ substantially compared to more shallow flood conditions. Research from temperate regions in Europe and North America have demonstrated high tolerance of first-year tree seedlings to partial inundation or saturated soil conditions (McDermott 1954, Tang and Kozlowski 1984, Jones et al. 1989, Siebel et al. 1998, Walsh et al. 2008, Siebel et al. 1998). This distinction between species’ flood tolerance levels and flood depth highlights the spectrum of possible outcomes produced by variation in flood intensity. At the community level, it indicates that floodplain tree species composition may be highly vulnerable to change – the collapse of flood variation into a narrower range of flood regimes for the purposes of flood control could favor a less diverse assemblage of species long-term.

The longest flood duration treatments had a greater effect on seedling morphology compared to 5-day treatment groups and non-flooded plants. This result was not surprising because the flooded plants typically experienced no growth, partial stem death, or leaf death while the control groups continued to develop during the long treatment period resulting in a more substantial difference in morphology compared to the shorter treatments and their controls. Gardiner et al. (1993) found reduced growth in stem height and diameter of Q. phellos seedlings grown in hypoxic soil conditions compared to controls. The same study also analyzed Q. lyrata seedlings and found a significant increase in growth in hypoxic soils compared to controls, which our study did not find through our submergence treatments. Seedlings of Quercus palustris, Quercus macrocarpa and Quercus bicolor have similarly displayed reduced or halted growth during flooding (Kabrick et al. 2007). Significant morphological differences between controls and 25-day submergence groups were more prevalent in the lighter-seeded species than the Quercus species. This variation may be explained by the apparent difference in growth rate between the Quercus seedlings and the U. americana, F. pennsylvanica, and C. laevigata seedlings. For example, the C. laevigata seedling grew from a mean of 8.48 cm at three weeks to a mean of 35.2 cm at nine weeks. In contrast, the Q. phellos seedlings had a mean of 12.6 cm at three weeks and grew to a mean of 16.3 cm at nine weeks. Additionally, these findings demonstrate how a lack of flooding may benefit lighter-seeded species over heavy-seeded species which do not experience as dramatic of a setback in growth during flooding.

**Implications**

Variation in flood regime intensity contributes to relatively high tree species diversity in floodplain forests (Connell 1978, Hughes and Cass 1997, Parolin 2012). The range of flood tolerance levels across species’ seedlings and their age groups presented in this study illustrates the importance of disturbance variation in producing diverse species assemblages from the earliest stages of life. The declines in species diversity in temperate floodplains of North America and Europe are primarily associated with a loss of flooding, reduction of flooding (i.e., frequency, depth, duration), and/or a stabilization of the flood regime (Johnson et al. 1976, Shankman 1996, Barnes 1997, Deiller et al. 2001, Gee et al. 2014). Homogenization of temperate floodplains forests could be driven, in part, by the elimination of the role of flooding in controlling germination opportunities and seedling mortality. For instance, the increase in C. laevigata in some North American floodplains (Oliver et al. 2005, Gee et al. 2014) and F. pennsylvanica in North American and European floodplains (Schmiedel and Tackenberg 2013,
Drescher and Prots 2016) may be consequence of alterations to these species’ regeneration niches (Grubb 1977). In effect, these hydrologic changes may have expanded their realized niche within the regeneration process by eliminating a key stressor (Hutchinson 1957).

In floodplains of the Southeastern U.S., these fundamental differences in seedling survival relative to flood dynamics provides some clues into shifts in composition from more flood-tolerant Quercus species to more mesic forests dominated by Celtis/ Fraxinus/ Ulmus spp. (Oliver et al. 2005, Hanberry et al. 2012, Gee et al. 2014). The latter species generate a high abundance of small seeds that produce delicate seedlings, all significantly more sensitive to flooding within the first few weeks post-germination compared to the three Quercus species in this study. It is likely spring flooding historically acted as an abiotic control on the distribution of the light-seeded species, either through inhibiting germination on flooded sites (chapter 4), or inducing high mortality of newly emerged seedlings. These species would have been limited to non-flooded sites, sites with earlier flood recession, or sites with shorter flood duration within a floodplain. Moreover, after a seedling survives its first year, annual flooding would continue to exert an effect on seedling composition (Streng et al. 1989, Jones et al. 1994). The greater flood duration tolerance of Quercus species would have armed them with a competitive edge in the presence of annual flood disturbance. In the absence of flooding at many floodplain sites in the Southeastern U.S., and beyond, less flood tolerant seedlings are likely experiencing an advantage in the regeneration process. It is reasonable that the earlier emergence of some light-seeded species, in combination with their greater volume of seeds and the lack of flooding at many floodplain sites, swings the competitive edge in their favor (Streng et al. 1989, chapter 4). A longer growing season, coupled with a more rapid growth rate in their first year compared to Quercus spp., as suggested by this study’s findings, may establish some light-seeded species in a more prominent position at the cohort level to reach canopy dominance long-term.

This study presents a meaningful range of species-specific responses to variation in flood timing and duration at the regeneration level. There remain additional questions about the regeneration process in the context of flood patterns and modified floodplain hydrology that require further investigation. Evaluating such relationships is necessary to understand how past and future changes to floodplain hydrology are affecting, and will continue to affect, future canopy structure and composition of these ecosystems.
CHAPTER 4. FIRST-YEAR TREE SEEDLING DYNAMICS IN FLOODPLAIN FORESTS OF THE LOWER MISSISSIPPI RIVER ALLUVIAL VALLEY

Introduction

Tree regeneration by seed is a known limiting process with long-term effects on forest species composition (Connell 1989, Clark et al. 1998, Hubbell et al. 1999). The process consists of multiple distinct stages including seed production, seed dispersal, germination, seedling emergence, establishment and survival. Each stage is driven by, and vulnerable to, natural biotic and abiotic forces that may have lasting effects on species composition (Grubb 1977, Parolin et al. 2004, Kroschel et al. 2016). The differentiation of the regeneration niche among species leads to a high diversity of species within an ecosystem due to variation in evolved regeneration strategies (Grubb 1977). Accurate interpretation of regeneration’s long-term influence necessitates the understanding of species’ regeneration strategies, as well as the environmental factors affecting the regeneration process (Dickinson et al. 2000, Proll et al. 2015, chapter 3).

In floodplain forests, flood disturbance is historically the most important environmental factor driving variation in regeneration patterns (Hughes 1990). Flooding can influence seed dispersal (Schneider and Sharitz 1988), seed germination (Murphy and Stanley 1975, Pierce and King 2007), seedling establishment, and survival (Streng et al. 1989, Jones et al. 1994). Within these relationships, individual components of the hydroperiod (duration, timing, frequency, depth/water level) can cause unique species composition patterns in early regeneration stages (Parolin et al. 2004). Flood duration is a known determinant of species composition and arrangement in floodplains worldwide (Bedinger 1971, Franz and Bazzaz 1977, Wassen et al. 2002, Parolin et al. 2004, Murray-Hudson et al. 2014). Likewise, water level fluctuations have been shown to shape floodplain tree species composition patterns (Nilsson and Keddy 1988, Van Splunder et al. 1995, Parolin et al. 2004). Perhaps as important as flood duration and water level, but less noted, is the influence of flood timing on woody composition and distribution outcomes (Toner and Keddy 1997, Mahoney and Rood 1998). Flood timing is an important control for successful Populus spp. seedling establishment in floodplains of the western U.S. (Mahoney and Rood 1998); and in the southeastern U.S., earlier timed spring flooding corresponds to high first-year woody seedling mortality for early germinating species (Streng et al. 1989, Jones et al. 1994). Aside from these important findings, the relationship between flood timing and woody seedling germination and establishment is generally understudied (Toner and Keddy 1997). Of the studies that have examined this relationship, many have focused primarily on Populus and Salix spp. (Johnson 1994, Van Splunder 1995, Mahoney and Rood 1998, Barsoum 2002). There is a need to extend the spotlight to additional floodplain forest ecosystems as well as diversify species of interest in order to gain a more robust understanding of the effects of flood timing on regeneration.

Flood timing can further be broken down into pre- and post-germination effects on seedling composition. Prior to germination, the timing of flooding can either inhibit or benefit seedling emergence. If a site remains flooded beyond seeds’ phenological germination windows (Streng et al. 1989, Sarneel et al. 2014), species will be precluded from colonizing that location.
for that growing season. However, if the flood waters recede before the seeds’ germination window closes, the site may be primed for germination opportunity (Parolin et al. 2004). The strength of this beneficial effect as expressed by individual species is generally unclear, though, because of the inherent overlap of internal physiological germination cues and external environmental germination triggers (e.g., flooding). Thus, determining how much germination reflects a phenological pattern or a flood effect is an additional question linked to flood timing. The post-germination effect of flood timing can influence early species composition via seedling mortality (chapter 3, Streng et al. 1989). A second growing season flood would have historically shaped seedling composition in various ways depending on the timing of this event (chapter 3, Streng et al. 1989, Toner and Keddy 1997); but these various outcomes can merely be speculative, at best. Overall, a process-based understanding of the effects of flooding on seed germination and seedling establishment is needed to better understand how historic hydrologic processes and current hydrologic modifications affect tree species composition within floodplain systems (King and Keim 2019).

Of the stages of regeneration, seed germination and seedling emergence are important drivers in species composition because of both the complexity and varying vulnerability of seedlings to mortality among stages (Grubb 1977, Streng et al 1989, Sarneel et al. 2014). Germination is defined as a seedling breaking through the protective seed coat, either through elongation of the radicle (hypogeal germination) or the expansion of the hypocotyl (epigeal germination). For example, germination in *Quercus* species is hypogeal germination whereas *Ulmus, Fraxinus,* and *Celtis* species have epigeal germination (Burn and Honkala 1990). In orthodox seeds, germination is preceded by dormancy break, which is a separate process. To produce a seedling, the conditions required for breaking dormancy must occur prior to the conditions required for germination (Baskin and Baskin 2014). In contrast to orthodox seeds, recalcitrant seeds lack a dormancy period and die below a critical moisture content threshold. Hence, recalcitrant seeds generally do not remain viable in the environment beyond a single growing season, and to produce seedlings, a germination opportunity must occur before the seeds reach their critical moisture content following dispersal. The seeds of many *Quercus* species are classified as recalcitrant (Xia et al. 2012), while seeds of *Ulmus, Fraxinus,* and *Celtis* species are classified as orthodox – seeds that are desiccation-tolerant (Royal Botanic Gardens Kew 2020). Following germination, trees enter the most vulnerable life stage for most woody species – the seedling stage. Once a seedling breaks its seed coat, it has lost all physical protection and must depend upon both its energy reserves and the environment for its survival. Species that exhibit epigeal germination must begin photosynthesis immediately after germination because relatively little energy is stored in the seed’s cotyledons. Species with hypogeal germination tend to possess thicker, more robust cotyledons that can support the seedling’s initial growth if environmental conditions lack adequate resources (Parolin et al. 2004). As could be expected, these characteristics tend to correlate with seed size, i.e. larger-seeded species such as *Quercus,* tend to demonstrate hypogeal germination and lighter-seeded species such as *Ulmus* usually exhibit epigeal germination. The function of seed size has been shown to contribute to differentiation in the regeneration niche among species (Grubb 1977, Streng et al. 1989). Recognizing the discrepancies among species’ physiological and morphological germination
characteristics will assist in our understanding of how flooding interacts with these regeneration stages.

In floodplains of the southeastern United States, these sensitive processes coexisted with dynamic water levels for ~18,000 years (Delcourt and Delcourt 1987, King et al. 2005), developing fundamental mechanisms that continue to shape the floodplain communities we see today. Correlations between species’ occurrence and floodplain hydrology, based on elevation or geomorphic features, were historically reliable in the absence of anthropogenic modifications because the natural mechanisms that produced observed species assemblages remained intact. While ecologists recognize the connection between these early life stages and long-term species composition (Streng et al. 1989), the details of the driving processes are unknown for most species (King and Keim 2019). In the past century, modifications to floodplains and rivers have changed the environment in which regeneration occurs, altering the fundamental patterns that drove the high diversity of species and structure unique to these systems (Conner and Sharitz 1999). Consequently, the predictive power of known species-hydrology correlations breaks down when the overstory composition is not reflective of the hydrologic conditions under which it established. Species’ responses to hydrologic changes may not be revealed for decades due to fundamental changes at the regeneration level. Compounding this effect are the imminent hydrologic shifts driven by a changing climate. There is evidence that transitions in precipitation patterns may destabilize historic woody species’ distributions via alterations to the regeneration niche (Weltzin and McPherson 2000, Walck et al. 2011). We currently lack the mechanistic understanding necessary to predict compositional outcomes under given flood regimes.

With nearly all southeastern floodplains affected by hydrologic modifications, the patterns from historic natural processes are becoming more obsolete as floodplains continue to adjust to new regimes. Evidence of compositional changes have been already exposed in some areas where flooding has been altered or eliminated (Oliver et al. 2005, Oswalt and King 2005, Gee et al. 2014). In lieu of reliable species-hydrology correlations, we must instead understand the fundamental processes that drove these correlations (King and Keim 2019). A process-level understanding of regeneration in the context of floodplain dynamics can define some of the fundamental components that will be crucial for ecologists and managers to understand modified and novel floodplain environments. The Lower Mississippi River Alluvial Valley (LMAV) of the southeastern U.S. has undergone extensive river modifications for flood control and navigation purposes, dramatically altering the natural hydrologic and geomorphic processes of the floodplains (Baker et al. 1991, Biedenharn and Watson 1997, Pinter et al. 2006, Hudson et al. 2008, Hupp et al. 2009, Hart and Breaker 2019). Recent research and anecdotal evidence suggests many floodplain forests in the LMAV are shifting from a flood-tolerant, shade-intolerant Quercus/Carya -dominated forest to less flood-tolerant, shade-tolerant communities such as Celtis/Ulmus/ Fraxinus (Oliver et al. 2005, Hanberry et a. 2012, Gee et al. 2014, LDWF pers. comm. 2015). This phenomenon is not unique to the LMAV, with similar loss of Quercus and increases in Fraxinus and/or Ulmus appearing in other temperate regions of the globe, such as Germany (Haase and Glaser 2009) and France (Tremolieres et al. 1998). It is suspected these changes are initiated at the regeneration level (Oliver et al. 2005, Gee et al. 2014), but species-specific relationships with hydrology at these stages remains unknown for LMAV systems (Shankman 1996).
In this study, I focus on the relationship between floodplain hydrology and germination ecology to describe the influence of flooding on first-year seedling composition in the LMAV. The purpose was to describe seedling emergence phenology and to address the following questions by individual species: (1) What is the effect of preceding total flood days on seedling emergence? (2) What is the relationship between seedling emergence and preceding water levels, including both groundwater and surface water? (3) Does the timing of flood recession demonstrate an effect on seedling emergence? (4) Does light availability affect seedling emergence? Lastly, (5) what is the effect of post-germination flooding on first-year seedling mortality? I hypothesized that generally lighter-seeded species, such as *Ulmus* and *Fraxinus* are more sensitive to longer duration flooding, higher water levels, flood timing, and post-germination flooding compared to heavier-seeded such as *Quercus*.

Table 4.1. Basal area (m$^2$/ha) of all woody stems $\geq$ 4.5 cm diameter at breast height (1.3 m) collected from 20 x 20 m plots at four sites within the Lower Mississippi River Alluvial Valley during summer 2018. The number of plots per site is indicated in parentheses. Species in bold indicate focal species referenced throughout the chapter.

<table>
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<th>Species (common name)</th>
<th>South A (4)</th>
<th>South B (4)</th>
<th>Boeuf (10)</th>
<th>Big Lake (11)</th>
</tr>
</thead>
<tbody>
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<td>Acer rubrum (red maple)</td>
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<td>Celtis laevigata (sugarberry)</td>
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<td><strong>3.22</strong></td>
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<td><strong>0.59</strong></td>
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<td>Liquidambar styraciflua (sweetgum)</td>
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<td>0.77</td>
<td>0.00</td>
<td>0.06</td>
</tr>
<tr>
<td>Quercus phellos (willow oak)</td>
<td><strong>0.00</strong></td>
<td><strong>0.00</strong></td>
<td><strong>6.83</strong></td>
<td><strong>5.72</strong></td>
</tr>
<tr>
<td>Quercus texana (Nuttall oak)</td>
<td><strong>2.45</strong></td>
<td><strong>6.07</strong></td>
<td><strong>0.45</strong></td>
<td><strong>5.43</strong></td>
</tr>
<tr>
<td>Taxodium distichum (bald cypress)</td>
<td>13.29</td>
<td>0.00</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Triadica sebifera (Chinese tallow)</td>
<td>0.00</td>
<td>0.32</td>
<td>0.00</td>
<td>0.00</td>
</tr>
<tr>
<td>Ulmus alata (winged elm)</td>
<td><strong>0.00</strong></td>
<td><strong>0.00</strong></td>
<td>&lt;0.01</td>
<td><strong>0.00</strong></td>
</tr>
<tr>
<td>Ulmus americana (American elm)</td>
<td><strong>4.78</strong></td>
<td><strong>4.67</strong></td>
<td><strong>0.20</strong></td>
<td><strong>1.02</strong></td>
</tr>
<tr>
<td>Ulmus crassifolia (cedar elm)</td>
<td><strong>0.00</strong></td>
<td><strong>0.00</strong></td>
<td><strong>0.24</strong></td>
<td><strong>7.51</strong></td>
</tr>
<tr>
<td>Total</td>
<td>38.78</td>
<td>29.27</td>
<td>22.85</td>
<td>30.35</td>
</tr>
</tbody>
</table>
Methods

Site Descriptions

All four sites are located within the LMAV in the state of Louisiana. Two sites are in north Louisiana on state wildlife management areas; the other two sites are located in Iberville Parish outside Baton Rouge on private land managed by A. Wilbert’s Sons, LLC (Fig. 4.1). In Caldwell Parish, Boeuf Wildlife Management Area (WMA), hereafter referred to as Boeuf, is located within the floodplain of the Boeuf River and is characterized by a pronounced elevation gradient (14.55 – 18.07 m) across the floodplain from the riverbank to a ridge running north-south on the west border. Generally, annual overbank flooding occurs with the hydroperiod affected by the elevational gradient. Soils are dominated by heavy, poorly drained clays of the Alligator and Perry series (Soil Survey Staff 2020). Fraxinus pennsylvanica, Celtis laevigata, Quercus phellos, and Ulmus spp. are dominants on ridge and mid-elevation sites. Carya aquatica, Gleditsia aquatica, and Q. lyrata are common canopy species on low sites with Forestiera acuminata and Planera aquatica in the midstory (Tables 4.1 and 4.2).

Table 4.2. Stem density (stems/ha) of all woody stems ≥ 4.5 cm diameter at breast height (1.3 m) collected from 20 x 20 m plots at four sites during summer 2018. The number of plots per site is indicated in parentheses.

<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>South A (4)</th>
<th>South B (4)</th>
<th>Boeuf (10)</th>
<th>Big Lake (11)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer negundo (boxelder)</td>
<td>118.8</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Acer rubrum (red maple)</td>
<td>212.5</td>
<td>143.75</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Carya aquatica (water hickory)</td>
<td>0.0</td>
<td>37.5</td>
<td>450.0</td>
<td>56.3</td>
</tr>
<tr>
<td>Carpinus caroliniana (American hornbeam)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>100.0</td>
</tr>
<tr>
<td>Celtis laevigata (sugarberry)</td>
<td>225.0</td>
<td>381.3</td>
<td>81.3</td>
<td>487.5</td>
</tr>
<tr>
<td>Cephalanthus occidentalis (buttonbush)</td>
<td>6.3</td>
<td>0.0</td>
<td>6.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Cornus drummondii (roughleaf dogwood)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>6.3</td>
</tr>
<tr>
<td>Crataegus sp. (hawthorn)</td>
<td>6.3</td>
<td>43.8</td>
<td>168.8</td>
<td>31.3</td>
</tr>
<tr>
<td>Diospyros virginiana (persimmon)</td>
<td>6.3</td>
<td>12.5</td>
<td>6.3</td>
<td>6.3</td>
</tr>
<tr>
<td>Forestiera acuminata (swamp privet)</td>
<td>0.0</td>
<td>0.0</td>
<td>893.8</td>
<td>25.0</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica (green ash)</td>
<td>12.5</td>
<td>175.0</td>
<td>31.3</td>
<td>56.3</td>
</tr>
<tr>
<td>Gleditsia aquatica (water locust)</td>
<td>0.0</td>
<td>6.3</td>
<td>75.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Gleditsia triacanthos (honey locust)</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>30.0</td>
</tr>
<tr>
<td>Ilex decidua (deciduous holly)</td>
<td>112.5</td>
<td>112.5</td>
<td>68.8</td>
<td>631.3</td>
</tr>
<tr>
<td>Liquidambar styraciflua (sweetgum)</td>
<td>0.0</td>
<td>143.8</td>
<td>0.0</td>
<td>6.3</td>
</tr>
<tr>
<td>Nyssa aquatica (water tupelo)</td>
<td>25.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Planera aquatica (water elm)</td>
<td>0.0</td>
<td>0.0</td>
<td>293.8</td>
<td>0.0</td>
</tr>
<tr>
<td>Quercus lyrata (overcup oak)</td>
<td>0.0</td>
<td>43.8</td>
<td>456.3</td>
<td>106.3</td>
</tr>
<tr>
<td>Quercus nigra (water oak)</td>
<td>0.0</td>
<td>37.5</td>
<td>0.0</td>
<td>25.0</td>
</tr>
<tr>
<td>Quercus phellos (willow oak)</td>
<td>0.0</td>
<td>0.0</td>
<td>475.0</td>
<td>137.5</td>
</tr>
<tr>
<td>Quercus texana (Nuttall oak)</td>
<td>6.3</td>
<td>93.8</td>
<td>81.3</td>
<td>81.3</td>
</tr>
<tr>
<td>Taxodium distichum (bald cypress)</td>
<td>118.8</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Triadica sebifera (Chinese tallow)</td>
<td>0.0</td>
<td>18.8</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td>Ulmus alata (winged elm)</td>
<td>0.0</td>
<td>0.0</td>
<td>6.3</td>
<td>0.0</td>
</tr>
<tr>
<td>Ulmus americana (American elm)</td>
<td>87.5</td>
<td>131.3</td>
<td>37.5</td>
<td>275.0</td>
</tr>
<tr>
<td>Ulmus crassifolia (cedar elm)</td>
<td>0.0</td>
<td>0.0</td>
<td>93.8</td>
<td>937.5</td>
</tr>
</tbody>
</table>
Big Lake WMA, hereafter referred to as Big Lake, is located within the Tensas River watershed in Franklin Parish. Pit-mound topography characterizes Big Lake and currently the area lacks large-scale overbank flooding. Historically, overbank flooding from the Tensas River and Bayou Macon were common (USACE 1972) but establishment of mainline levees of the Mississippi River in the early 20th century eliminated this process. Limited areas of the site annually flood from precipitation-driven ponding and backwater collection in sloughs. A small channel named Big Roaring Bayou cuts through the WMA and produces small-scale flooding along select areas of its banks. The elevation ranges from approximately 17.22 to 18.87 m and soils are primarily heavy clays in the Sharkey series (Soil Survey Staff 2020). *Celtis laevigata*, *F. pennsylvanica*, *Gleditsia triacanthos*, *Quercus* spp., and *Ulmus* spp. are common canopy species (Tables 4.1 and 4.2). The Louisiana Department of Wildlife and Fisheries manages both Bueuf and Big Lake for wildlife habitat and sections of both WMAs have been harvested for timber since the 1980s.

Figure 4.1. The location of four study sites (2016-2018) within the Lower Mississippi River Alluvial Valley: Bueuf Wildlife Management Area, Big Lake Wildlife Management Area, South A, and South B. See text for site descriptions.
The third site, henceforth referred to as South A, is located just south of Bayou Sorrell, Louisiana about 35 km southwest of Baton Rouge. This site receives annual overbank flooding from the adjacent Port Allen Lock channel and the soils are in the Fausse and Schriever series (Soil Survey Staff 2020). Elevation ranges from approximately 1.06 to 1.33 m. *Acer rubrum*, *C. laevigata*, *Nyssa aquatica*, *Q. texana*, *Taxodium distichum*, and *U. americana* are dominant overstory species (Tables 4.1 and 4.2). The last harvest on this site occurred prior to 1980 (A. Wilbert Son’s, pers. comm. 2020). The fourth site, about 17 km west of Baton Rouge near Grosse Tete, Louisiana, is referred to as South B. This site is hydrologically disconnected from a river channel but historically received flooding from the Mississippi River. Small sloughs and depressions allow for some precipitation-driven flooding, but otherwise no overbank flooding occurs. Elevation varies from about 1.96 to 2.09 m. The soils are in the Sharkey series (Soil Survey Staff 2020). *Acer rubrum*, *C. laevigata*, *F. pennsylvanica*, *Liquidambar styraciflua*, *Q. texana*, and *U. americana* dominate the overstory (Tables 4.1 and 4.2). The last timber harvest to affect the site occurred in 1994 and the forest has since naturally regenerated (A. Wilbert Sons, pers. comm. 2020).

**Field Sampling**

We established a total of 21 plots (20 x 20 m) at two sites in 2016 (10 at Boeuf and 11 at Big Lake) using a stratified random selection process to locate plots. Locations were limited to an area within 50 - 800 m of a road or ATV trail to minimize trail effects and to promote efficient detection for revisits. Boeuf has roughly 35 km of trails and Big Lake has about 20 km of trails throughout the WMA; each road or trail was limited to five or fewer plots to allow a greater distribution of study locations. Within these limitations plot locations were generated randomly. Inside each plot we established five stratified subplots (1 x 1 m, n = 105) to survey seedling dynamics. During the 2016, 2017, and 2018 growing seasons, subplots were surveyed, on average, every two weeks except for when flooding or hunting seasons prohibited us from visiting some plots. Extreme flooding in the spring of 2016 prevented us from initiating seedling surveys until early May; we initiated surveys in February in 2017 and 2018. Data collection included seedling emergence, height, and mortality of all seedlings ≤ 50 cm. Individual seedlings were marked, identified to species, and measured during each survey; seedling markers allowed me to distinguish between new and already present individuals. Seedlings already present at the time of the first survey and resprouts were documented as such, and new germinants were recorded. Often seeds remained attached or adjacent to newly emerged seedlings, assisting in their identification. Surveys ran through the end of September of each year.

We established four plots (20 x 20 m) at each of our other two sites, South A and South B, in the spring of 2017 using methods identical to the first two sites. Five subplots (1 x 1 m) were established in each plot using the same protocol as our north sites (n = 40). Seedling surveys initiated in early February and continued through September of 2017 and 2018. We surveyed using two-week intervals and followed the same protocol as our first two sites by marking individual seedlings and documenting species, emergence, height, and mortality.

In December of 2015 five water level monitoring stations were established at our large sites (three at Boeuf WMA and two at Big Lake WMA) to characterize the hydrology of each floodplain (see Johnson 2015). I constructed shallow wells using vented PVC pipe with 1 m of
the well extending above the surface and 2 m extending below the surface. Each well was equipped with a pressure transducer (HOBO; Onset, Bourne, Mass., USA) strung from the top of the well to within 5 cm of the well bottom. The pressure transducers recorded data at 30-minute intervals from December 8, 2015 to April 2019. In 2017 one additional water-level monitoring station was added to Boeuf and two more stations were added to Big Lake. In the fall of 2016, I installed a water level monitoring station at both the South A and South B sites using the same procedures as the prior stations. Water level was logged from November 21, 2016 to April 2019.

To estimate changes in water level per plot, I used elevation data from the Louisiana Lidar Project (Atlas 2008) to determine the elevation of each plot and the elevation of each water level monitoring station. Five elevation points were averaged at each plot location from the lidar DEM to account for variation at the plot level and within the DEM’s horizontal resolution (5 x 5 m; Atlas 2008). Vertical accuracy of the lidar was 6.18 cm RMSE. Plot water level was back calculated using the difference in elevation between the nearest water level station and the plot. Ground-truthing of subplot water level estimates were conducted during each biweekly survey to the extent of observed surface flooding; we could not verify estimated belowground water levels at the time of survey.

Light availability was collected using digital hemispherical photos taken at each subplot during 2016, 2017, and 2018 at the north sites, and during 2017 and 2018 at the south sites. Photos were taken mid-growing season after leaf-out (i.e., June-July) from a level surface in the center of each subplot, 10-15 cm above the soil, oriented north. A smartphone (iPhone SE) with a fish-eye lens attachment was used to collect canopy photographs (Smith and Ramsay 2018, Wan et al. 2018). I used ImageJ (Rueden et al. 2016) to analyze the photos following the protocol outlined by Smith and Ramsay (2018). I applied a uniform circular mask to each photo to crop the outer square frame away from the circular canopy image. This allowed me to determine relative canopy closure for each subplot during each summer.

Species Selection

I selected five species and one genus (*Ulmus* spp.) to examine species-specific responses to multiple environmental gradients. All five species are considered relatively flood tolerant as mature trees but vary by their shade tolerance and seed size (Table 4.3). I grouped *U. americana*, *U. alata*, and *U. crassifolia* due to similarities in first-year seedling morphology and henceforth refer to them as one of the six focal species for simplicity, but note that ‘*Ulmus* spp.’ represents three species. The relatively light-seeded species include *C. laevigata*, *F. pennsylvanica*, and *Ulmus* spp. The latter two species produce samaras dispersed predominantly via wind and water (Middleton 2000, Schmiedel and Tackenberg 2013); the former species produces a drupe dispersed by wildlife and water (Kennedy 1990). The other three species are the heavier-seeded, *Quercus phellos*, *Q. texana*, and *Q. lyrata*. All three species are gravity-dispersed, but particularly *Q. phellos* and *Q. texana* are of high wildlife value which also aids in their dispersal (Filer 1990, Schlaegel, 1990). Hydrochory is an important dispersal agent of *Q. lyrata*, as its seeds have a corky seed coat giving them the ability to float (Solomon 1990).
Table 4.3. The flood and shade tolerance classifications of six focal species (McKnight et al. 1980).

<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>Flood tolerance</th>
<th>Shade tolerance</th>
<th>Seed mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Celtis laevigata (sugarberry)</td>
<td>moderately tolerant</td>
<td>very tolerant</td>
<td>0.065</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica (green ash)</td>
<td>moderate</td>
<td>intermediate</td>
<td>0.025</td>
</tr>
<tr>
<td>Quercus lyrata (overcup oak)</td>
<td>moderate</td>
<td>intolerant</td>
<td>6.048</td>
</tr>
<tr>
<td>Quercus phellos (willow oak)</td>
<td>moderate – weak</td>
<td>intolerant</td>
<td>1.152</td>
</tr>
<tr>
<td>Quercus texana (Nuttall oak)</td>
<td>moderate</td>
<td>intolerant</td>
<td>5.040</td>
</tr>
<tr>
<td>Ulmus spp. (elm)</td>
<td>moderate – weak</td>
<td>tolerant</td>
<td>0.006</td>
</tr>
</tbody>
</table>

*Mean seed mass based on seeds supplied from Louisiana Forest Seed Co. (2017). Mass represents only the nulet of the seed, not the full drupe.

**Data Analyses**

Hydrologic variables were calculated per survey per plot for each of the three years. Although natural microtopographic variation was common at our sites, I could not accurately account for small differences in elevation across a single plot, therefore I assumed the hydrologic metrics were representative of the full plot and its subplots. For each plot, I calculated the total number of days flooded (TFD) as the cumulative number of days the water was above the soil surface since January 1 of each year until the day of the survey. The average water level (WL) for each plot was determined by averaging the water level across both the 30 days and the 15 days prior to a survey – this included groundwater levels down to 2 m belowground and surface flooding depth. I found no significant difference between the 30-d and 15-d averages (p > 0.05); therefore, I used the 15-day average because it coincided with our biweekly survey intervals and was more representative of recent water level dynamics. The number of days since the last flood event (DSLF), i.e., the timing of flood recession, was determined each survey by quantifying the number of days since the last flood event for each plot within a growing season. I defined a flood event as a period in which the water level was continually above the soil surface for a minimum of 24 hours (Jones et al. 1994).

For each plot, I determined seedling emergence by documenting presence/absence per species. Emergence presence was documented for a species if any of the subplots included a newly emerged seedling at the time of survey. I defined emergence absence by a species’ seeds being present but exhibiting no evidence of emergence. Seeds of a species were assumed present at a plot if a seedling of that species emerged at any point during that growing season within one of the subplots. I similarly calculated first-year seedling mortality by documenting whether a species experienced a mortality event between each survey.

For each species, I calculated first-year seedling emergence abundance per plot by averaging the number of newly emerged seedlings by subplot, thereby producing an average
abundance value per square meter. Seedling mortality totals were similarly averaged by subplot for each plot. Again, I quantified values by species per plot, per survey for all years.

I used logistic regression to separately model emergence probability and mortality probability for each species as a function of the hydrologic variables: total flood days, water level, and days since the last flood (ter Braak and Looman 1986, Trexler and Travis 1993). Specifically, I first ran generalized linear models with a logit link function using both linear and quadratic functions for each species’ emergence and mortality responses as they related to each hydrologic variable. Models were assessed using a -2-log likelihood approach; model fit was based on the change in deviance between the model and the null model (no variables included). A change in deviance greater than the critical Chi square determined whether the modeled relationship was significant. Next, I assessed associated effects of our hydrologic variables. I increased model complexity by combining independent variables, and function terms (linear or quadratic), from the models that showed a significant relationship (i.e., serial nesting). All models were compared to the null model and the previously supported simpler model; a difference in deviance greater than the critical Chi square value at α = 0.05 determined whether the more complex model was retained. Lastly, I added an interaction term between the independent variables in each model (e.g., TFD x WL) to see if model fit was improved. If the model with the interaction term was significant based on deviation from the simpler supported model, I selected the model with the interaction term as the best-fit model.

A linear regression model was used to test the effects of each of the hydrologic variables on emergence abundance and average mortality values. To test the effects of canopy closure on seedling presence-absence, I again used logistic regression to model the probability of seedling occurrence at a plot versus canopy closure, for each year. The relationship between seedling abundance and canopy closure was analyzed using a linear regression model. All analyses were performed in R (The R Core Team 2020).

I assessed overall first-year seedling composition associations, and trends with environmental factors, through a nonmetric multidimensional scaling ordination (NDMS: Krustal 1964) using the protocol described by Battaglia et al. (1999) and the DECODA package (Minchin 1989). I standardized species’ average abundance values based on unit maxima to account for natural variation among quantities of species’ seedling abundance. Disparity in species composition was conveyed using the Bray-Curtis dissimilarity index (Bray Curtis 1975) across an ordination space. Next, I fit vectors representing the hydrologic variables across the ordination space using the maximum correlation technique outlined by Dargie (1984; Kantvilas and Minchin 1989). Vector direction represented the best correlation with the seedling composition across the ordination space. I used 1000 random permutations of each hydrologic variable to test if each vector correlation was significant.
Table 4.4. Hydrology characteristics of four sites within the Lower Mississippi River Alluvial Valley, including elevation of the lowest plot and highest plot measured at each site and corresponding annual number of total flood days for 2016-2018. There was not data for the south sites in 2016. Number of plots (20 x 20 m) given in parentheses.

<table>
<thead>
<tr>
<th>Site</th>
<th>Elevation Range (m)</th>
<th>Mean (m)</th>
<th>Annual Total Days Flooded</th>
<th>2016</th>
<th>2017</th>
<th>2018</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boeuf (10)</td>
<td>14.55 – 18.07</td>
<td>15.91</td>
<td></td>
<td>178 – 20</td>
<td>86 – 0</td>
<td>155 – 0</td>
<td>73.7</td>
</tr>
<tr>
<td>Big Lake (11)</td>
<td>17.22 – 18.87</td>
<td>18.03</td>
<td></td>
<td>168 – 11</td>
<td>125 – 0</td>
<td>147 – 0</td>
<td>87.9</td>
</tr>
<tr>
<td>South A (4)</td>
<td>1.06 – 1.33</td>
<td>1.17</td>
<td></td>
<td>206 – 20</td>
<td>299 – 108</td>
<td>183.4</td>
<td></td>
</tr>
<tr>
<td>South B (4)</td>
<td>1.96 – 2.09</td>
<td>2.02</td>
<td></td>
<td>138 – 45</td>
<td>155 – 39</td>
<td>94.0</td>
<td></td>
</tr>
</tbody>
</table>

Results

Hydrology

There was a greater range in elevation among our plots at Boeuf compared to Big Lake (Table 3.4). Boeuf had a greater number of total flood days in 2016 (178 – 20 d) and 2018 (155 – 0 d) compared to Big Lake (168 – 11 d in 2016; 147 – 0 d in 2018), but in 2017 Big Lake (125 – 0 d) surpassed Boeuf (86 – 0) on maximum number of days flooded. South A showed a greater elevation range in plots compared to the South B; the former site also displayed a higher average of total flood days. The year 2016 was particularly wet at our northern two sites (we did not have 2016 data for the southern sites), with all plots experiencing an estimated 11 or more flood days (Table 3.4). Both Boeuf and South A showed greater variability in total flood days at the plot level from year to year compared to the other two sites (Fig. 4.2). Boeuf and South A maintain hydrologic connectivity to a nearby channel and received overbank flooding during the years of study, whereas the other two sites exhibit precipitation-driven ponding.

Based on 573 subplot surveys over the course of three growing seasons, water level estimates based on elevation and long-term data loggers were reliable for 94.4% of our field observations (n = 541). Twenty of the 32 inconsistent water level estimates were 20 cm or less from the soil surface (Fig. 4.3). Most of the inconsistencies estimated water level below the soil surface when we observed surface flooding. Ponding of water in localized areas from precipitation may have been the cause of the inconsistencies between estimated and observed water levels, but we were unable to confirm this.
Figure 4.2. The estimated annual total flood days for 29 plots (20 x 20 m) located at four sites within the Lower Mississippi River Alluvial Valley. Data is from 2016 to 2018 and is based on long-term data loggers. Two sites (South A and South B) did not have data for 2016.

Figure 4.3. The frequency of inaccurate plot (20 x 20 m) water level estimates based on data-logger records and ground-truthed field observations for 573 subplots (1 x 1 m) surveyed for the 2016-2018 growing seasons at four sites within the Lower Mississippi River Alluvial Valley. A water level of zero represents the soil surface, negative values represent water below the soil surface, and positive values represent surface flooding.
Variation in water level (i.e., flood depth and groundwater) within and among sites was evident when comparing hydrographs of the lowest and highest elevation plots per site (Fig. 4.4 a-d). Boeuf experienced greater than 5 m of flooding at its lowest elevation plot in 2016 and 2018, while the highest plot was only briefly flooded (n = 20 d) in 2016. Boeuf included seedlings of several flood tolerant species, such as *C. aquatica*, *F. acuminata*, *G. aquatica*, *P. aquatica*, and *Q. lyrata* which exhibited relatively high emergence densities in 2016 and 2018 (Table 4.5). In 2017 when Boeuf had relatively little overbank flooding (Fig. 4.4a), there was zero or limited emergence of these species compared to the other two years. A similar pattern was observed in 2017 at South B which experienced a relatively dry year in 2017 followed by a wet year in 2018 (Fig. 4.4d). This site had a different seedling composition compared to Boeuf, but also displayed limited emergence abundance for all species in 2017 compared to 2018.

![Graph showing emergence frequency of seedlings in relation to site hydrology at four sites within the Lower Mississippi River Alluvial Valley.](image)

Figure 4.4. Emergence frequency of seedlings in relation to site hydrology at four sites within the Lower Mississippi River Alluvial Valley. Hydrographs represent the lowest elevation 20 x 20 m plot (low) and the highest elevation 20 x 20 m plot (high) at the site. The dashed horizontal line represents the soil surface. Data includes seedlings of all species encountered. Note y-axes scales are different on each figure. Sites are a) Boeuf WMA, b) Big Lake WMA c) South A and d) South B. See text for site locations and descriptions.
Figure 4.4 continued. Emergence frequency of seedlings in relation to site hydrology at four sites within the Lower Mississippi River Alluvial Valley. Hydrographs represent the lowest elevation 20 x 20 m plot (low) and the highest elevation 20 x 20 m plot (high) at the site. The dashed horizontal line represents the soil surface. Data includes seedlings of all species encountered. Note y-axes scales are different on each figure. Sites are a) Boeuf WMA, b) Big Lake WMA c) South A and d) South B. See text for site locations and descriptions.
Figure 4.4 continued. Emergence frequency of seedlings in relation to site hydrology at four sites within the Lower Mississippi River Alluvial Valley. Hydrographs represent the lowest elevation 20 x 20 m plot (low) and the highest elevation 20 x 20 m plot (high) at the site. The dashed horizontal line represents the soil surface. Data includes seedlings of all species encountered. Note y-axes scales are different on each figure. Sites are a) Boeuf WMA, b) Big Lake WMA c) South A and d) South B. See text for site locations and descriptions.
Table 4.5. Mean annual abundance (± SE) per subplot (1 x 1 m) of first-year seedlings at four sites within the Lower Mississippi Alluvial Valley. Focal species are in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Boeuf (50)</th>
<th>Big Lake (55)</th>
<th>South A (20)</th>
<th>South B (20)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum</td>
<td>0.0 0.00</td>
<td>1.0 0.03</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Carya aquatica</td>
<td>3.3 0.26</td>
<td>0.0 0.00</td>
<td>7.2 0.40</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Celtis laevigata</td>
<td>0.0 0.00</td>
<td>1.0 0.00</td>
<td>1.7 0.33</td>
<td>1.5 0.21</td>
</tr>
<tr>
<td>Cephalanthus occidentalis</td>
<td>1.0 0.02</td>
<td>0.0 0.00</td>
<td>2.5 0.07</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Crataegus spp.</td>
<td>1.0 0.02</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Forestiera acuminata</td>
<td>50.8 7.90</td>
<td>0.0 0.00</td>
<td>8.7 1.30</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>1.6 0.30</td>
<td>1.2 0.17</td>
<td>1.0 0.00</td>
<td>1.4 0.22</td>
</tr>
<tr>
<td>Gleditsia aquatica</td>
<td>4.5 0.19</td>
<td>0.0 0.00</td>
<td>1.0 0.03</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Gleditsia triacanthos</td>
<td>1.0 0.02</td>
<td>1.0 0.02</td>
<td>0.0 0.00</td>
<td>1.8 0.09</td>
</tr>
<tr>
<td>Ilex decidua</td>
<td>1.0 0.03</td>
<td>1.0 0.03</td>
<td>0.0 0.00</td>
<td>1.5 0.04</td>
</tr>
<tr>
<td>Liquidambar styraciflua</td>
<td>0.0 0.00</td>
<td>1.0 0.02</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Planera aquatica</td>
<td>8.2 0.77</td>
<td>2.2 0.13</td>
<td>2.8 0.14</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Quercus lyrata</td>
<td>3.9 0.64</td>
<td>1.0 0.00</td>
<td>1.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Quercus nigra</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>1.0 0.00</td>
<td>1.4 0.30</td>
<td>1.0 0.00</td>
<td>0.5 0.00</td>
</tr>
<tr>
<td>Quercus texana</td>
<td>1.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>1.3 0.25</td>
</tr>
<tr>
<td>Taxodium distichum</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Triadica sebifera</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
<td>0.0 0.00</td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td>3.1 0.71</td>
<td>1.4 0.40</td>
<td>3.2 0.55</td>
<td>2.0 0.33</td>
</tr>
</tbody>
</table>
Table 4.6. Abundance of first-year seedlings (< 1 year old) at four floodplain sites in the Lower Mississippi Alluvial Valley during the 2016-2018 growing seasons. Focal species are in bold.

<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>2016</th>
<th>2017</th>
<th>2018</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer rubrum (red maple)</td>
<td>0</td>
<td>522</td>
<td>939</td>
</tr>
<tr>
<td>Carya aquatica (water hickory)</td>
<td>31</td>
<td>1</td>
<td>37</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Celtis laevigata</strong> (sugarberry)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><strong>26</strong></td>
<td><strong>33</strong></td>
<td><strong>92</strong></td>
</tr>
<tr>
<td>Cephalanthus occidentalis (buttonbush)</td>
<td>1</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Crataegus spp. (hawthorn)</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Forestiera acuminata (swamp privet)</td>
<td>1077</td>
<td>0</td>
<td>78</td>
</tr>
<tr>
<td><strong>Fraxinus pennsylvanica</strong> (green ash)</td>
<td><strong>45</strong></td>
<td><strong>611</strong></td>
<td><strong>1207</strong></td>
</tr>
<tr>
<td>Gleditsia aquatica (water locust)</td>
<td>19</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Gleditsia triacanthos (honey locust)</td>
<td>15</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>Ilex decidua (deciduous holly)</td>
<td>3</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Liquidambar styraciflua (sweetgum)</td>
<td>0</td>
<td>2</td>
<td>7</td>
</tr>
<tr>
<td>Planera aquatica (water elm)</td>
<td>82</td>
<td>11</td>
<td>17</td>
</tr>
<tr>
<td>Quercus lyrata (overcup oak)</td>
<td><strong>67</strong></td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Quercus nigra (water oak)</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Quercus phellos (willow oak)</td>
<td><strong>8</strong></td>
<td><strong>58</strong></td>
<td>5</td>
</tr>
<tr>
<td>Quercus texana (Nuttall oak)</td>
<td><strong>7</strong></td>
<td><strong>22</strong></td>
<td>5</td>
</tr>
<tr>
<td>Taxodium distichum (bald cypress)</td>
<td>0</td>
<td>32</td>
<td>10</td>
</tr>
<tr>
<td>Triadica sebifera (Chinese tallow)</td>
<td>0</td>
<td>14</td>
<td>5</td>
</tr>
<tr>
<td>Ulmus spp. (elm)</td>
<td><strong>82</strong></td>
<td><strong>2597</strong></td>
<td><strong>8040</strong></td>
</tr>
</tbody>
</table>

Seedling Dynamics

A total of 15832 first-year seedlings representing 17 species and two genera (Crataegus and Ulmus) were documented across the three growing seasons. This included 1664 seedlings of 14 species in 2016, 3916 seedlings of 15 species in 2017, and 10452 seedlings of 16 species in 2018 (Table 4.6). The most widely distributed species were C. laevigata (18 % subplots), F. pennsylvanica, (31.4 % subplots) and Ulmus spp. (47.3 % subplots) which occurred at all four sites in all years with the exception of the absence of C. laevigata at Boeuf in 2016 (Table 4.7). Quercus texana also occurred at all sites, but not every year and not in as many subplots (6.1 % subplots) as the other three species. Combining all three years, Boeuf had the highest species richness of first-year seedlings with 18 species, followed by Big Lake with 12 species. At South A and South B, seven and six species of first-year seedlings were found, respectively. At the plot scale, Ulmus spp. were found in all but two of our 29 plots during the three years; C. laevigata and F. pennsylvanica were the next most common species across all plots, occurring in 23 and 22 plots, respectively. Of the oaks, Q. phellos was found at 13 plots, Q. texana occurred in 12 plots, and Q. lyrata was in seven plots (Table 4.8).
Table 4.7. Percent of subplots in which first-year seedlings were detected during the 2016-2018 growing seasons at four sites within the Lower Mississippi Alluvial Valley. Total subplots (1 x 1 m) per site (N) is given in parentheses. Focal species are in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Boeuf (50)</th>
<th>Big Lake (55)</th>
<th>South A (20)</th>
<th>South B (20)</th>
<th>Overall (400)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Acer rubrum</em></td>
<td>0.0</td>
<td>4.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Carya aquatica</em></td>
<td>7.7</td>
<td>0.0</td>
<td>10.0</td>
<td>0.0</td>
<td>1.8</td>
</tr>
<tr>
<td><em>Celtis laevigata</em></td>
<td>0.0</td>
<td>2.0</td>
<td>6.0</td>
<td>30.9</td>
<td>21.8</td>
</tr>
<tr>
<td><em>Cephalanthus occidentalis</em></td>
<td>0.6</td>
<td>0.0</td>
<td>4.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Crataegus spp.</em></td>
<td>0.6</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Forestiera acuminata</em></td>
<td>12.9</td>
<td>0.0</td>
<td>18.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Fraxinus pennsylvanica</em></td>
<td>38.0</td>
<td>12.0</td>
<td>8.0</td>
<td>18.2</td>
<td>27.3</td>
</tr>
<tr>
<td><em>Gleditsia aquatica</em></td>
<td>2.6</td>
<td>0.0</td>
<td>4.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Gleditsia triacanthos</em></td>
<td>0.6</td>
<td>2.0</td>
<td>0.0</td>
<td>14.5</td>
<td>5.5</td>
</tr>
<tr>
<td><em>Ilex decidua</em></td>
<td>1.3</td>
<td>4.0</td>
<td>0.0</td>
<td>3.6</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Liquidambar styraciflua</em></td>
<td>0.0</td>
<td>2.0</td>
<td>0.0</td>
<td>0.0</td>
<td>7.3</td>
</tr>
<tr>
<td><em>Planera aquatica</em></td>
<td>6.5</td>
<td>10.0</td>
<td>12.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Quercus lyrata</em></td>
<td>34.0</td>
<td>4.0</td>
<td>2.0</td>
<td>0.0</td>
<td>3.6</td>
</tr>
<tr>
<td><em>Quercus nigra</em></td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.8</td>
</tr>
<tr>
<td><em>Quercus phellos</em></td>
<td>14.0</td>
<td>14.0</td>
<td>4.0</td>
<td>3.6</td>
<td>32.7</td>
</tr>
<tr>
<td><em>Quercus texana</em></td>
<td>4.0</td>
<td>0.0</td>
<td>0.0</td>
<td>7.3</td>
<td>21.8</td>
</tr>
<tr>
<td><em>Taxodium distichum</em></td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Triadica sebifera</em></td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
</tr>
<tr>
<td><em>Ulmus spp.</em></td>
<td>24.0</td>
<td>10.0</td>
<td>24.0</td>
<td>41.8</td>
<td>67.3</td>
</tr>
</tbody>
</table>
Table 4.8. The distribution (presence/absence) of six focal tree species in 29 plots (20 x 20 m) at four sites within the Lower Mississippi River Alluvial Valley from 2016-2018 (Boeuf and Big Lake) and 2017-2018 (South A and South B).

<table>
<thead>
<tr>
<th>Species</th>
<th>Boeuf</th>
<th>Big Lake</th>
<th>South A</th>
<th>South B</th>
</tr>
</thead>
<tbody>
<tr>
<td>Celtis laevigata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quercus lyrata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quercus phellos</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Quercus texana</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Emergence**

Species with generally high first-year seedling abundance per subplot in one or more years included *A. rubrum, C. aquatica, F. pennsylvanica, F. acuminata, P. aquatica*, and *Ulmus* spp. (Table 4.5). South A and South B sites, though not as rich in species as the more northern sites, displayed substantially higher densities of *A. rubrum*, *F. pennsylvanica*, and *Ulmus* spp. compared to the other sites. South A had the greatest distribution of these three species and highest densities relative to the other sites. Boeuf showed the highest densities of the heavy-seeded species, *C. aquatica* (3.3 – 7.2 seedlings/m²) and *Q. lyrata* (1.0 – 3.9 seedlings/m²). Species varied widely in both the length and timing of their emergence “windows” (Fig. 4.5). Some species emerged throughout most of the growing season (e.g., *Q. texana*) while others exhibited short pulses of emergence (e.g., *F. acuminata* and *P. aquatica*). The earliest seedlings appeared around the 70th day of the year (~mid-March), with some of the first emergents being *A. rubrum*, *F. pennsylvanica*, *T. distichum*, and *Ulmus* spp. Generally lighter-seeded species, such as *F. pennsylvanica* and *Ulmus* spp. emerged during the first half of the growing season compared to heavier-seeded species such as *C. aquatica* and *Q. lyrata*.

Of the six focal species, the month of May had the highest percent emergence for four of the species. *Ulmus* spp. peaked in percent emergence prior to the other species (March) and *Q. lyrata* showing the latest maximum percent emergence in July (Fig. 4.6). There was high variability in first-year seedling abundance among years and species (Fig. 4.7). Abundance roughly separated out based on seed size. The lightest-seeded species, *F. pennsylvanica* and *Ulmus* spp., were the most abundant of the six species, with more than 8000 *Ulmus* spp. individuals documented in 2018 (Fig. 4.7). The two south sites were particularly prolific in 2017 and 2018, which contributed to the spike in abundance among these species. *Quercus lyrata* likely experienced a mast year in 2016 at the northern sites, with relatively high abundance and dramatically reduced numbers the following years. A similar pattern occurred with *Q. phellos* at the northern sites in 2017.
Figure 4.5. Annual emergence timing of floodplain forest woody species at four sites within the Lower Mississippi River Alluvial Valley during 2016-2018. Total number of documented first-year seedlings is given after each species’ name; only species with N ≥ 5 are presented. Day 70 is approximately mid-March and day 245 is approximately early September. Focal species are in bold.
Figure 4.6. Monthly emergence by percent of six focal floodplain species at four sites in the Lower Mississippi River Alluvial Valley during 2016, 2017 and 2018. Data represents March 2016 through September 2018.
Seedling Composition

The results from the ordination showed greater dissimilarity in species composition of first-year seedlings at Boeuf relative to the other three sites (Fig. 4.8a); Boeuf also had the most species represented in first-year seedling composition (Table 4.5). Of the two southern sites, South A displayed a high dissimilarity in seedling composition, more so than South B. The only difference in species richness between these two sites is the presence of *T. distichum* at South A (Table 4.5). The three independent hydrologic variables (TFD, WL, and DSLF) were all significantly related to species composition; WL had the greatest correlation with seedling composition through time. The TFD and DSLF were somewhat correlated with each other, as expected, with more flood days corresponding to fewer days since the last flood. The perpendicular relationship between WL and the other two vectors indicates that water level being high or low does not translate into more or less flood days at a location. In fact, it suggests that some plots may have experienced relatively high-water levels, such as near the soil surface, but fewer days flooded (i.e., stable conditions), while others may have undergone many days flooded followed by a dramatically reduced water level (i.e., “flashy” flood conditions). This pattern was evident when plots were categorized by total flood days (Fig. 4.8b). Some plots with 100 or more total flood days corresponded to lower water levels based on the direction of the WL vector. Interestingly, the greatest outlier points had relatively few total flood days and these points represented the lowest elevation plots at Boeuf during 2017 when the site had limited flooding (Fig. 4.4a). The composition of these points was *Q. lyrata* + *Ilex decidua*, and *P. aquatica*. 

Figure 4.7. Annual first-year seedling abundance for six focal species at four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons. Note y-axes differ in scale.
Figure 4.8. NDMS ordination of first-year seedling composition at four sites within the Lower Mississippi River Alluvial Valley (2016-2018). The fitted vectors depict the direction and degree of correlation between the variable and seedling composition; longer vectors indicate greater correlation. Variables include the total number of days flooded from January 1 to time of survey, values increase from left to right (TFD, p < 0.001); average water level, values increase top to bottom (WL, p < 0.001); and number of days since the last flood, values decrease left to right (DSLF, p = 0.01). Points are categorized by a) the site at which the plot was located; and b) the estimated total flood days at the plot prior to survey.
Species-Specific Responses

Emergence vs Total Flood Days

Of our six focal species, the total number of days flooded prior to emergence was not a significant factor explaining seedling emergence patterns (Appx A, Fig. A.1). I went a step further and examined four other species known to be flood-tolerant and among these species I did find significant relationships (Chi sq. < 0.05) between emergence probability and total flood days. These species included A. rubrum, C. aquatica, F. acuminata, and P. aquatica. Except for A. rubrum, species showed the highest probability of emergence with >100 total flood days (Appx A, Fig. A.2).

Figure 4.9. The probability of seedling emergence (±SE in gray) vs plot mean water level of the 15 days prior to emergence detection for six focal species. All models were statistically significant for all species shown (Chi sq. < 0.05). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.
Figure 4.9 continued. The probability of seedling emergence (±SE in gray) vs plot mean water level of the 15 days prior to emergence detection for six focal species. All models were statistically significant for all species shown (Chi sq. < 0.05). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.

Emergence vs Water Level

All six focal species demonstrated a significant relationship between emergence probability and the average water level at a plot (Chi sq < 0.05; Fig. 4.9). With the exception of Q. texana, all species showed a unimodal response to water level. During their emergence windows (Fig. 4.5), Ulmus spp. and F. pennsylvanica expressed the greatest emergence probability of 0.35 and 0.37, respectively, when the water level centered around the soil surface. The probability of emergence (P(e)) was greatest for both C. laevigata (P(e) = 0.25) and Q. phellos (P(e) = 0.27) at a water level between -1 m and -0.5 m. The probability of encountering newly emerged Q. lyrata (P(e) = 0.37) and Q. texana (P(e) = 0.50) was highest around a water level of -1 m and -2 m, respectively. Additional species’ relationships are presented in Appx A, Fig. A.4.

Emergence vs Days Since the Last Flood

The number of days since the last flood (DSLF), i.e., the timing of flood recession, was statistically significant as a predictor of emergence for all six species (Figs. 4.10 and 4.11a). Again, the best models were non-linear and illustrated unimodal species’ responses. Fraxinus pennsylvanica (P(e) = 0.40) and Ulmus spp. (P(e) = 0.36) had the highest probability of emergence close to 25 days post-flood (Chi sq. < 0.05). Following a flood event, the next most likely species to emerge within 50 days were C. laevigata and Q. phellos (P(e) = 0.25; Chi sq. < 0.05). Quercus texana (P(e) = 0.34; Chi sq. < 0.10) and Q. lyrata (P(e) = 0.54; Chi sq. < 0.05) demonstrated the latest peak emergence probability, and unlike the other species, maintained over 25% chance of emergence 100 days after a flood.
The day of the year (DOY) also showed a significant relationship with emergence timing, reflecting species’ emergence phenology windows (Fig. 4.5). This was significant for four of our six species (Chi sq. < 0.05); *Q. lyrata* and *Q. texana* did not demonstrate a significant relationship with DOY (Chi sq. > 0.05; Fig. 4.11b). To separate the effects of flood recession timing and DOY, we examined the mean dates of flood recession and emergence onset across all sites and also for a single site per species (Table 4.9). Across all sites, the annual length of time between the average last flood day and average emergence day varied within species. At a single site, the comparisons showed tighter patterns between the last flood day and emergence day, with the difference only ranging from 38.6-45.7 days for *Q. lyrata*. Both *F. pennsylvanica* and *Ulmus* spp. exhibited short durations between average last flood day and emergence day, with 20.4-29.4 days, and 12.7-23.0 days, respectively. Seedling abundance also showed significant relationships with both DOY and DSLF; however, the window of time varied between these two relationships, with DSLF corresponding to a shorter duration emergence response compared to DOY (e.g., Fig. 4.13). This was true for *Ulmus* spp. (Fig. 4.13), *F. pennsylvanica*, *Q. phellos*, and *Q. lyrata*, but not for *C. laevigata* and *Q. texana* (Appx A, Figs. A.4-8). The shorter response period between emergence and DSLF may indicate the relationship is stronger than DOY for species that displayed this pattern. This was also true for four other additional species we examined in detail (Appx A, Figs. A.9-12).

Figure 4.10. The probability of seedling emergence (±SE in gray) vs the number of days since the last flood (DSLF). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.
Figure 4.10 continued. The probability of seedling emergence (±SE in gray) vs the number of days since the last flood (DSLF). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.
Figure 4.11. The probability of seedling emergence vs. a) the number of days since the last flood (DSLF); and b) the day of the year (DOY). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons. All species demonstrated a significant relationship with DSLF (Chi sq. < 0.05); all species except for *Quercus lyrata* and *Quercus texana* demonstrated a significant relationship with DOY (Chi sq. < 0.05).
Figure 4.11 continued. The probability of seedling emergence vs. a) the number of days since the last flood (DSLF); and b) the day of the year (DOY). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons. All species demonstrated a significant relationship with DSLF (Chi sq. < 0.05); all species except for *Quercus lyrata* and *Quercus texana* demonstrated a significant relationship with DOY (Chi sq. < 0.05).

Emergence vs Multiple Variables

Combining both water level (WL) and the number of days since the last flood (DSLF) produced the best explanation for emergence probability for all focal species (Table 4.10). The unimodal emergence response of the three lighter-seeded species to both water level and time since the last flood event produced a best-fit model when the variables were combined with an interaction term (Chi sq. < 0.05). In contrast, an interaction between the two variables was not important for explaining emergence probability of the *Quercus* species, and relatively simpler models using the two variables were the better fit.
Table 4.9. Mean and median day of the year when the last flood ended (±SE) and mean and median day of emergence per species. Statistics included only plots where each species was present. Mean and median values considered all sites, and a single site for each species.

<table>
<thead>
<tr>
<th>Species</th>
<th>Year</th>
<th>Plots (N)</th>
<th>Day of Last Flood Overall</th>
<th>Day of Emergence Overall</th>
<th>Difference in Means</th>
<th>Plots (N)</th>
<th>Day of Last Flood One Site</th>
<th>Day of Emergence One Site</th>
<th>Difference in Means</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cultis laevigata</td>
<td>2016</td>
<td>12</td>
<td>122.2 (± 2.1)</td>
<td>124.1</td>
<td>156.2 (± 5.3)</td>
<td>144.0</td>
<td>33.9</td>
<td></td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>21</td>
<td>99.4 (± 9.9)</td>
<td>94.4</td>
<td>113.5 (± 8.8)</td>
<td>122.0</td>
<td>14.1</td>
<td>7</td>
<td>87.4 (± 25.6)</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>29</td>
<td>112.1 (± 3.4)</td>
<td>115.5</td>
<td>144.4 (± 7.9)</td>
<td>138.5</td>
<td>32.4</td>
<td>8</td>
<td>122.5 (± 1.8)</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>2016</td>
<td>22</td>
<td>138.5 (± 6.0)</td>
<td>129.5</td>
<td>164.7 (± 4.4)</td>
<td>158.0</td>
<td>26.2</td>
<td></td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>47</td>
<td>102.6 (± 6.9)</td>
<td>95.8</td>
<td>118.6 (± 6.6)</td>
<td>102.5</td>
<td>15.9</td>
<td>11</td>
<td>114.1 (± 9.6)</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>42</td>
<td>99.4 (± 4.3)</td>
<td>6.9</td>
<td>122.5 (± 6.7)</td>
<td>121.0</td>
<td>23.1</td>
<td>21</td>
<td>94.9 (± 3.7)</td>
</tr>
<tr>
<td>Quercus lyrata</td>
<td>2016</td>
<td>14</td>
<td>158.2 (± 7.9)</td>
<td>140.1</td>
<td>196.8 (± 7.8)</td>
<td>191</td>
<td>38.6</td>
<td>14</td>
<td>158.2 (± 7.9)</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>5</td>
<td>152.0 (± 45.0)</td>
<td>164.4</td>
<td>192.2 (± 43.2)</td>
<td>207.5</td>
<td>40.2</td>
<td>3</td>
<td>139.7 (± 108.2)</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>1</td>
<td>138.3 (± 0.0)</td>
<td>138.3</td>
<td>184.0 (± 0.0)</td>
<td>184</td>
<td>45.7</td>
<td>1</td>
<td>138.3 (± 0.0)</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>2016</td>
<td>6</td>
<td>150.0 (± 13.1)</td>
<td>157.3</td>
<td>190.7 (± 5.4)</td>
<td>195.5</td>
<td>40.6</td>
<td>2</td>
<td>153.3 (± 29.2)</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>24</td>
<td>158.3 (± 9.9)</td>
<td>160.8</td>
<td>171.5 (± 8.4)</td>
<td>165.0</td>
<td>13.3</td>
<td>18</td>
<td>162.0 (± 12.4)</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>6</td>
<td>116.0 (± 1.3)</td>
<td>116.8</td>
<td>156.2 (± 11.3)</td>
<td>157.0</td>
<td>40.1</td>
<td>4</td>
<td>115.8 (± 1.7)</td>
</tr>
<tr>
<td>Quercus texana</td>
<td>2016</td>
<td>6</td>
<td>125.9 (± 2.4)</td>
<td>128.6</td>
<td>176.8 (± 15.7)</td>
<td>166.0</td>
<td>50.9</td>
<td>6</td>
<td>125.9 (± 2.3)</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>14</td>
<td>155.3 (± 12.2)</td>
<td>177.0</td>
<td>195.7 (± 15.9)</td>
<td>178.0</td>
<td>40.3</td>
<td>14</td>
<td>155.3 (± 12.2)</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>3</td>
<td>112.4 (± 14.7)</td>
<td>126.2</td>
<td>175.7 (± 46.3)</td>
<td>222.0</td>
<td>63.3</td>
<td></td>
<td>--</td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td>2016</td>
<td>20</td>
<td>128.8 (±5.2)</td>
<td>126.6</td>
<td>160.1 (± 3.7)</td>
<td>158.0</td>
<td>31.2</td>
<td></td>
<td>--</td>
</tr>
<tr>
<td></td>
<td>2017</td>
<td>50</td>
<td>94.5 (± 5.5)</td>
<td>94.8</td>
<td>106.9 (± 4.6)</td>
<td>101</td>
<td>12.3</td>
<td>15</td>
<td>82.2 (± 13.3)</td>
</tr>
<tr>
<td></td>
<td>2018</td>
<td>72</td>
<td>99.5 (± 3.3)</td>
<td>106.6</td>
<td>115.1 (± 4.6)</td>
<td>112.0</td>
<td>15.6</td>
<td>11</td>
<td>96.5 (± 12.0)</td>
</tr>
</tbody>
</table>
Figure 4.12. Average emergence abundance of *Ulmus* spp. seedlings during 2017 and 2018 at South A relative to a) the day of the year, and b) number of days since the last flood.
Table 4.10. Logistic regression models of the probability of seedling emergence by species in relation to average water level (WL) and the number of days since the last flood (DSLF).

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameters of final supported model</th>
<th>Change in deviance</th>
<th>df</th>
<th>Terms in simpler supported model(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Celtis laevigata</td>
<td>logit ( P = -1.7427 + (-2.7879<em>WL) + (-1.4542</em>WL^2) + (0.0198<em>DSLF) + (-0.0002</em>DSLF^2) + (0.0192*(WL*DSLF)) )</td>
<td>4.20</td>
<td>1</td>
<td>WL, WL^2, DSLF, DSLF^2</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica</td>
<td>logit ( P = -0.5959 + (-0.3872<em>WL) + (-0.9811</em>WL^2) + (0.0349<em>DSLF) + (-0.0005</em>DSLF^2) + (-0.0011*(WL*DSLF)) )</td>
<td>6.69</td>
<td>1</td>
<td>WL, WL^2, DSLF, DSLF^2</td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td>logit ( P = -0.6269 + (-0.5000<em>WL) + (-1.2536</em>WL^2) + (0.0275<em>DSLF) + (-0.0006</em>DSLF^2) + (-0.0155*(WL*DSLF)) )</td>
<td>9.39</td>
<td>1</td>
<td>WL, WL^2, DSLF, DSLF^2</td>
</tr>
<tr>
<td>Quercus phellos</td>
<td>logit ( P = -1.6258 + (-0.9519<em>WL) + (0.0156</em>DSLF) + (0.0293*(WL*DSLF)) )</td>
<td>4.93</td>
<td>1</td>
<td>WL, DSLF</td>
</tr>
<tr>
<td>Quercus texana</td>
<td>logit ( P = -2.5205 + (-1.3935<em>WL) + (0.0005</em>DSLF) )</td>
<td>12.53</td>
<td>2</td>
<td>WL, DSLF</td>
</tr>
<tr>
<td>Quercus lyrata</td>
<td>logit ( P = -1.6049 + (-1.2062<em>WL) + (0.0001</em>DSLF) )</td>
<td>11.21</td>
<td>2</td>
<td>WL, DSLF</td>
</tr>
</tbody>
</table>

The change in deviance is the difference in deviance between the final supported model and the previous simpler supported model. The reported changes in deviance are all greater than the critical Chi square value at \( \alpha = 0.05 \).

Light Availability

Light availability at most plots was relatively low in response to canopy closure values of 80 to 90 percent (Fig. 4.13). The probability of detecting first-year *F. pennsylvanica* seedlings at a plot significantly declined with increasing canopy closure (Fig. 4.14). The other five species did not demonstrate a significant \((P > 0.05)\) relationship with light availability \((P > 0.05; \text{Appx A, Fig. A.13})\). We did not detect a relationship between first-year seedling abundance and canopy closure.
Figure 4.13. Percent canopy closure during the 2016-2018 growing seasons at four sites within the Lower Mississippi River Alluvial Valley. Values were calculated from hemispherical photos taken during mid-summer of each year.

Figure 4.14. The probability of occurrence (±SE in gray) for first-year *Fraxinus pennsylvanica* seedlings relative to percent canopy closure. Data is based on the 2016-2018 growing seasons at four sites within the Lower Mississippi River Alluvial Valley.
Table 4.11. Percent mortality of first-year seedlings (< 1 year old) and established seedlings (≥ 1 year old) at four floodplain sites in the Lower Mississippi Alluvial Valley during the 2016-2018 growing seasons. Only stems ≤ 50 cm were documented. The total number of first-year seedlings (N) per year is given in parentheses. Focal species are in bold.

<table>
<thead>
<tr>
<th>Species (common name)</th>
<th>Mortality (%) seedlings &lt; 1 yr</th>
<th>Mortality (%) established seedlings ≥ 1 yr*</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2016</td>
<td>2017</td>
</tr>
<tr>
<td>Acer rubrum (red maple)</td>
<td>--</td>
<td>(0)</td>
</tr>
<tr>
<td>Carya aquatica (water hickory)</td>
<td>72 (31)</td>
<td>0 (1)</td>
</tr>
<tr>
<td>Carpinus caroliniana (American hornbeam)</td>
<td>-- (0)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Carya illinoinsis (pecan)</td>
<td>-- (0)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Celtis laevigata (sugarberry)</td>
<td>69 (26)</td>
<td>82 (33)</td>
</tr>
<tr>
<td>Cephalanthus occidentalis (buttonbush)</td>
<td>0 (1)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Crataegus spp. (hawthorn)</td>
<td>100 (1)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Cornus drummondii (roughleaf dogwood)</td>
<td>-- (0)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Diospyros virginiana (persimmon)</td>
<td>-- (0)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Forestiera acuminata (swamp privet)</td>
<td>98 (1077)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Fraxinus pennsylvanica (green ash)</td>
<td>56 (45)</td>
<td>92 (611)</td>
</tr>
<tr>
<td>Gleditsia aquatica (water locust)</td>
<td>84 (19)</td>
<td>-- (0)</td>
</tr>
<tr>
<td>Gleditsia triacanthos (honey locust)</td>
<td>93 (15)</td>
<td>50 (4)</td>
</tr>
<tr>
<td>Ilex decidua (deciduous holly)</td>
<td>67 (3)</td>
<td>75 (4)</td>
</tr>
<tr>
<td>Liquidambar styraciflua (sweetgum)</td>
<td>-- (0)</td>
<td>50 (2)</td>
</tr>
<tr>
<td>Planera aquatica (water elm)</td>
<td>96 (82)</td>
<td>91 (11)</td>
</tr>
<tr>
<td>Quercus lyrata (overcup oak)</td>
<td>40 (67)</td>
<td>25 (4)</td>
</tr>
<tr>
<td>Quercus nigra (water oak)</td>
<td>-- (0)</td>
<td>0 (1)</td>
</tr>
<tr>
<td>Quercus phellos (willow oak)</td>
<td>63 (8)</td>
<td>38 (58)</td>
</tr>
<tr>
<td>Quercus texana (Nuttall oak)</td>
<td>29 (7)</td>
<td>41 (22)</td>
</tr>
<tr>
<td>Taxodium distichum (bald cypress)</td>
<td>-- (0)</td>
<td>97 (32)</td>
</tr>
<tr>
<td>Triadica sebifera (Chinese tallow)</td>
<td>-- (0)</td>
<td>71 (14)</td>
</tr>
<tr>
<td>Ulmus spp. (elm)</td>
<td>63 (82)</td>
<td>95 (2597)</td>
</tr>
</tbody>
</table>

*Inconsistency in total (N) values between years of established seedlings can be attributed to overwinter mortality, herbivory, and additional plots set up in 2017
Mortality

First-year seedling mortality was generally higher compared to older seedlings (≥ 1 year; Table 4.11). Light-seeded species, such as A. rubrum (89-99%), F. pennsylvanica (56-92%), and Ulmus spp. (82-95%), tended to have some of the highest mortality in their first year when compared to heavy-seeded species like Quercus lyrata (0-40%) and C. aquatica (0-72%). But that pattern does not appear to extend beyond the first growing season.

First-year seedling mortality tended to be later for many of the more flood tolerant species (Fig. 4.15), which also generally emerged later in the season (Appx A, Fig. A.14). The median mortality frequency for C. aquatica, F. acuminata, G. aquatica, and P. aquatica all occurred at approximately the 230th day of the year (~mid-August). The earliest emergents of the growing season experienced some of the earliest mortality beginning around week 12, e.g., A. rubrum, C. laevigata, F. pennsylvanica, and Ulmus spp.

Figure 4.15. First-year seedling mortality timing of floodplain forest woody species at four sites within the Lower Mississippi River Alluvial Valley during 2016-2018. Only species with N ≥ 5 are presented. Day 70 is approximately mid-March and day 245 is approximately early September. Focal species are in bold.
Figure 4.16. The hydrographs of four plots (20 x 20 m) at site South A, located in the Lower Mississippi River Alluvial Valley, during 2017. Water level is relative to the soil surface (y = 0). Each line represents water level at a plot location; plot elevations are presented in the legend.

Figure 4.17. Cumulative percent mortality of first-year seedlings at site South A, located in the Lower Mississippi River Alluvial Valley, during 2017. High water levels during June and July prevented accurate surveys of seedlings, therefore mortality values in August include mortality from June and July as well.
The South A site experienced a prolonged second flood (May – July) in 2017 at all plots (Fig. 4.16) which resulted in complete morality of documented first-year seedlings. Prior to inundation, mortality was below 30% for all species. Following the second flood, mortality rose to ≥ 40% for all species, though it should be noted these values represent the cumulative loss throughout both June and July. I could not accurately census seedlings at the time of peak flooding (June - July), therefore mortality was visually confirmed when flooding receded in August (Fig. 4.17).

Mortality vs Total Flood Days

*Fraxinus pennsylvanica, Ulmus spp., and Q. phellos* had a significantly higher probability (Chi sq. < 0.05) of mortality at plots with greater number of days flooded. *Ulmus* spp. showed about a 60 percent or higher probability of mortality at locations flooded for ≥100 days; *F. pennsylvanica* displayed a 50 percent or higher probability of mortality at the same duration, and *Q. phellos* displayed about a 20 percent or higher chance at ≥100 days of flooding. The total number of days flooded at plot was not a significant predictor of mortality for *C. laevigata, Q. texana*, or *Q. lyrata* (Chi sq. > 0.05; Appx A, Fig. A.15)

Mortality vs Water Level

The probability of mortality of *F. pennsylvanica* increased with rising water level, reaching 50 percent with water at the soil surface (Chi sq. < 0.05; Appx A, Fig. A.16b). I did not detect a relationship between water level and mortality of *C. laevigata or Ulmus* spp. because the former exhibited relatively low mortality across the water level gradient (0.25 - 0.50%) whereas the latter displayed a consistently high chance of mortality (0.50 - 0.75%) across this gradient (Fig. 4.12a,c). We also found a positive relationship between water level and *Q. phellos* mortality (Chi sq. < 0.10). In contrast, we found both *Q. texana* (Chi sq. < 0.05) and *Q. lyrata* (Chi sq. < 0.10) mortality declined with increasing water level (Appx A, Fig. A.16e-f). Notably, the documented flood depth did not average greater than one meter prior to observed emergence at any of our plots, and rarely did it average more than 0.5 meters prior to observed emergence.

Mortality vs Days Since the Last Flood

*Fraxinus pennsylvanica* showed a unimodal relationship between mortality and the number of days since the last flood (Chi sq. < 0.05; Appx A, Fig. A.16). Mortality probability increased in the days following a flood, surpassing 0.50 and peaking around 0.75 days post-flood; but then the probability of mortality declined throughout the remainder of the season. *Ulmus* spp. similarly displayed a unimodal mortality pattern, but it was not statistically significant, nor was the low chance of mortality for *C. laevigata*. The only *Quercus* species to show a significant relationship with this variable was *Q. phellos*, which declined in mortality probability after a flood (Chi sq. < 0.05). The other two *Quercus* species showed a steady chance of mortality following a flood (Appx A, Fig. A.17).
Mortality vs Multiple Variables

The probability of mortality of *F. pennsylvanica* was best explained by all three of the hydrologic variables and an interaction between them (Appx A, Table A.1). Mortality of both *Ulmus spp.* and *Q. phellos* was further explained by combining both total days flooded at a plot and the time since the last flood event.

Discussion

The results of this study indicate that first-year seedling species composition is significantly influenced by interrelationships in the timing of flooding relative to species-specific germination and establishment processes. Flood duration preceding a seed’s germination window inhibited germination when it fully overlapped with a species’ phenological germination window. At locations with prolonged flooding (i.e., beyond May), this event precluded early germinant species (e.g., *C. laevigata, F. pennsylvanica*, and *Ulmus spp.*) from colonizing these areas. This finding helps answer my first and second questions about the effects of preceding total flood days and water levels on seedling emergence. The results additionally revealed that flooding promotes germination if flooding recedes prior to the close of a species’ germination window, presumably facilitating imbibition and soil water access of nondormant seeds. Thus, regarding my second and third questions, a dynamic water level and the timing of flood recession can significantly influence seedling germination processes. Additionally, results showed that seedling emergence was generally unaffected by light availability, with the exception of one species (*F. pennsylvanica*). Finally, post-germination flood timing significantly affected seedling composition in the event of a second flood via seedling mortality. These findings are similar to prairie pothole wetlands in that the timing of flooding relative to germination and establishment events can serve as an important environmental sieve that controls species composition of the seedling layer (van der Valk 1981). Topographic variability across the floodplain, temporal variability in rainfall and flooding, along with variation in seed production (Downs and McQuilkin 1944, Clark et al. 1999a), creates diverse flood probabilities at any given spot on the floodplain and leads to varied germination and establishment outcomes over time. Furthermore, once established, floodplain species can further direct subsequent establishment events through their effects on light availability – a widely recognized secondary filter influencing seedling and sapling recruitment (Battaglia et al. 2000, Lin et al. 2004, Mann et al. 2008).
Figure 4.18. The same square meter subplot on a) March 28, 2017 and on b) March 23, 2018. First-year seedlings of *Acer rubrum*, *Celtis laevigata*, *Fraxinus pennsylvanica*, and *Ulmus* spp. are present in the second image.
Nondormant seeds were prevented from germinating when their location was inundated beyond their phenological germination window. Specifically, *C. laevigata*, *F. pennsylvanica*, and *Ulmus* spp. were susceptible to lost germination opportunities at sites flooded past the 150th day of the year (~end of May; e.g., Fig. 4.18), whereas *Quercus* spp. tended to avoid this restriction. Notably the former three species still exhibited limited emergence during the summer months, but in substantially lower quantities. Among the six focal species, viable seeds were still able to reach and/or survive sites until flooding receded. Thus, emergence disparity among species was significant only when abundance was considered in addition to occurrence (Table 8). Nearly all species associated with the number of flood days at a plot were hydrophilic species, such as *C. aquatica*, *F. acuminata*, and *Q. lyrata*. The fact that flood duration lacked significance as a predictor for emergence occurrence but was significant when abundance was incorporated illustrates the challenge of evaluating the intricacies of the dynamic regeneration processes. Seeds of *Q. lyrata* (Pierce and King 2007) and *F. pennsylvanica* (Schmiedel and Tackenberg 2013) both exhibit improved germination after being inundated for extended periods. Flooding can also aid in seed dispersal (Schneider and Sharitz 1988, Thebaud and Debussche 1991, Middleton 2000, Schmiedel and Tackenberg 2013), and some seeds may not be dispersed until flood waters recede (Stapanian 1982). Thus, flood recession must occur prior to the end of a species’ phenological germination window to allow germination to proceed; and though long flood durations do not necessarily eliminate regeneration, they can significantly reduce seedling abundance of some species.

Flooding can favor germination if flooding recedes prior to the close of a species’ germination window. In this situation, nondormant seeds can benefit through flood-induced imbibition and soil water access which stimulates germination. *Fraxinus pennsylvanica* and *Ulmus* spp. displayed evidence of this pattern with higher germination probability correlated to groundwater near the soil surface. This presumably indicated a high soil moisture and suggests germination was triggered by imbibition. Although we did not measure it directly, seed imbibition is required to initiate the germination process (Finch-Savage and Leubner-Metzger 2006). We could not specifically distinguish whether these effects were driven by flooding or by a high water table, but in the presence of microtopographic variation, a high water table immediately below the soil surface in one location may concurrently results in a limited extent of flooding in another nearby location. *Fraxinus pennsylvanica* is known to germinate better following flooded conditions (DuBarry 1963, Walls et al. 2005) and in one study showed an increase in germination following 15 days of inundation compared to seeds flooded for fewer days (Schmiedel and Tackenberg 2013). Both *F. pennsylvanica* and *Ulmus* spp. species have samaras with membranous seed coats making them more permeable to water as well as vulnerable to fungal attacks (Halloin 1986). They also demonstrate epigeal germination, indicating that a relatively quick response to imbibition is advantageous to avoid damping off and to secure a rapid growth opportunity. Further research that directly examines seed imbibition would help explain how this physiological process affects germination timing of floodplain forest species.

Both *C. laevigata* and *Q. phellos* exhibited the highest probability of emergence when the groundwater level was relatively lower, about 0.75 m below the soil surface. The harder seed
coat of both species, compared to species with samaras, may translate to emergence in relatively drier soil conditions as groundwater declines later in the growing season (Fig. 4). Thicker seed coats can take longer to respond to imbibition (Hernandez and Oriolo 1985, Baskin and Baskin 2014), therefore while a water level close to the soil surface may trigger germination, the lag in seedling response to break through the seed coat may correspond to a receding water level (Schopmeyer 1974).

Seed size could also help explain the relatively lower water levels corresponding to peak emergence probabilities of *Q. lyrata* and *Q. texana*. Like hard seed coats, larger seed size can cause a lag time between the start of imbibition and the subsequent emergence of the radical (Castro et al. 2005). Aside from seed size, the time interval between seed germination and seedling emergence could have also created a disconnect between high water level and emergence; I observed multiple *Quercus* seedlings emerging from the soil surface, indicating germination of the buried acorns could have occurred several days prior. In addition, most *Quercus* species have recalcitrant seeds (Olson 1974, Iakovoglou et al. 2009, Baskin and Baskin 2014) with limited or no dormancy, therefore dormancy does not require breaking prior to the onset of germination. *Quercus lyrata* is known to germinate during humid cold stratification without inundation (Schopmeyer 1974). It is therefore likely that soil moisture was still high when *Quercus* germination occurred, presumably through rainfall and capillary fringe in the clay floodplains soils. Had the locations been too dry, viability of these recalcitrant acorns would likely have been lost. Actual soil moisture values are unknown, however. These characteristics could help explain the separation between high water levels and emergence timing for the *Quercus* species. Other regeneration studies of bottomland species have documented higher numbers of first-year seedlings emerging on wetter sites compared to drier locations (Streng et al. 1989, Jones et al. 1994). This pattern has potentially long-lasting effects on composition; Leyer et al. (2012) reported the probability of occurrence for young trees in European floodplains was highest with an average water level at 0 ± 1 m relative to the soil surface. Additional research on the relationship between soil moisture and seed germination is necessary to better understand how water levels directly and indirectly affect the germination process. This applies, too, to low water tables. Floodplains adjacent to entrenched river channels generally drain faster and experience reduced water tables compared to non-entrenched systems (Bornette et al. 1996, Heine and Lant 2009), but the effect of this on soil moisture and the germination process warrants further investigation.

Germination windows and flood events are naturally correlated with the spring season in southeastern bottomlands (Streng et al. 1989), thus the timing of germination relative to flood recession may reveal clues in in species’ regeneration strategies. *Fraxinus pennsylvanica* and *Ulmus* spp. emerged the earliest (~20-25 days) following a flood event, which agrees with their earlier emergence windows (Fig. 6). This supports a strategy of getting an early start to the growing season to lengthen the development period during their first year (Streng et al. 1989, Jones et al. 1997). Both *C. laevigata* and *Q. phellos* emerged 30-40 days after a flood event with longer likelihood of emergence compared to the former two species. This ties into their slower response to germination that stretches out that probability curve over time. Both *Q. texana* and *Q. lyrata* displayed the broadest germination window; at the time when emergence tapered off
for the other four species, 100 days since a flood event, emergence persisted well beyond this point for these two oaks.

Further study is required to specifically separate the effects of flood recession from species’ germination phenology. The time of year can explain emergence probability for most of our focal species except for *Q. lyrata* and *Q. texana*. When the number of days since flood recession was used to explain emergence probability across all sites, species displayed significant relationships. But when site-specific evaluations of emergence abundance were considered, both variables (time of year or time of flood recession) were significant predictors for all species except *C. laevigata* and *Q. texana*. Across years, the average last flood day varied, as would be expected, but so did the average day of emergence even within a single site. If emergence responded more directly to flooding than to time of year, we would expect a similar length of time between the last flood day and average emergence day. This was generally true when considering the margins of error about the means for each species. What may be the most compelling evidence to separate these factors are the differences in duration of the emergence response times. Among the site-specific assessments, the emergence response time relative to flood recession was often shorter than the response time based on the day of the year (Fig. 13). Some species, including *Ulmus* spp., *F. pensylvanica*, expressed both high emergence probability and abundance within 30 days of a flood. When we examined additional species (*A. rubrum, C. aquatica, F. acuminata, and P. aquatica*), they all expressed peak emergence probability within 50 days of a flood, whereas their emergence probability relative to the day of the year showed much broader response curves. Furthermore, *A. rubrum* occurred at a different site than the other three species and experienced earlier flood recession, and when flood recession was used to explain emergence probability, all four species’ emergence windows overlapped (Appx A, Fig. A.18). It is evident that day of year, flood recession timing, and germination timing are intricately related, but disassembling these factors from one another requires further research.

Among woody forest species, light availability tends to increase in importance for survival after the first growing season, and our results generally aligned with this finding (Grime and Jeffrey 1965, Hall and Harcombe 2001). Canopy closure was high across all four sites (Fig. 4.14). The availability of light was not an important predictor for the occurrence of first-year seedlings of any of our focal species, except *F. pensylvanica* which decreased in occurrence probability with increasing canopy closure. Light is important for seedling emergence of some species (Battaglia and Sharitz 2000), for instance, germination rates of *C. laevigata* and *Ulmus* spp. have been found to increase in high light conditions (Burns and Honkala 1990, Nijjer et al. 2002). But *F. pensylvanica* is not known to require light to germinate (Schopmeyer 1974), though more research is needed to confirm this. The low variation among our plots and sites in canopy closure (Fig. 4.14) likely made it more difficult to detect patterns in first-year seedling presence relative to light if they occurred. Further examination on the direct effects of light and first-year seedling dynamics could strengthen our understanding of this relationship and how it affects the early stages of the regeneration process.

Lastly, post-germination flood timing can significantly influence seedling composition in the event of a second flood. Species that emerged in March had a greater risk of experiencing a second flood at locations with dynamic flood regimes (Fig. 4). Light- versus heavier-seeded
species generally displayed high and lower percentages of first-year seedling mortality, respectively. This was illustrated by light-seeded *F. pennsylvanica* and the more moderately-sized seeds of *C. laevigata*; the former species was critically sensitive to differences in all three of our hydrologic variables, whereas the latter species was not. *Celtis laevigata* mortality probability remained the same across the hydrologic gradients (i.e., total flood days, days since the last flood, and average water level), but it was relatively low, often below 50%. The mortality probability met or exceeded 50% in all three of our *F. pennsylvanica* models. Complete inundation of young first-year seedlings of both species results in similar mortality rates (chapter 3). It may be that this difference in response between the two species is due to the timing of species’ emergence. Light-seeded *Ulmus* spp. also showed sensitivity to the number of days flooded at a site – both *F. pennsylvanica* and *Ulmus* spp. have early, overlapping emergence windows in the spring. *Celtis laevigata* emergence extended slightly later than these other species, providing some limited opportunity to avoid early-season flooding (Fig. 4).

The pattern between seed size and seedling vulnerability to flooding extended to variability among the three *Quercus* species. The *Quercus* species with the smallest seed, *Q. phellos*, was vulnerable to more days flooded, to higher water levels, and was more sensitive shortly after a flood event. In contrast, *Q. texana* and *Q. lyrata* were less vulnerable to high water levels and showed no significant change in mortality with number of days flooded at a site and time since the last flood. *Quercus phellos* seedlings are more susceptible to mortality than the other two species when subject to complete submergence (chapter 3). Seed size likely provides *Q. texana* and *Q. lyrata* more tolerance to flooding due to their higher energy storage and helps explain their distribution on floodplains at lower sites compared to *Q. phellos*. Previous studies have also demonstrated lower flood tolerance of *Q. phellos* relative to other bottomland species (Hosner and Boyce 1962, Bedinger 1971, King and Grant 1996).

*Seedling Composition*

This is the first study to provide a comprehensive assessment of a floodplain forest seedling composition representative of the LMAV. This aspect provides foundation-level understanding of ecological processes that are critical to evaluating forest community responses to environmental change in this region. The most ubiquitous species through both space and time during the study were *C. laevigata*, *F. pennsylvanica*, and *Ulmus* spp. The latter two species illustrate the potential of wind-dispersed species, extending germination opportunities spatially where other species are more limited. At the South A site, *F. pennsylvanica* had a relatively low basal area (0.75 m²/ha) and density (12.5 stems/ha; Tables 1 and 2) but was the second most abundance species in first-year seedlings following *U. americana* (Table 5). This pattern highlights the regeneration strategy of producing many relatively small seeds to improve chances of seeds reaching favorable germination conditions. Moreover, these species and *C. laevigata* reached maximum germination potential by mid-May (Fig. 7), but emergence did not completely cease until late July, thereby the germination opportunity extended through time as well, albeit more diminished. This implies spring flooding would not entirely preclude germination of these species if flooding receded before late July, but it is likely late season flooding plays a role in suppressing establishment opportunities for these species.
Producing fewer relatively heavy seeds was also a regeneration strategy. Species such as *C. aquatica*, *Q. lyrata*, and *Q. texana* occurred in lower densities at fewer sites compared to the light-seeded species (Table 5). These heavy-seeded species emerged from late May through the end of the growing season (Fig. 6). Late season germination potential allows species to avoid stress driven by early-season disturbance, but it reduces the timeframe for seedling development (Streng et al. 1989). High carbohydrate reserves, accompanied by hypogeal germination, of the seeds of these species alleviates immediate dependency on environment resources. Seedlings were often robust and generated substantially greater height within a month of emergence compared to light-seeded species, a disparity which was also found in 3-week-old seedlings in my controlled greenhouse experiments (chapter 3).

Other species’ emergence patterns diverged from either of these strategies. For instance, *T. distichum* was an early germinant with relatively light seeds, but occurred in low density at the one site in which it was found (Table 5). This species disperses during the fall and winter and is transported effectively by water (Schneider and Sharitz 1988) and research suggests seeds readily germinate after 30 days of soaking (Schopmeyer 1974, Murphy and Stanley 1975). It is plausible that the regeneration strategy of *T. distichum* is linked to a dependence on prolonged (>30 d) flood disturbance to induce germination. Other flood tolerant species with moderate-sized seeds displayed similar emergence patterns, with maximum emergence following prolonged flood events. *Planera aquatica* and *F. acuminata*, though only abundant at a single site, showed diminished emergence in 2017 when flood duration was reduced. But in 2016 and 2018 when flooding was >150 flood days, distribution and density of these species was relatively high (Tables 5 and 7), suggesting extended flooding may have promoted germination.

Even within a single growing season, our results suggest dynamic flooding promotes coexistence of a greater diversity of species compared to sites with more stable hydrology. Elevation gradients and microtopography variation create differences in flood duration that diversify germination potential overt time. Plots with more flood days were generally different in seedling composition relative to less flooded plots, and seedling composition was correlated with floodplain hydrology (Fig. 9). All sites experienced some degree of flooding, extensive ponding included. The microtopography at Big Lake likely enhances the diversity of seedling composition to an extent (Schaetzl et al. 1989, Battaglia et al. 2000, Gardiner et al. 2004), but the lack of an overbank flood pulse at the Big Lake and South B may be a limitation on species diversity long-term. Along the Upper Rhine River, Deiller et al. (2001) found that a disconnected site lacking overbank flooding increased in species richness over time from colonization of flood-intolerant species, but species diversity remained highest in the flooded site due to the stronger ecological gradient imposed by flooding. Further research on species’ relationships with the flooding hydroperiod is needed to improve our insight into different species’ regeneration responses and how they interact with hydrology to influence composition.

**Implications**

This study suggests dynamic flood conditions across space and time contribute to increased diversity of first-year seedling composition in the LMAV. Variability in flood duration and timing produced a greater diversity of opportune germination conditions for seeds at
locations across a floodplain and at locations throughout a growing season. Although we could not fully separate the effects of flood recession and time of year, there is evidence that a flood disturbance preceding or ending within a species’ phenological emergence window enhances emergence probability. Furthermore, high water levels near the soil surface are beneficial for producing the best regeneration opportunity. All species demonstrated emergence at sites with no overbank flooding, indicating that spring rainfall produced adequate moisture to trigger germination. Flood duration may limit regeneration by precluding emergence of species if seeds cannot reach an exposed soil surface. Flood duration can also affect first-year seedling mortality if flooding occurs after emergence (chapter 3).

Environmental changes within and beyond the LMAV are contributing to the creation of novel ecosystems, now only best understood through ecological processes because historic patterns have been disrupted or eliminated. Many of the observed floodplain forest community transitions in LMAV are linked to altered hydrology, but where the changes are occurring along the regeneration timeline has not been identified or necessarily understood. Gee et al. (2014) identified a positive correlation between the reduction of flooding and the recruitment of *C. laevigata* in a bottomland historically dominated by *Q. lyrata*. Mechanisms within the regeneration process were suspected to be the drivers behind the community transition. Additional studies in the LMAV found similar evidence of floodplain forest community transitions. Smith (1996) documented evidence of *Quercus*-dominated canopies shifting to more shade-tolerant species. Hanberry et al. (2012) found that present-day floodplain forests have lower stocking comprised of young, small-diameter trees compared to historic floodplain forests which had greater average basal area and lower densities. They identified a forest transitioning from shade-intolerant species to shade-tolerant species within LMAV bottomlands. In these studies, the loss or reduction of flooding was hypothesized as a driving factor behind these phenomena.

One of the earliest effects on tree species composition from changes to floodplain hydrology could be within first-year seedling composition. The absence of extended flooding (>150 d) tends to favor early-season germinants that can capitalize on a longer growing season while avoiding flood-stress (Streng et al. 1989). Modified regions of the LMAV that have reduced or altered flood regimes likely promote emergence conditions for species such as *F. pennsylvanica*, *U. americana*, *U. crassifolia*, and *C. laevigata* and may help explain the high density of these species in more contemporary floodplains (Gee et al. 2014, Battaglia et al. 2002). All four sites in this study have been hydrologically modified from nearby channelization or disconnected from the main channel; Boeuf and South A still experience overbank flooding, but Big Lake and South B are hydrologically disconnected and flood via precipitation-driven ponding. While basal area of *C. laevigata*, *F. pennsylvanica*, and *Ulmus* spp. is comparable among sites, the density of these species is much higher at Big Lake relative to Boeuf, and at South B relative to South A. The shade-tolerance of these species creates further advantage beyond the early regeneration stages, especially relative to shade-intolerant oaks. Oliver et al. (2005) determined shade-intolerant red oaks grow at competitive rates with that of other floodplain forest species, but in shaded conditions growth of red oaks slows more than growth of other species. Alternatively, other research has attributed composition change to harvest
management of floodplain forests which has promoted the replacement of shade intolerant
species with shade tolerant species in the canopies (Dey 2014).

Late-season flooding (July or later) would be advantageous for regeneration of later-
emerging species, which also tend to be more flood tolerant (e.g., *C. aquatica, Q. lyrata, Q. texana*). Flooding not only aids in the dispersal of many of these species (Schneider and Sharitz 1988, Solomon 1990), but my results suggest it may also stimulate germination based on rapid
emergence following flood recession, and increased germination abundance during wetter years
compared to drier years. In the absence of extended flooding the function of a second-season
flood may facilitate the limitation of light-seeded species and favor later-germinants. At the
South A site in 2017, a second mid-season flood affected all plots until August, resulting in
complete mortality of first-year seedlings of six species, primarily *A. rubrum, F. pennsylvanica,*
and *Ulmus* spp. The sooner a second flood were to occur post-emergence, the greater the
probability of mortality for the light-seeded species, including *C. laevigata, F. pennsylvanica,*
and *U. americana* (chapter 3). Prior research also suggests heavier-seeded oak species (*Q. lyrata*
and *Q. texana*) are more likely to survive flooding up to 25 days (chapter 3).

The variation in flooding both spatially and temporally is the key driver in maintaining
diversity of first-year seedling composition within a floodplain. The lack of flooding has been
tied to changing forest composition (Shankman 1996, Oliver et al. 2005, Hanberry et al. 2012,
Gee et al. 2014), but so has increased flooding (Oswalt and King 2005). The general stabilization
of floodplain hydrology tends to reduce species diversity (Johnson et al. 1976, Barnes 1997); but
the precise agents of change, as a result of more stable hydrology, are difficult to identify
because it may take decades for a forest response to manifest. Evidence of compositional change
within the regeneration process offers valuable insight that may have long term implications.

In addition to historic and current hydrologic modifications, impending future changes
associated with drought and water management must be considered when evaluating
regeneration of floodplain forest species composition (Allen et al. 2010). In Texas, issues such
as drought, riverbed incision, and depleted water tables have caused major die-offs in some
floodplain forests and possibly inhibited regeneration of current tree species (TPWD pers. comm.
2014, Moore et al. 2016). Some evidence suggests conditions in the LMAV are shifting to
warmer temperatures and decreased streamflow (Ouyang et al. 2017). The ongoing depletion of
the Mississippi River Valley Alluvial Aquifer could further challenge river-floodplain
relationships in the future, potentially increasing surface water demand and reducing water
availability for floodplain ecosystems (Reba et al. 2017). These cases further support the need to
understand how river modifications have, and potentially will, curb the historic trajectory of
floodplain stand development.

**Conclusion**

First-year seedling species composition was significantly influenced by floodplain
hydrology through relationships between the timing of flooding and species-specific germination
and establishment processes. Flood duration preceding a seed’s germination window inhibited
germination when it fully overlapped with a species’ phenological germination window.
Flooding also benefited germination when it receded prior to the close of species’ germination
windows. Additionally, post-germination flood timing significantly influenced seedling composition through the event of a second flood inducing seedling mortality. How well species’ germination windows are synchronized, or varied, in relation to the floodplain hydrology is therefore a key factor directing seedling composition via the regeneration process (Streng et al. 1989, Sarneel 2014). Spatial and temporal variation in the timing of flood recession would diversify species’ opportunities to benefit from flooding because of the unique emergence windows demonstrated by LMAV species. This would ultimately lead to diversification in seedling species composition in both space and time. Where this spatial and temporal variation in flooding has been lost or stabilized, so too has an important ecological control that likely helped shape historic regeneration patterns and seedling composition within the LMAV. These results highlight the need for additional study on species’ relationships with flood hydroperiod – particularly flood recession – soil moisture, and seed imbibition, and the nature of these relationships within the regeneration process.
CHAPTER 5. GENERAL CONCLUSION

This dissertation evaluated mechanisms affecting seedling establishment and survival processes in relation to variations in flood hydroperiod. This is the first study to provide a comprehensive assessment of a floodplain forest seedling composition representative of the LMAV. Different regeneration strategies were highlighted among floodplain forest woody species that will aid in ecological interpretation of early life stage patterns not only in the LMAV but in other floodplain systems. This research provides foundation-level understanding of ecological processes that are critical to evaluating forest community responses to environmental change.

Evolved regeneration strategies have resulted from the differentiation of the regeneration niche among species, which increases diversity within an ecosystem (Grubb 1977). The wide variation in flood tolerance levels of floodplain forest species within their first year post-germination (chapter 3) illustrates the importance of the timing of flood disturbance relative to species-specific germination windows in affecting the species composition of the seedling layer in southeastern floodplain systems. In floodplains of the LMAV, these fundamental differences in seedling survival relative to flood dynamics provides important insight into compositional changes from more flood-tolerant Quercus species to less flood-tolerant Celtis/Fraxinus/Ulmus forest communities (Oliver et al. 2005, Hanberry et al. 2012, Gee et al. 2014). The latter species generate a high abundance of small seeds that produce delicate seedlings, all significantly more sensitive to flooding within the first few weeks post-germination compared to Quercus species. Historically, spring flooding likely limited colonization of the lighter-seeded species both temporally and spatially through preventing germination at flooded sites (chapter 4) or causing high post-germination mortality of light-seeded species (chapter 3). These processes would have restricted light-seeded species to non-flooded sites, sites with earlier flood recession, or sites with shorter flood duration within a floodplain. Tolerance to longer flood durations (chapter 2) and later emergence windows (chapter 4) of Quercus species would have been advantageous to establishment of individuals in the presence of annual flood disturbance. Locations in the LMAV that have eliminated or reduced flooding have expanded the regeneration opportunity for light-seeded species by reducing or removing flooding-imposed limitations on seedling establishment and survival (Streng et al. 1989, chapter 4). A longer growing season, coupled with a more rapid growth rate in their first year compared to heavy-seeded Quercus spp. and a general greater tolerance to shade may establish light-seeded species in a more prominent position at the cohort level to reach canopy dominance.

The declines in species diversity in temperate floodplains of North America and Europe are primarily associated with a loss of flooding, reduction of flooding (i.e., frequency, depth, duration), and/or a stabilization of the flood regime (Johnson et al. 1976, Shankman 1996, Barnes 1997, Deiller et al. 2001, Gee et al. 2014). The increase in C. laevigata in some North American floodplains (Oliver et al. 2005, Gee et al. 2014) and F. pensylvanica in North American and European floodplains (Schmiedel and Tackenberg 2013, Drescher and Prots 2016) may be driven, in part, by changes to these species’ regeneration niches (Grubb 1977, chapter 2).
The spatial and temporal variation in flooding will be an important component in maintaining diversity of first-year seedling composition within a floodplain. Reduced flooding has been linked to changing floodplain forest composition (Shankman 1996, Oliver et al. 2005, Hanberry et al. 2012, Gee et al. 2014), but so has increased flooding (Oswalt and King 2005). The general stabilization of floodplain hydrology tends to decrease species diversity (Johnson et al. 1976, Barnes 1997); but the precise agents of change, as a result of more stable hydrology, are difficult to identify because it may take decades for a forest response to manifest. The evidence of differences in species composition in relation to flooding within the regeneration process offers valuable insight that may have long term implications for floodplain forest composition.
Figure A.1. The probability of seedling emergence (±SE in gray) vs total flood days prior to emergence detection for six focal species. All models were not statistically significant (Chi sq. > 0.05). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.
Figure A.2. The probability of seedling emergence (±SE in gray) vs total flood days prior to emergence detection for four hydrophilic woody species. All models were statistically significant (Chi sq. < 0.05). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.
Figure A.3. The probability of seedling emergence vs the plot mean water level of the 15 days prior to emergence detection. All four species were statistically significant (Chi sq. < 0.05). Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons.
Figure A.4. Average emergence abundance (±SE in gray) of *Celtis laevigata* seedlings during 2017 and 2018 at South A relative to a) the day of the year and b) number of days since the last flood. Neither relationship was statistically significant (P > 0.05).
Figure A.5. Average emergence abundance (±SE in gray) of *Fraxinus pennsylvanica* seedlings during 2017 and 2018 at South B relative to a) the day of the year and b) number of days since the last flood.
Figure A.6. Average emergence abundance (±SE in gray) of *Quercus phellos* seedlings during 2016, 2017, and 2018 at Big Lake relative to a) the day of the year and b) number of days since the last flood.
Figure A.7. Average emergence abundance (±SE in gray) of *Quercus texana* seedlings during 2016 and 2017 at Big Lake relative to a) the day of the year and b) number of days since the last flood. Neither relationship was statistically significant (P > 0.05).
Figure A.8. Average emergence abundance (±SE in gray) of *Quercus lyrata* seedlings during 2016, 2017, and 2018 at Boeuf relative to a) the day of the year and b) number of days since the last flood.
Figure A.9. Average emergence abundance (±SE in gray) of *Planera aquatica* seedlings during 2016, 2017 2018 at Boeuf relative to a) the day of the year and b) number of days since the last flood.
Figure A.10. Average emergence abundance (±SE in gray) of *Carya aquatica* seedlings during 2016 and 2018 at Boeuf relative to a) the day of the year and b) number of days since the last flood.
Figure A.11. Average emergence abundance (±SE in gray) of *Forestiera acuminata* seedlings during 2018, 2017 2018 at Boeuf relative to a) the day of the year and b) number of days since the last flood.
Figure A.12. Average emergence abundance (±SE in gray) of *Acer rubrum* seedlings during 2017 and 2018 at South A relative to a) the day of the year and b) number of days since the last flood.
Figure A.13. The probability of occurrence (±SE in gray) for first-year seedlings of five focal species relative to percent canopy closure. Relationships were not statistically significant (P > 0.05). Data is based on the 2016-2018 growing seasons at four sites within the Lower Mississippi River Alluvial Valley.
Figure A.14. Emergence rate by percent of five floodplain species at four sites in the Lower Mississippi River Alluvial Valley. Data is represented from March 2016 through September 2018.
Figure A.15. The probability of first-year seedling mortality (±SE in gray) vs the total flood days at a plot prior to mortality detection. Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons. Fraxinus pennsylvanica, Ulmus spp., and Quercus phellos were statistically significant (Chi sq. < 0.05), but other species were not.
Figure A.16. The probability of first-year seedling mortality (±SE in gray) vs the plot mean water level of the 15 days prior to mortality detection. Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons. *Celtis laevigata* and *Ulmus* spp. were not statistically significant (Chi sq. > 0.10), but other species were significant at Chi sq. < 0.10 or Chi sq. < 0.05.
Figure A.17. The probability of first-year seedling mortality (±SE in gray) vs the number of days since the last flood. Data was collected from four sites within the Lower Mississippi River Alluvial Valley during the 2016-2018 growing seasons. *Fraxinus pennsylvanica* and *Quercus phellos* were statistically significant (Chi sq. < 0.5), the other four species relationships were not.
Table A.1. Logistic regression models of the probability of first-year seedling mortality by species in relation to the total number of days flooded (TDF), average water level (WL) and the number of days since the last flood (DSLF).

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameters of final supported model</th>
<th>Change in deviance</th>
<th>df</th>
<th>Terms in simpler supported model(s)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Fraxinus pennsylvanica</em></td>
<td>logit $P = -2.3700 + (0.0186\times TDF)$ + (0.0270\times WL) + (0.5445\times WL^2)$ + (0.0701\times DSLF) + (0.0061\times (TDF\times WL))$ + (-0.0004\times (TDF\times DSLF)) + (0.0481\times (WL\times DSLF))$ + (-0.0002\times (TDF\times WL\times DSLF))$</td>
<td>15.39</td>
<td>5</td>
<td>TDF, WL, WL^2, DSLF</td>
</tr>
<tr>
<td><em>Ulmus spp.</em></td>
<td>logit $P = -0.8999 + (0.0134\times TDF)$ + (0.0040\times DSLF)$</td>
<td>19.74</td>
<td>2</td>
<td>TDF, DSLF</td>
</tr>
<tr>
<td><em>Quercus phellos</em></td>
<td>logit $P = -1.8208 + (0.0079\times TDF)$ + (-0.0177\times DSLF)$</td>
<td>7.76</td>
<td>2</td>
<td>TDF, DSLF</td>
</tr>
</tbody>
</table>

The change in deviance is the difference in deviance between the final supported model and the previous simpler supported model. The reported changes in deviance are all greater than the critical Chi square value at $\alpha = 0.05$. 
a) Probability of Emergence vs. Day of Year

b) Probability of Emergence vs. Days Since Last Flood
Figure A.18. The probability of emergence first-year seedling mortality relative to a) the day of the year, all species statistically significant at the Chi sq. < 0.05 level except for *Carya aquatica*; and b) number of days since the last flood, all species statistically significant at the Chi sq. < 0.05 level.
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LIST OF REFERENCES

Alldredge, B. and G. Moore. 2014. Assessment of riparian vegetation sensitivity to river hydrology downstream of a major Texas dam. River Research and Applications 30, 244.


Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec’s southern boreal forest. Ecology 81(6), 1500-1516.


Bonner, F.T. and J.L. Gammage. 1967. Comparison of germination and viability tests for Southern hardwood seed. Southern Forest Experiment Station, Forest Service, USDA.


110


Meitzen, K.M. 2009. Lateral channel migration effects on riparian forest structure and composition, Congaree River, South Carolina, USA. Wetlands 29(2), 465-475.


Minchin, P.R. 1989. DECODA user’s manual. Research School of Pacific Studies, Australian National University, Canberra.


Murphy, J.B. and R.G. Stanley. 1975. Increased germination rates of baldcypress and pondcypress seed following treatments affecting the seed coat. Physiologia Plantarum 35(2), 135-139.


Poorter, L. 2007. Are species adapted to their regeneration niche, adult niche, or both? The American Naturalist 169, 433-442.


VITA

Whitney Kroschel was born in St. Paul, Minnesota in 1987 and raised in Afton, Minnesota where her experience in the countryside, a nearby state park, and taking summer trips up north to the cabin fueled her love for ecology. She attended Minnesota-State University – Mankato where she majored in Biology and Geography and competed in D2 track and field as a pole vaulter for the Mavericks. After graduating with a B.S. she moved to Huntington, West Virginia to attend graduate school at Marshall University where she studied herpetology. She graduated with her M.S. in Biological Sciences in 2012 and moved to Winnemucca, Nevada where she worked as a contractor for the Bureau of Land Management assisting with environmental policy compliance (NEPA). The desire to expand her skillset and expertise in ecology brought her to Baton Rouge, Louisiana in 2014 for a PhD program in the School of Renewable Natural Resources studying wetland ecology. Following the completion of her PhD, Whitney hopes to continue her work with wetlands through employment with a government agency to influence and improve management and policy of these important ecosystems.