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WOODY PLANT COMMUNITIES OF THREE URBAN WETLANDS
AND THE SUCCESS OF AN INVASIVE SHRUB (*LONICERA MAACKII*) OVER
NATURAL AND EXPERIMENTAL FLOODING GRADIENTS

By

Meghan Rhea Langley
B.S., Centre College, 2004

A Dissertation Submitted to the Faculty of the
College of Arts and Sciences of the University of Louisville
In Partial Fulfillment of the Requirements
for the Degree of

Doctor of Philosophy in Biology

Department of Biology
University of Louisville
Louisville, Kentucky

May 2016

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A Dissertation Approved on

June 3, 2016

by the following Dissertation Committee:

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Dr. Margaret Carreiro

Dr. Christopher Barton

Dr. Gary Cobbs

Dr. Sarah Emery

Dr. Wayne Zipperer

DEDICATION

This dissertation is dedicated to my parents

Robert Franklin Langley

and

Michele Mann Langley

for encouraging curiosity, valuing education and supporting me
through all my academic endeavors.

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I offer sincere gratitude to the many people who contributed to my Ph.D. work with their advice, time, effort, and support. My committee chair, Dr. Margaret Carreiro provided her expertise, encouragement, lab space and financial support. I credit her and my current committee members—Dr. Chris Barton, Dr. Gary Cobbs, Dr. Sarah Emery and Dr. Wayne Zipperer—with keeping me motivated and on the path to completion. Past members of my advisory committee (Dr. Hwa-Seong Jin and Dr. Clara Leuthart) also provided valuable insights. Dr. Jeff Jack, my former advisor, also deserves remembrance for accepting me into his lab and piquing my interest in wetland research before his untimely passing.

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ABSTRACT

WOODY PLANT COMMUNITIES OF THREE URBAN WETLANDS AND THE SUCCESS OF AN INVASIVE SHRUB (*LONICERA MAACKII*) OVER NATURAL AND EXPERIMENTAL FLOODING GRADIENTS

Meghan R. Langley

June 3, 2016

Globally, wetlands are known for providing important ecosystem services that enhance the quality of human life and regulating global biogeochemical cycles. Despite the wide recognition of their value, temperate forested wetlands are the least protected type of ecosystem world-wide, and are threatened by human activities such as logging and development. The ecology of forested wetlands remaining in urbanized areas is impacted by a multitude of anthropogenic threats, including fragmentation (which decreases the amount of interior habitat and increases edge habitat), hydrologic modification (ditching and draining of wetlands) and the incursion of invasive species (which are frequently introduced by human activities).

In the first study presented in this dissertation (Chapter 2), I examined how woody plant communities of three urban wetlands—the dominant biota of these ecosystems—changed along edge-to-interior and hydrologic gradients. Detailed measurements of elevation, surface water levels, and ground water levels were made to estimate the number of days each transect was flooded. The three study forests were surveyed in transects along edge-to-interior gradients (0-60 meters from the forest edge) and were

found to exhibit a gradient of flooding (measured as the number of days flooded in sampled areas). Ordination with non-metric multidimensional scaling (NMS)—using Importance Values (IVs) of adult trees, saplings, tree seedlings, shrubs and vines in transects at 1, 5, 10, 30 and 60 m from the edge—was used to see if patterns in the woody plant community related to distance from edge, number of days flooded and other environmental variables.

Distance from the forest edge and number of days flooded were the two variables shown to be most correlated with ordination axes generated from the species matrix ($r^2 \geq 0.15$), and each was associated with a different axis. The shrub community was most indicative of community differences along the hydrologic gradient (Axis 1); *Lindera benzoin* (a facultative shrub) and *Cornus foemina* (a facultative wetland shrub) were the species most associated with drier and wetter transects, respectively. The invasive shrub species, *Lonicera maackii*, was present at all sites, but more important at the two driest sites. Because the relative elevation (within a transect) of *L. maackii* plants increased with the number of days flooded, it appeared that higher elevation microsites may have provided refugia for the establishment and/or persistence of this invasive species in flooded areas. *Fraxinus pennsylvanica* (green ash) was a major component of the tree canopy species at all sites, and the imminent threat posed by the emerald ash borer (*Agrilus planipennis*) will most certainly result in the formation of large canopy gaps.

Following the findings of Chapter 2, two manipulated experiments were conducted to determine the degree to which *L. maackii* was impacted by flooding at early life history stages. In the first experiment (Chapter 3), seedlings of *L. maackii* were subjected to factorial treatment combinations of simulated canopy cover (2 levels),

flooding duration (3 levels) and flooding depth (4 levels) in experimental mesocosms for 40 days. Flooding events were followed by a recovery period. Inundation and saturation of seedlings for 10 to 17 days had a markedly negative effect on honeysuckle seedlings as shown by slow vertical growth or dieback and loss of leaves. No seedlings inundated for 17 days survived.

In the second experiment (Chapter 4), I measured the germinability and mean germination time (MGT) of *L. maackii* seeds stratified under cool-moist, cool-saturated, or cool-inundated conditions and transitioned to a second set of conditions intended to mimic natural drawdown or flooding events. A constantly moist control was included. Only MGT, but not germinability, of moist-to-inundated transitions (a simulated flooding treatment) differed significantly from moist controls. Seeds subjected to simulated drawdown conditions did not differ from moist controls, indicating that seeds of *L. maackii* seeds can remain viable in flooded areas, and that temporary, winter flooding of wetland microsites may not impose a major limitation on *L. maackii* germination.

The results of these three studies underscore the threats posed by invasive plant and insect species to the native woody plant community of these study systems. Evidence from the field and mesocosm studies suggest that flooding does pose a barrier to *L. maackii* colonization, but that higher elevation “safe sites” (with shorter flooding durations and/or depths) may enhance the ability of this species to invade wetter areas. At the time of field data collection (2010), emerald ash borer was largely absent from these forests, but has now caused widespread tree death in the region. Because *Lonicera maackii* is known to benefit from increased light availability, the opening of the tree

canopy could have a beneficial effect on the spread of this invasive plant species within wetland sites.

TABLE OF CONTENTS

	PAGE
DEDICATION	iii
ACKNOWLEDGEMENTS	iv
ABSTRACT	vi
LIST OF TABLES	xii
LIST OF FIGURES	xiv
 Chapter I: Introduction	 1
 Chapter II: Patterns of Woody Plant Communities Over Hydrologic and Edge-To-Interior Gradients: A Study of Three Urban Wetlands.....	 5
Introduction	5
Methods	8
Results	25
Discussion	37
Conclusions	41
 Chapter III: Effects of Flooding Duration, Flooding Depth and Light on the Growth and Survival of <i>Lonicera Maackii</i> in an Experimental Mesocosm	 67
Introduction	67
Methods	71
Results	83
Discussion	90
Conclusions	94
 Chapter IV: Effects of Simulated Flooding on Germination of <i>Lonicera Maackii</i> Seeds	 119
Introduction	119
Methods	121
Results	128
Discussion	129
Conclusions	135
 REFERENCES	 140
 APPENDICES	 148
Appendix Table 1	148
Appendix Table 2	151
Appendix Table 3	152

Appendix Table 4	153
Appendix Table 5	154
Appendix Table 6	155
Appendix Table 7	158
Appendix Table 8.....	162
Appendix Table 9	163
Appendix Table 10	166
Appendix Table 11	167
Appendix Table 12	169
Appendix Table 13	170
Appendix Table 14	171
Appendix Table 15	174
Appendix Table 16	177
Appendix Figure 1	179
Appendix Figure 2	180
Appendix Figure 3	181
Appendix Figure 4	182
Appendix Figure 5	183
Appendix Figure 6	184
Appendix Figure 7	185
Appendix Figure 8	186
Appendix Figure 9	187
Appendix Figure 10	188
Appendix Figure 11	189
 CURRICULUM VITAE	 190

LIST OF TABLES

Table 2-1: Summary of research site characteristics	42
Table 2-2: Number of days flooded for edge-to-interior transects and sites	43
Table 2-3: Summary of environmental variables in edge-to-interior transects	44
Table 2-4: Correlations between environmental variables	45
Table 2-5: Density, Importance Values and basal area of adult trees by site	46
Table 2-6: Species richness and diversity measures for all vegetation layers	48
Table 2-7: Density, Importance Values and frequency of tree saplings by site	49
Table 2-8: Density, Importance Values and frequency of tree seedlings by site	50
Table 2-9: Density, Importance Values and frequency of shrub species by site	51
Table 2-10: Density, Importance Values and frequency of shrub species by site	52
Table 2-11: Summary of environmental and biotic and environmental variables associated with NMS ordination axes	53
Table 2-12: Correlation data for relationships between days flooded, total shrub stem density, and stem density of important shrub species	54
Table 3-1: Results of mixed model regression testing effects of experimental variables on plant growth response of <i>Lonicera maackii</i> seedlings	96
Table 3-2: Results of mixed model regression testing effects of experimental variables on leaf number response of <i>Lonicera maackii</i> seedlings	97
Table 3-3: Mean, minimum and maximum days lived of <i>Lonicera maackii</i> seedlings for all combinations of flooding depth and flooding duration	98
Table 3-4: Results of mixed model regression testing effects of experimental variables on final aboveground biomass of <i>Lonicera maackii</i> seedlings	99
Table 3-5: Results of mixed model regression testing effects of experimental variables on final belowground biomass of <i>Lonicera maackii</i> seedlings	100

Table 3-6: Results of mixed model regression testing effects of experimental variables on final root-shoot ratio of <i>Lonicera maackii</i> seedlings	101
Table 4-1: Summary of stratification and post-stratification treatments for all five treatment groups in germination assay	137
Table 4-2: Means of mean germination time (MGT) for all flooding treatments and moist controls	138
Table 4-3: Means of total seed germinability for different flooding treatments	139

LIST OF FIGURES

Figure 2-1: Layout and dimensions of sampling units	55
Figure 2-2: Visual aid explaining terms used in quantifying site hydrology	56
Figure 2-3: Hydrographs depicting water levels in water monitoring wells in each of the three research sites.....	57
Figure 2-4: Seedling density of important species in north and south-facing edges with varying distance from the edge.....	58
Figure 2-5: Mean stem density of the four most abundant shrub species, at each site.....	59
Figure 2-6: Height class distribution of <i>Lonicera maackii</i> stems at each site.....	60
Figure 2-7: Total percent cover of <i>Lonicera japonica</i> vines with distance from the forest edge at all three research sites.....	61
Figure 2-8: Biplot of environmental variables with NMS ordination axes 1 and 3 based on woody plant species Importance Values (IVs) in all sampling units (parallel transects) from all three study sites.....	62
Figure 2-9: Biplot of biotic variables with NMS ordination axes 1 and 3 based on woody plant species Importance Values (IVs) in all sampling units (parallel transects) from all three study sites.....	63
Figure 2-10: Biplot of biotic variables with NMS ordination axes 1 and 2 based on woody plant species Importance Values (IVs) in all sampling units (parallel transects) from all three study sites.....	64
Figure 2-11: Stem densities of dominant shrub species vs. days flooded in parallel transects across all sites.....	65
Figure 2-12: Factor–ceiling distribution of the number of days flooded vs. the rank elevation of all <i>Lonicera maackii</i> individuals sampled.....	66

Figure 3-1: Graphical summary of split-split plot experimental design, showing nested structure of variables.....	102
Figure 3-2: Photographs illustrating construction of outdoor mesocosms.....	103
Figure 3-3: Graphical summary of split-split plot design for each experimental tank....	104
Figure 3-4 Illustration of flood depth and flood duration manipulations.....	105
Figure 3-5: Daily fluctuation in temperature for soil, water and air in experimental mesocosms, as measured on a single date.....	106
Figure 3-6: Mean observed vs. predicted growth curves for seedlings over the duration of the experiment.....	107
Figure 3-7: Stem growth response of seedlings subjected to different flooding depths for three days over the duration of the experiment.....	108
Figure 3-8: Stem growth response of seedlings subjected to different flooding depths for ten days over the duration of the experiment.....	109
Figure 3-9: Stem growth response of seedlings subjected to different flooding depths for seventeen days over the duration of the experiment.....	110
Figure 3-10: Mean observed vs. predicted curves for change in seedling leaf number over the duration of the experiment.....	111
Figure 3-11: Change in leaf number for seedlings subjected to different flooding depths for three days over the duration of the experiment	112
Figure 3-12: Change in leaf number for seedlings subjected to different flooding depths for ten days over the duration of the experiment	113
Figure 3-13: Change in leaf number for seedlings subjected to different flooding depths for seventeen days over the duration of the experiment	114
Figure 3-14: Mean aboveground biomass for all combinations of light, flood depth and flood duration.....	115
Figure 3-15: Interaction plot showing final mean aboveground biomass of surviving seedlings for all combinations of light, flood depth and flood duration.....	116
Figure 3-16: Mean belowground biomass for all combinations of light, flood depth and flood duration.....	117

Figure 3-17: Mean root-shoot-ratio for all combinations of light, flood depth and flood duration.....118

Figure 4-1: Mean daily temperature in experimental germination chamber from days 14-96.....136

CHAPTER I

INTRODUCTION

Wetlands, in their many forms, are recognized as some of the most important ecosystems in the world. According to Costanza et al. (1997), per unit of area, wetland ecosystems are the most valuable terrestrial ecosystem globally, because of the multitude of ecosystem services they provide. In a review of ecosystem services in urban areas, urban wetlands were the only ecosystem type regarded by Bolund and Hunhammar (1999) as providing all identified services, including air filtration, regulation of micro-climate, regulation of rainwater drainage, waste treatment, and cultural/recreational values.

While benefits of wetlands are recognized by the scientific community, these ecosystems continue to be threatened as a result of both direct and indirect human activities. Only 3.9% of the world's temperate forested wetlands are protected; this is the lowest figure for any forest type globally (Schmitt et al. 2009). Although legislation in the United States strictly regulates the development and draining of wetlands, wetland losses continue. From the 1950s through the mid-80s over 9 million acres of freshwater forested wetlands were lost from the conterminous United States (Dahl 2016). For approximately two decades thereafter, promising gains were made, and forested wetland area increased. Unfortunately, from 2004-2009, this trend saw a reversal, with losses of over 600,000 acres (1.2%) of forested wetland. Urbanization accounted for

26% of losses during this time period. Since this type of conversion generally involves draining, filling and building on wetlands, these represent permanent losses of wetland area and their associated ecosystem services.

Remnant wetlands in urbanized areas face a number of threats. Urban forests are likely to be highly fragmented because of their association with high road densities and development, thus decreasing the amount of forest interior. Wetland forest fragments in urbanized areas must contend with the combined threats of air, soil, and water pollution, invasive species, altered hydrology, and the urban heat island effect, each of which has the potential to affect the survival, growth, reproduction and distribution of wetland flora and fauna, and can affect the ability of wetlands to perform ecosystem services (Faulkner 2004).

Many aspects of the urban environment mirror changes in climate, disturbance regimes, and species movements that are currently occurring at a global scale (Carreiro & Tripler 2005). Thus, study of urban wetlands may be seen as an opportunity to “flash-forward” and make predictions about the future condition of forests that may be increasingly affected by human activities, invasive species, and global climate change.

Personal Reflections and Dissertation Objectives

Recognizing both the value and scarcity of forested wetlands in my local area (Louisville, Kentucky), my initial motivations for pursuing this topic were both scientific and personal. From a scientific perspective, these systems offered the opportunity to explore ecological patterns along gradients of stress and resource availability. From a personal perspective, I wanted to explore these locally rare—and often isolated—

systems, documenting and describing the plant communities of these systems before they vanished permanently.

Finding and gaining access to research sites was an eye-opening experience that helped to shape my research goals and furthered my curiosity about these systems. Knowing that much of southwest Jefferson County had, at one time, been covered by swamp land, I was taken aback by how relatively few patches of wetland forests remained in the area. Furthermore, most of these areas were privately owned, with uncertain prospects for the future. One site (Site 3), was completely landlocked in a sea of concrete, between a shipping yard, train depot, and commercial developments. The boundary between the forest and gravel was abrupt, with semi-trucks touching the tree branches, and frogs jumping out of puddles made by their huge wheels.

With this boundary between the industrial world and nature in mind, my initial research goals for this work were to study changes in woody plant community composition occurring along an edge-to-interior gradient. Studies from upland forest systems showed that changes in resources availability and microclimate occurring at the forest edge affected ecosystem pattern (Chen et al. 1992, Cadenasso and Pickett 2001, Harper et al. 2005) and process (Weathers et al. 2001), but I was not familiar with as much work on edge effects in wetland areas.

After conducting a pilot study, I was somewhat frustrated by my inability to demonstrate what variables were most responsible for controlling important community patterns—such as the presence of invasive species—which did not always show the clear associations with edge habitats I had expected. Adjusting my focal lens to the wetland

context, I realized I needed to quantify the hydrology of these systems to truly understand the extent of edge effects, as hydrology is of fundamental importance to wetland species distributions. In Chapter II, I show the results of my field research in three forested wetlands, where I link species distributions within and among wetlands to both hydrology and proximity to edge. Special attention is paid to the apparent influence of hydrology on the distribution of an invasive shrub species, *Lonicera maackii* (Amur honeysuckle).

Following this evidence, I conducted two manipulated experiments testing the effects of simulated flooding on *L. maackii* at two critical life history stages: seed and seedling. In Chapter 3, the impact of flooding depth and duration, and its potential interaction with light levels, on *L. maackii* seedling growth and survival is examined in detail. In Chapter 4, I conducted a germination assay of *L. maackii* seeds subjected to different treatments of simulated flooding and drawdown.

CHAPTER II

PATTERNS OF WOODY PLANT COMMUNITIES OVER HYDROLOGIC AND EDGE-TO-INTERIOR GRADIENTS: A STUDY OF THREE URBAN WETLANDS

Introduction

Current policy in wetland management permits the continued loss of naturally occurring wetlands, a factor that undoubtedly results in a net loss of ecosystem services and wildlife habitat (Faulkner 2004, Mitsch and Gosselink 2007). As a result, remaining forested wetland areas are often highly fragmented. Such fragmentation may have a number of effects that can alter the structure and function of these forest types (Saunders et al. 1991).

Urban forests, generally speaking, are threatened by fragmentation and tend to be smaller than rural counterparts (Medley et al. 1995). Fragmentation increases the perimeter-area ratio of forests, reducing the area of interior forest, increasing the area of forest susceptible to edge effects, and modifying the microclimate of forest boundaries. Edge effects include changes in the forest microclimate—such as light, temperature, soil moisture—and have been demonstrated for various forest types in a number of studies (Matlack 1993, 1994, Chen et al. 1995, Delgado et al. 2007). This perturbation of the abiotic environment has been shown to affect the distribution of individual species, as well as induce changes at the community level (Harper et al. 2005). This is due both to

species' individual requirements and tolerances, as well as from competitive interactions that may result when the resource environment is altered. Potential differences in herbivore activity along edges as opposed to forest interiors (Jules and Rathcke 1999, Cadenasso and Pickett 2000) may also shape species distributions.

Plant community composition and structure in edge habitats are also affected by species movements through or along edges. For instance, the role of edge habitats facilitating forest colonization by invasive plant species has been the subject of a number of papers (Moran 1984, Brothers and Spingarn 1992, Hutchinson and Vankat 1997, Cadenasso and Pickett 2001, Honnay et al. 2002, With 2002, Pauchard and Alaback 2004, Borgmann and Rodewald 2005, Bartuszevige et al. 2006). This effect is thought to be due to the high light environment of edge habitats, and the proximity of edges to disturbed landscape matrices, which may foster “weedy” species. Edges may also act as filters of plant propagules into a forest, the extent to which is related to the mode of seed dispersal, and the physical structure and composition of edge vegetation (Cadenasso and Pickett 2001).

Most studies of edge effects on plant communities have been conducted in upland systems. In these systems, which are defined by the presence of surface, or near-surface water on an intermittent or continuous basis, site hydrology is the major factor influencing plant distributions. While the surrounding landscape matrix and within-site legacy determine the potential pool of species available to colonize wetland sites, hydrologic conditions are the primary filter determining which species are able to persist. Thus, any potential edge effects due to increased light, propagule pressure, or edaphic factors must be considered in the context of the hydrologic conditions. For instance,

exotic wetland species from the surrounding landscape matrix may not be able to tolerate wetland flooding, which could offer these systems some resistance to exotic species invasion. Because hydrology is the primary driver of plant species distributions in wetlands, any attempt to measure edge effects must quantify site hydrology and determine if it is affected by the proximity to the forest edge, or if it varies independently of this factor.

With this in mind, the main objectives of this study were as follows:

- 1) Describe the woody plant community of urban wetlands along edge-to-interior gradients and determine if environmental variables, edge proximity and/or edge orientation is associated with changes in plant community composition.
- 2) Quantify variation in hydrology between and within research sites and determine its potential association with changes in woody plant composition and structure, with special consideration to the occurrence of invasive woody species.
- 3) Determine if site hydrology varies with distance to edge.
- 4) Determine which patterns in community composition (i.e. importance of exotic species, importance of obligate and facultative wetland species and species richness) appeared to be driven primarily by hydrology, and which by distance from the forest edge.

Methods

Site Descriptions

All study sites are contained within the boundaries of Jefferson County, Kentucky (total land area of 1000 km²) and includes the full extent of the incorporated metropolitan area of Louisville, Kentucky. The northern border of the county is formed by the Ohio River. Within the county borders, the range of elevations observed is 383 to 902 feet above sea level. Jefferson County land use and land cover ranges from highly developed at the urban core, to forest, pasture and cropland towards the county boundary.

The majority of sites selected for this study lies in southwestern Jefferson County in the Pond Creek watershed. This low-lying, 231 km² watershed has large portions of land that are subject to frequent flooding and ponding, and historically has had the most wetland area in the county (MSD 2006). The low gradient terrain that characterizes this area formed as a result of glacial outwashes from the Quaternary period. In the last century, the creation of ditches (Northern and Southern Ditch) has aided in draining this area for development, which is primarily residential (MSD 2010). However, the shallow elevational gradient in this area still promotes the maintenance of wetland hydrology and vegetation on hydric soils in certain areas. The Louisville Metropolitan Sewer District (MSD) considers the destruction of wetlands in the Pond Creek watershed as a contributor to frequent flooding episodes and water pollution (MSD 2006).

Table 2-1 summarizes the area and soil characteristics of all wetlands selected for inclusion in this study. Study sites were identified using the National Wetlands Inventory (USFWS 2016), county soils data from the Soil Survey Geographic Database (SSURGO;

Soil Survey Staff, 2009), and high-resolution digital color imagery in ArcGIS. All data sets were used together to locate potential study areas in Jefferson County, but sites had to be identified as meeting hydric criteria according to the SSURGO soils database to be considered further. Potential sites were also disqualified for the following reasons: 1) Forest did not appear to be primarily closed canopy, 2) the forest did not appear to have well-defined north and south-facing edges, 3) forest was < 1 hectare in size, 3) forest consisted only of thin strips of riparian forest, or 4) landowner information obtained from the Jefferson County Property Evaluation Administrator (PVA) revealed that the property ownership was in a state of flux. Landowner permission was obtained by phone, or mail using addresses on file with the Jefferson County Property Evaluation Administrator (PVA). Access permission was granted by 8 out of ~ 35 landowners. Of these 8, the three with the largest area were chosen.

Soil series determination from each transect location (see Sampling Design) were verified in the field by NRCS personnel. Transects in Site 1 (Max Sawyer), were located on the Melvin soil map unit characterized as frequently flooded, silt loam. Transects in Sites 2 and 3 (Evangel and Trinity), were located on the Zipp soil map unit. NRCS soil descriptions (NRCS 2005) indicate both soil map units meet hydric criteria and have seasonally high water tables present at 0-0.8 feet of the soil surface. Both soil series are classified as having apparent (i.e. endosaturated), rather than perched (i.e. episaturated) water tables, indicating that zone of soil saturation is continuous from a depth of 2 m or more to the top of the water table (NRCS 1999).

Site 1 (Max Sawyer) was located in a primarily residential area, adjacent to a major transportation corridor (I-65). Based on my observations, Site 1 (later referred to

as the “dry” site in this chapter) had undergone the most modification and was the most hydrologically disconnected from the surrounding landscape. Surrounded by residential land use and an interstate, this area has been heavily ditched around the periphery to drain water away from the area (i.e. where transects were located). However, standing water is still present at this site during portions of the growing season, and areas near the water monitoring well routinely had knee-deep water in winter and spring. In some instances, the land immediately outside the forest boundary was lower than that inside the forest; this was most likely a result of grade alterations made in residential plots to drain water away from houses, towards ditches. Although this soil series is characterized as frequently flooded (i.e. inundated by flowing water from stream overflow, or runoff from the adjacent landscape), the extent of ditching through and around the site perimeter appeared to limit flooding events. For instance, drainage ditches running parallel to the forest edge were present at 3 out of the 4 transect locations, effectively intercepting runoff from the adjacent landscape at the forest edge. Additionally, a large ditch runs through the middle of the wetland and drains to nearby Fishpool Creek. This feature is extremely incised, and I never personally observed water levels high enough to overflow onto the adjacent wetland areas. Based on these observations, it appeared that the presence of standing water or near surface water was driven mostly by the influence of the water table and/or precipitation. There was frequent evidence of human disturbance in this site, including numerous waste items, ATV tracks and construction debris.

Site 2 (Evangel) was located adjacent to I-65, but was surrounded on three sides by a fairly large tract of undeveloped open space and pasture. Large ditches ran to the north and south of the site, approximately 100 m and 200 m from research areas at the

forest edge, respectively. In contrast to Site 1, these ditches were further from the forest edge, and the elevation of the land immediately surrounding the forest edge was similar to the elevation within the forest. I later will refer to this wetland as the “intermediate” site.

Site 3 (Trinity, later referred to in the paper as the “wet” site) was the most isolated from other forest and undeveloped spaces, being surrounded by a rail depot, shipping container storage yard, and commercial or industrial space. There was minimal evidence of recent human activity in the wetland and minimal ditching at the forest edge (shallow concrete ditches were present on the north and west sides). This was the only Site where I ever observed any visible sheet flow of water; this was observed near the sampling well in the forest interior.

Sampling Design

Before establishing sampling transects, aerial imagery of each site was examined, and areas with well-defined north- and south-facing edges were identified. In the field, segments of edge on the north and south forest with continuous canopy cover were identified (i.e. no large canopy gaps along the edge, or within ~100 m of the edge). The boundaries of this candidate area were flagged, and a random number table was used to choose a point along the edge to be the starting point of the edge-to-interior transect. Two edge locations were flagged on both north- and south-facing edges at each site. Care was given to avoid locating transects within 100 m of one another on the same edge, or within 60 meters of an adjacent forest edge. Aerial images of all research sites are included in Appendix Figures 1, 2 and 3 with the location of transects.

Fig. 2-1 shows the transect design and components. The edge boundary was marked at each of the four flagged edge points at each site. This was done by moving from the surrounding landscape matrix towards the forest edge until the canopy cover transitioned to approximately 80% cover. A flag was placed at this point, and at 1, 5, 10, 30 and 60 m from this point towards the forest interior, in a straight line, thus forming the edge-to-interior transect.

At each of the five marked distances along the edge-to-interior transect, a second set of 12 m long transects running parallel to each other were delineated. These were referred to as parallel transects. During environmental and plant sampling procedures (see following sections), four temporary 2 x 2 m quadrats delineated by PVC frames were placed 1 m apart from each other, centered along the midpoint of parallel transects. A second set of 12 x 12 m plots for measuring adult trees was centered over the 6 m and 60 m midpoints of the edge-to-interior transect.

To summarize, each site contained four edge-to-interior transects (two on the north- and two on the south-facing sides) running from the forest edge to 60 m towards the forest interior. Parallel transects (12 x 2 m) were established at 1, 5, 10, 30 and 60 m along each edge-to-interior transect. Four 2 x 2 m quadrats were nested within each 12 x 2 m parallel transect.

Data Collection Dates

All woody plant (see Plant Data Collection, below), ground cover and elevation data (see Environmental Data Collection, below) were collected during the summer of

2010. Dates of data collection in 2010 for each site were: August 17 to September 9 at Site 1, June 29 to July 19 at Site 2, and July 23 to August 13 at Site 3.

Hydrologic data—including surface water elevations along each edge-to-interior transect and groundwater level data—was collected the following summer of 2011. Together with ground surface elevations taken during 2010, this data was used to estimate the average number of days each transect was flooded (see Environmental Data Collection). Although this data was not collected during the same time period as plant data, I felt it was valid to apply this data to characterize the flooding of each transect and relate to woody vegetation community data. In systems with highly dynamic microtopography, this could be problematic because surface elevations could vary greatly year to year. There were two reasons I felt this was not an issue in these systems. For one, personal observations made for three consecutive seasons indicated that there was minimal disturbance of microtopography between years. This was assessed by noting that large soil deposits on top of leaf litter were rare, and that observed water in all but one perpendicular transect was always ponded, stagnant water, with no observable flow. At Site 2, transect “S2” was the only exception to this, but noticeable flow was minimal and occasional. If microtopography were highly dynamic, I would have expected to observe frequent deposits of soil. Based on my familiarity with these sites, I felt it was reasonable to estimate the number of days each transect was flooded based on 2010 elevation data in combination with ground and surface water data obtained the following summer. Furthermore, since I was dealing with woody, perennial species, whose distributions are reflective of long-term environmental trends, I felt it was

reasonable to view flooding trends in 2011 as a *relative* measure of overall hydrologic differences between transects and sites, and relate these to plant data from 2010.

Environmental Data Collection

In each sampling quadrat, the ground cover of several variables was estimated. These variables were: 1) percent bare soil, 2) percent leaf litter 3) percent coarse woody debris (widths > 10 cm, 4) percent herbaceous cover. While bare soil and litter were considered mutually exclusive (additive) cover types, others were not. For instance, herbaceous cover or coarse woody debris could occupy the same two-dimensional space as leaf litter or bare soil. Thus, total ground cover could be greater than 100%. In some instances, leaf litter was covered by a relatively thin layer of sediment (~1-4 mm) due to recent flooding events, but leaf litter was still clearly distinguishable underneath this layer; this was counted as leaf litter cover. Bare soil was primarily evident in areas of relatively high relief (i.e. mounds, sides of ditched areas) where leaf litter did not accumulate. Coarse woody debris was defined as woody material having an average diameter of 10 cm or greater. The percent cover of each ground cover type was recorded as falling in one of the following classes: < 5%, 6-25%, 26-50%, 51-75%, 76-95% or 95+%. The canopy closure of each transect (a proxy for light availability) was estimated using a spherical densiometer held ~1 m from the ground surface in each transect (Robert E. Lemmon, Forest Densiometers, Bartlesville, OK).

Hydrologic conditions in each parallel transect were quantified by combining data from three datasets: 1) detailed surveys of microtopography in each parallel transect during 2010, 2) readings of water levels in wells made throughout the growing season in

2011, and 3) surface water levels recorded in each transect on select dates in 2011. The following paragraphs detail how this data was collected and combined to estimate hydrologic conditions.

During the summer of 2010 (when plant data was collected), detailed surveys of transect microtopography were conducted. A permanent elevation benchmark (i.e. a nail in a tree, or piece of rebar in a high elevation area) was established at each edge-to-interior transect (Fig.2-2). Using a surveyor's level and stadia rod (CST/Berger SAL Level), an assistant and I recorded the elevation of 10 points in each 2 x 2 m quadrat. These elevations were made relative to the established benchmark at each edge-to-interior transect. Elevation sampling points within quadrats were randomly chosen along lengths of PVC placed in each half of the quadrat.

In spring of 2011, a shallow ground water well 1 m deep was installed at each of the three wetland sites (Appendix Fig. 4). Each was placed in an interior location (> 100 m from forest edges) where flooded conditions were evident in the immediate vicinity. However, to avoid surface water entering the wells, wells were installed in locally high sites that did not appear to be frequently flooded above the soil surface. Following established protocols for installing groundwater monitoring wells (Sprecher 2008), slotted well casings (with an unslotted riser within 35 cm of the soil surface) extended 1 m below the soil surface. These were surrounded with packed, coarse sand (~5 cm below the well bottom and to the sides). The sand extended ~5-10 cm above the slotted portion of the well. Bentonite clay was then packed around the riser to the soil surface, and a mixture of field soil and bentonite was mounded around the base of the well above the ground surface. Above the mounded soil, wells were vented (i.e. a hole was drilled) to

equalize pressure between the well environment and open air pressure. The location of the wells in areas of slightly higher elevation than adjacent flooded areas, and the bentonite clay seal were intended to prevent surface water entering the wells directly, so that groundwater levels could be accurately measured. PVC housing constructed for a water level data logger was mounted on top of each well casing, and equipped with a waterproof cap. The total length of each well with the housing was 1.75 m (0.75 m extending above the soil surface). Each well was equipped with a Global Water WL15 water level data logger (Global Water, College Station, Texas). This device uses a pressure transducer to measure the amount of water above the sensor. Following manufacturer procedures, each device was calibrated to accurately record water levels. Sensors were placed at the well bottom. Water levels in each well were recorded continuously on an hourly basis from 5/2/2011 to 8/26/2011, a total of 123 days.

Monitoring points for measuring surface water depth were established at approximately 10, 30 and 60 meters along each edge-to-interior transect in May 2011. These were lengths of PVC pipe approximately 0.75 m long that were pounded into the soil (Fig. 2-2). The elevation of the top of these monitoring points was recorded relative to the permanent site benchmark established the previous summer. On 3 to 4 dates, when surface water was present at each site, the distance between the top of the monitoring point and the water surface was measured. These values were ultimately used to reference the elevation of the of the water surface to the site elevation datum, and determine the difference between the daily average water table elevation and surface water levels (see below). This enabled the prediction of daily surface water levels in each parallel transect.

A final elevation survey at each site was conducted to measure the elevation of permanent elevation benchmarks relative to one another, thereby registering them to the same datum and one of the four permanent elevation benchmarks at each site was used as a reference point for the whole site. The elevation of the top of the water monitoring well was also recorded during this survey. To summarize, for each site the resulting dataset had all of the following information relativized to the respective site's datum: 1) ground surface elevations in quadrats where plants were collected in 2010, 2) the elevations of surface water monitoring points, and 3) elevation of the top of the groundwater monitoring well.

Fig. 2-2 provides a visual aid for interpreting the following calculations. Daily mean height of water in each well was calculated. The average water table surface elevation on each day (E_{wt}) was calculated by subtracting 1.75 m (total well length) from the top of well elevation (E_{well}) and adding the daily mean height of the water table above the sensor h_{wt} (Eq. 1). For each day water surface elevations were measured (3-4 days at each point) the elevation of the water surface (E_{ws}) at each monitoring point was calculated by subtracting the distance measured from the top of the water monitoring point to the water surface (D_{ws}) from the elevation of the top of the monitoring point (E_{wmp} , Eq. 2). Finally, the height difference between the water surface (in each transect) and the water table (Δwt) surface was calculated for each day water surface measurements were made. This was done by subtracting the elevation of the water table (E_{wt}) from the water surface elevation (E_{ws}). This calculation is given in Eq. 3.

Eq. 1

$$E_{wt} = E_{wmp} - 1.75 + h_{wt}$$

Eq. 2

$$E_{ws} = E_{well} - D_{ws}$$

Eq. 3

$$\Delta wt = E_{ws} - E_{wt}$$

Average values of Δwt were calculated for each water monitoring point, and this number was added to daily values of mean water table elevations to estimate the average elevation of the water table at each monitoring point, for each day of the monitoring period. Since the water surface was not always level (e.g. because of ditching) these values could be very different along an edge-to-interior transect. Water table elevations generated from 10 m monitoring points were applied to parallel transects at 1, 5 and 10 m. Water table elevations from 30 m and 60 m monitoring points were applied to parallel transects at their respective distances.

Using the ground surface elevations measured in 2010, I used predicted values of the water table elevation in each parallel transect to estimate how many days each ground surface elevation data point was flooded in 2011 (40 points/transect). For every day of the monitoring period, a point was considered “flooded” if it was equal to, or lower than, the predicted water level. Thus, every elevation point, in every quadrat, had a corresponding value for “days flooded”. These values were averaged over a quadrat, and quadrats were averaged over the parallel transect. The resulting value, describing the wetness of each parallel transect, is referred to as “days flooded” or “number of flooded

days” for the rest of the chapter. Because this estimate incorporated elevation data, it is reflective of how microtopography impacts the overall “wetness” of a local area.

During June of 2011, leaf area index (LAI) data was recorded. A LAI-2000 Plant Canopy Analyzer was used to measure LAI (LI-COR, Lincoln, Nebraska). LAI is a unitless ($\text{m}^2 \text{ leaf}/\text{m}^2 \text{ ground surface}$) measure of foliage quantity, and commonly used as a measure of productivity. This was of interest directly, and because it should be inversely related to light availability at the forest floor. Standard protocols for measuring LAI were followed as per the manufacturer’s recommendations (LI-COR 1992). LAI was measured in 4 locations per parallel transect, in the approximate quadrat locations from the previous season of field work. Measurements were made away from tree trunks, as the sensor registers any light blocking object as leaf area. I also used an equipped filter to block my own outline from the sensor, and made measurements of LAI approximately 0.5 m from the ground surface. Sensor data was downloaded and the manufacturer software was used to compute values of LAI.

Plant Data Collection

Plants were sampled in area units described in *Sampling Design*. Adult trees were defined as those with a diameter at breast height (dbh) greater than 2.5 cm. The species identity and dbh of all living trees in 12 x 12 m edge and interior plots was recorded (4 edge and 4 interior plots at each site). All other plant data was collected within 2 x 2 m quadrats in each parallel transect. Woody vines falling in each quadrat were identified, and recorded as % cover in the following ranges: < 5%, 6-25%, 26-50%, 51-75%, 76-95% or 95+%. Vine cover on the ground and in the canopy above a quadrat was tallied

separately. Stem counts of saplings species (< 2.5 cm dbh and > 30 cm tall) and shrub species in each quadrat were also recorded. For tree seedlings, a distinction was made between “recent germinants” and “established seedlings”. Recent germinants generally only had 1-2 pairs of leaves and/or cotyledons. Established seedlings had some woody tissue formation and/or more than 2 pairs of leaves.

For shrubs, stem counts for individual plants were tallied when possible, but this was difficult for clonally growing species such as *Cornus foemina*. Because the growth habit of shrubs varied, I tried to sample stem counts in a consistent manner. First, individual shrubs (or a definable clump of clonally growing shrubs) were placed into a height category based on the average height of plant stems. These categories were <0.25 m, 0.25-0.5 m, 0.5-1.0 m, 1.0-2.0 m, and over 2 m (2+ m). The number of stems originating within the first 0.3 m of the ground was recorded as the stem number of the individual. Finally seedlings (<0.3 m tall) were counted by species.

The elevation of all *Lonicera maackii* shrubs was also recorded. Using data from the ground elevation survey, each shrub was assigned an elevation rank, based on its relative elevation within a parallel transect. Ranks were calculated using the “PERRANK” function in MS Excel, which returns a ranking of a value (range: 0-1) as a percentage of a range of values. For individual plants, this function was used to calculate the elevation rank of all *L. maackii* shrubs, based on the range of sampled ground elevation values in a parallel transect (80 sampled elevation points). Therefore shrubs near the highest sampled ground elevation point would rank close to 1, and those near the lowest points would rank close to 0. In a few instances, the elevation of plants fell outside the range of sampled elevation points. In these cases, the plant was assigned a

rank of “0” if it was lower than the lowest sampled elevation point and “1” if it was higher than the highest sampled elevation point.

The intention of obtaining this data was to examine the relationship between rank elevations of *L. maackii* and the number of flooded days in parallel transects where they occurred. If flooding constrained the range of suitable habitat for *L. maackii*, I expected the rank elevation of shrubs to increase with the number of days flooded.

Data Treatments

Stem counts for saplings, seedlings and shrubs per quadrat were totaled over each parallel transect by adding quadrat level data. Stem counts for each species and vegetation layer (i.e. seedlings, saplings, etc.) were converted to density in $\text{m}^2 \text{ha}^{-1}$. For vines, values of total percent cover were determined by adding together the percent cover of vines on the ground and in the canopy. Thus, it was possible for vines to have greater than 100% cover. For each vegetation layer, the frequency, relative frequency, relative density (relative cover for vines) and importance value (IV) were calculated. For a species, *X*, these measures were calculated as follows for each vegetation layer, in each parallel transect.

$$\text{Density} = \frac{\text{total \# of stems of species } X \text{ in parallel transect}}{16 \text{ m}^2} \times 10,000 \frac{\text{m}^2}{\text{ha}} = \text{stems/ha}$$

$$\text{Frequency} = \frac{\text{number of quadrats containing species } X}{4}$$

$$\text{Relative Frequency} = \frac{\text{frequency of species } X}{\text{sum of all species frequencies}}$$

$$\text{Relative Density (or \% Cover)} = \frac{\text{density (or \% cover) of species } X}{\text{sum of all species densities (or total \% cover)}}$$

$$\text{IV} = \frac{\text{Relative Frequency} + \text{Relative Density}}{2} \times 100$$

Adult basal area was calculated by summing the total cross sectional area (in m²) of species by plot and expressing it in terms of m²/ha.

$$\text{Basal Area} = \frac{\text{total cross sectional area of species } X \text{ (m}^2\text{)}}{144 \text{ (m}^2\text{)}} \times 10,000 \frac{\text{m}^2}{\text{ha}} = \frac{\text{m}^2}{\text{ha}}$$

Relative basal area and IV values were then calculated as above, substituting basal area for “density”.

For ordination (see Statistical Analysis), “Exotic Vine IV” and “Exotic Shrub IV” were calculated by summing the total importance values of species meeting those criteria within each parallel transect. “Exotic” was defined as having provenance outside of North America.

Species richness was calculated by vegetation layer as the total number of species. Shannon diversity (Magurran 2013) was calculated according to the following equation, where p is the relative density or relative cover of a species.

$$H = \sum_{i=1}^s p_i \ln p_i$$

Environmental variables were averaged at the parallel transect level for analyses listed below.

Statistical Analyses

For certain variables of interest (species richness of individual plant strata and abundance of species of interest), I performed multiple regression using a mixed linear model (PROC MIXED in SAS 9.4) to test if these response variables varied with fixed effects of site, edge orientation, or distance from edge, and included all 2 and 3-way interactions between these variables. Parallel transects represented individual samples. The ID of an edge-to-interior transect was included as a random blocking effect within site and side (i.e. north vs. south). For count data (density or number of species) I first tried modeling the data using the Poisson distribution (recommended for count data) and the link=logit method. In all instances, data were over-dispersed as indicated by model output indicating X^2 values divided by degrees of freedom were substantially greater than one. In this case the negative binomial distribution was used, which is recommended for over-dispersed data, and the logit link. Failure of the model to fit random effects indicated over-fitting of the model and the random blocking effect was removed from the model. The model was then rerun with only fixed effects in PROC MIXED or PROC GENMOD. When comparing the number of days flooded between sites, number of days flooded was treated as a continuous variable. Model residuals were examined for normality and homoscedasticity. Percent cover data were modeled using the arcsine transform where:

$$Y \text{ (Transformed)} = \arcsine(y^{-2})$$

Non-metric multidimensional scaling (NMS) is an ordination method often used to find patterns in plant community data. I used the PC-ORD software following guidelines recommended in McCune et al. (2002) to run this procedure. The species matrix was composed of importance values of all species, for each parallel transect separated by vegetation layer. For instance, *Fraxinus* sp. seedlings and saplings were entered as separate “species”. Adults were not included because they were sampled at a different scale. Species occurring in fewer than three transects were removed from the matrix (~5% of transects), as recommended. The outlier analysis function in PC-ORD was used to find transects that were outliers (>2 standard deviations from the mean) and these were removed from the analysis due to concerns over model stability. Three transects from Site 3 were removed from the analysis because of this. I used PC-ORD autopilot mode (“slow and thorough” method) to run the ordination and checked that model stress was within an acceptable range, as recommended in (McCune et al. 2002).

Secondary matrices summarizing environmental data variables and biotic variables were created in Excel and imported into PC-ORD. These data were used for creating biplots depicting relationships between these variables and ordination axes. Variables included in the environmental matrix were: days flooded, distance from edge, percent herb cover, percent coarse woody debris, LAI, and percent canopy closure. Percent bare soil was not included because it was highly correlated with percent leaf litter and contributed essentially no unique information. The biotic matrix contained summary variables about exotic species, wetland indicator status and the total density or cover of plants from individual vegetation layers (i.e. saplings, tree seedlings, shrubs, vines). Wetland Indicator Status (WIS) information was obtained from PLANTS Database

(USDA 2016). I used regional statuses for the Eastern Piedmont Region. These designations indicate the association of particular species with wetland habitats. The WIS for species from this study are shown in Appendix Table 16. The total IV of species with facultative wetland (FACW) or obligate wetland (OBL) status was calculated for each vegetation layer and included in the matrix. Other biotic variables were: exotic shrub IV, exotic vine IV, total seedling density, total sapling density, total vine cover, and total shrub stem density.

Results

Environmental Variables

Site-Level Environment

The three sites differed in hydrology, as shown by differences in the number of days flooded ($X^2(2) = 28.24$, $p < 0.0001$; Table) and visual comparison of site hydrographs (Fig. 2-3). Site 1 transects had the fewest number of flooded days (i.e. days where surface water level was \geq ground level, mean of 3.9 ± 1.9 days) with 5 out of the 15 transects experiencing an average of zero days of flooding. At Site 2, days flooded ranged from 0.4 ± 0.2 to 71.9 ± 4.9 days flooded, (mean of 19.9 ± 3.7). Site 3 transects experienced the highest number of flooded days, (range: 0 to 84.5 ± 0.4 ; mean of 39.4 ± 7.6 days). Tukey's pairwise comparisons confirmed a significant difference in days flooded between Site 1 and 3 (Tukey's adjusted $p < 0.0001$) and Sites 2 and 3 (Tukey's adjusted $p < 0.0001$ for both comparisons, Table 2-2). Based on these findings, Sites 1, 2 and 3 are hereafter referred to as the "dry", "intermediate" and "wet" sites, respectively. The mean number of days flooded for all parallel transects, edge-to-interior transects and sites is given in Table 2-2.

All values for mean days flooded, other environmental variables (averaged over edge-to-interior transects) and sites are given in Table 2-3. Mean LAI was highest for the dry site (4.42 ± 0.12), with values of 2.76 ± 0.12 and 3.80 ± 3.0 for the intermediate and wet sites, respectively. Percent canopy closure was similar among sites, and ranged from $89.0 \pm 1.5\%$ at the wet site to 91.1 ± 1.6 at the intermediate site. Herb cover varied greatly between sites, being lowest in the dry site ($13.4 \pm 3.5\%$) and similar in the other sites ($60.3 \pm 17.1\%$ and $56.4 \pm 2.5\%$, for the intermediate and wet site, respectively). Environmental data at the transect scale is listed in Appendix Table 2.

Associations among Environmental Variables

Pearson correlations between environmental variables at the landscape scale (calculated by including transects from all sites) are given in Table 2-4. Percent leaf litter and percent bare soil were essentially redundant variables that were highly correlated ($r = -0.98$, $p < 0.0001$). Days flooded was also positively correlated with % herbaceous cover ($r = 0.31$, $p = 0.023$), % bare soil ($r = 0.41$, $p = 0.008$) and negatively correlated with % canopy closure ($r = -0.3662$, $p = 0.006$). Herb cover and LAI were negatively correlated ($r = -0.63$, $p < 0.0001$).

At this scale of examination, considering transects from all sites, no environmental variables correlated with distance from edge. However, because flooding and distance from forest edge were both expected to be important factors affecting plant communities, it was necessary to know if these variables were still independent of one another at the site level. At the landscape scale, when transects from all sites were included, these variables were not shown to be related ($r = 0.1160$, $p = 0.4$). At the

intermediate site, there was a marginally significant, positive correlation between days flooded and distance from edge ($p = 0.07$, $r = 0.41$), indicating a probable lack of independence between these factors at this location. At the other two sites, distance from edge was not correlated days flooded ($r = 0.19$, $p = 0.49$ at the dry site; $r = 0.01$, $p = 0.96$ at the wet site). Therefore, based on these three forested wetlands, the assumption that distance from edge will necessarily be correlated with hydroperiod cannot be made.

Woody Plant Communities

Adult Trees

The total basal area of adult trees ranged from 32.5 ± 4.1 to $47.1 \text{ m}^2 \text{ ha}^{-1}$ in the wettest and driest site, respectively (Table 2-5). *Acer rubrum* (red maple, FAC) adults had the highest IV and basal area at all three sites (Table 2-5). At the wet and intermediate site, *Fraxinus pennsylvanica* (green ash, FACW) and *Celtis laevigata* (sugarberry, FACW) were in the top three highest importance values. At the driest site *F. pennsylvanica* and *Liquidambar styraciflua* (FAC) were the second and third most important species, respectively.

Adult tree species richness was highest at the dry site (15 species, 5.8 ± 1.0 species/144 m^2 plot, Table 2-6), but there was no significant difference among sites ($p > 0.8$). Total species richness of adult trees at the intermediate and wet sites was 10 and 12 species (4.8 ± 0.4 and 5.3 ± 0.6 species/144 m^2 plot, Table 2-6), respectively. Six species of trees occurred only at the dry site; of these 6 species, 5 were found in the edge (first 10 m) only (*L. styraciflua*, *Liriodendron tulipifera*, *Ulmus rubra*, *Populus deltoides* and *Nyssa sylvatica*; Appendix Table 3). Of these five species, all except *N. sylvatica*

were facultative upland species. Considering all sites, mean adult richness was higher at the edges (6.58 ± 0.65 species/144 m² plot) than the interior (3.92 ± 0.08 species/144 m² plot) and this difference was significant ($X^2(1) = 7.8$, $p = 0.005$, Appendix Table 4). Across sites, mean adult diversity (H) was 1.32 ± 0.05 and 1.00 ± 0.09 in edge and interior plots, respectively (Appendix Table 5).

Saplings

The total density of saplings ranged from $12,094 \pm 3273$ to 4594 ± 4593 stems ha⁻¹, at the wet and dry sites, respectively (Table 2-7), and decreased with distance from the edge (Appendix Figure 5). Mean frequencies, densities and importance values of sapling species at all distances from the edge, at each site, are presented in Appendix Table 7.

F. pennsylvanica saplings had the highest mean density of any species at all three sites, and the highest importance values at the wet and dry site (Table 2-7). At the wet site, it had the highest density of any species at all distances from the edge, with importance values ranging from (mean: 35 ± 6 , range: 20 ± 11 to 50 ± 20). *A. rubrum* had the second highest mean density and IV at the wet site. At the intermediate site, *C. laevigata* and *F. pennsylvanica* had the highest two importance values and/or densities at all distances. This pattern was similar at the dry site, with those two species maintaining high densities and/or importance values at all distances. *Asimina triloba* (pawpaw, FAC) was unique to the dry site and had higher densities than other species at 30 and 60 m from the forest edge.

Species richness of saplings declined with distance from the forest edge ($F_{1,42} = 6.8$, $p = 0.013$, Appendix Tables 5 and 6). Seven species (plus one unidentified species)

were found exclusively in transects from 1-10 meters, while only two species were found exclusively in the 30 or 60 m transects. Species found exclusively at the edge included FACU, FAC, FACW and OBL species, and all were fairly rare within sampled areas. These species included *L. tulipifera* saplings (FACU) and *Nyssa sylvatica* (FAC), which were only found at the wet site, but limited to the edge (5 and 10 m). Four of these seven species are considered shade intolerant (*L. tulipifera*, *Salix nigra*, *Platanus occidentalis* and *Sassafras albidum*), while *N. sylvatica* is considered shade tolerant. The other two species (*Prunus* sp. and *Crataegus* sp.) were only identified at the genus level.

Seedlings

Total seedling density ranged from 2906±644 to 7156±1855 stems ha⁻¹ for the dry and intermediate sites, respectively (Table 2-8). *F. pennsylvanica* had the highest importance value and density of seedlings at all sites. *Celtis laevigata*, which was the second most important and abundant species at the intermediate and dry site, was very uncommon at the wet site, despite having basal area of adults comparable to those in the other sites. According to Burns and Honkala (1990), this species is intolerant of flooding in the seedling stage and this may explain its low abundance at this site. No relationships between species richness and site, edge orientation or distance from edge were found.

Seedling density appeared to differ in north vs. south facing plots. This was tested for significance. Mixed-model regression indicated a significant interaction between edge orientation and distance from edge on seedling density ($F_{1,41} = 6.26$, $p = 0.016$, Appendix Table 8), with no significant effects of site. Since seedling density did not appear to have a clear relationship with distance from edge (Appendix Fig. 6), the

significance of this interaction is most likely due to seedling density being generally higher in south sides at all distances except 60m, where they were approximately equal. As seen in figure (Fig. 2-4), *F. pennsylvanica* was a major contributor to high seedling densities in south-facing transects. At all sites, *F. pennsylvanica* maintained high, if not the highest, importance values in the seedling layer at all distances from the edge (Appendix Table 9). *C. laevigata* was generally the next most important species at the intermediate and dry site, at all distances; an exception was the intermediate site at 30 m. *Quercus palustris* (pin oak, FACW) was another relatively important seedling species that reached its highest densities at 30 and 60 m, but appeared to have a stable distribution throughout the edge zone (1-10 m) as well.

Two species that were present as adult trees at the intermediate site, but did not appear as seedlings (or saplings) were *Populus deltoides* (cottonwood, FAC) and *Platanus occidentalis* (American sycamore, FACW).

Shrubs

Shrub species richness differed significantly by site ($F_{2,9} = 10.3$, $p = 0.005$, Appendix Table 10) and the dry site had significantly higher species richness than the two other sites (Tukey adjusted $p = 0.005$ for dry site vs. intermediate site, Tukey adjusted $p = 0.03$ for wet vs. dry site). Thirteen shrub species were present at the dry site (Table 2-9), with four species found only at that site. These species were: *L. benzoin*, *Euonymus alatus* (burning bush, an exotic species, wetland indicator status undetermined), *Euonymus americanus* (bursting-heart, FAC), and a *Prunus* sp. In contrast, only three shrub species were present at the intermediate site: *Lonicera maackii*

(Amur honeysuckle, an invasive exotic), *Rubus* sp. and *Cornus foemina* (stiff dogwood, a FACW native). Eight species of shrubs were found at the wet site, and two of those—*Cephalanthus occidentalis* (buttonbush, a native wetland OBL) and *Aralia spinosa* (devil's walking stick, FAC)—were unique to that site.

The shrub species with the highest importance value differed for all three sites (Table 2-9). The most important shrub species at each site were: *Lindera benzoin* (dry site, IV = 41±5.3), *Lonicera maackii* (intermediate site, IV = 43.1±9.5) and *Cornus foemina* (wet site, IV = 40.1±8.7). *L. benzoin* (spicebush) was found exclusively at the dry site, but the other two species were present at all sites. The stem density of these three shrub species at each site is compared in Fig. 2-5, along with *Rubus* spp., which also occurred at all sites.

At 1 m from the forest edge, *Rubus* sp. had the highest stem density and/or importance value across sites, and tended to decline in importance with distance from the forest edge (Appendix Table 11). In the wet site, *C. foemina* was the most important species at all distances from the forest edge. In the dry site, *L. benzoin* was dominant from 5 to 60 m from the edge, with *L. maackii* and *Rubus* sp. maintaining lower, but relatively stable, importance values in the same areas. At the intermediate site, *L. maackii* appeared 5 m from the forest edge, then maintained high importance values at 5, 10 and 30 m from the forest edge (IV values of 75±15, 92±8 and 44±18, respectively), then substantially decreased in density at 60 m, leaving *C. foemina* as the dominant shrub. Total shrub stem density did not appear to have any relationship to distance from edge (Appendix Fig. 7). Densities of *L. maackii* clearly declined with distance from edge at the intermediate site, but this trend was not seen at the other sites (Appendix Fig. 8).

As discussed previously, the number of days flooded increased with distance from the edge at the intermediate site only. In view of this, it seems likely that hydrology, not proximity to the forest edge, was a more likely driver of this pattern at the intermediate site.

Density of *L. maackii* differed significantly between sites, with both the dry and intermediate sites having greater stem densities than the wet site (Tukey adjusted $p = 0.01$ for both comparisons, Appendix Table 12). The size class structure of *L. maackii* stems was similar among sites, though the dry site had a greater density of stems in the largest height category (>2 m tall), but this was not tested for significance (Fig. 2-6). Because *L. maackii* has been negatively correlated with native shrub densities in other studies, I examined correlation values between the density of this species and the three other dominant shrubs. None of these correlations was significant ($p > 0.3$).

Vines

The vine community at the wet and intermediate sites was dominated by *Toxicodendron radicans* (poison ivy, FAC), which had importance values of 49 ± 8 and 58 ± 6 at each site, respectively (Table 2-10). At the dry site, *Lonicera japonica* (Japanese honeysuckle, an exotic, invasive species) was the most important species ($IV = 38 \pm 4$). Total vine cover generally declined towards the forest interior (Appendix Fig. 9). Along edge-to-interior transects in the intermediate and dry site, *T. radicans* retained the highest importance values and percent cover at all distances from the forest edge (Appendix Table 14). At the dry site, *L. japonica* had the highest importance values and percent

cover at all distances except 30 m, where *Euonymus fortunei* (wintercreeper, an exotic invasive species) was more abundant. No vine species were unique to any one site.

Lonicera japonica had significantly different cover between sites. ($F_{2,12.5} = 7$, $p = 0.009$, Appendix Table 12) with coverage in the dry site being higher than the two other sites. It also showed a pattern of decreasing cover with distance from the forest edge at all three sites (Fig. 2-7) and this trend was significant ($F_{1,42} = 7$, $p = 0.01$, Appendix Table 12).

NMS Ordinations: Community Patterns and Environmental Correlates

The initial run of the NMS used mean woody species IVs calculated from all parallel transects at all sites. The solution resulted in three axes explaining 72.2% of the variation in the plant community composition with a final stress of 17.64. The environmental biplot in Fig. 2-8 shows the position of transects and species by strata (vines, shrubs, tree seedling, and saplings) based on their association with the resulting NMS axes, as well as vectors indicating environmental variables also associated with these axes. Fig. 2-9 shows transects and species by strata plotted identically as in Fig. 2-8, but displayed with vectors indicating axis associations with biotic variables such as wetland indicator status, exotic status and total abundance by stratum (i.e. shrub stem density). Referring to both figures, it is possible to make indirect associations between species distributions, environmental variables and community patterns. Table 2-11 summarizes the predominant species, environmental variables, and biotic variables that were most strongly associated with Axis 1 and 3.

Plotting transects in relationship to Axis 1 and 3 (Fig. 2-8) revealed clear compositional differences between Site 1 (dry site) and the two other sites, based on their

position in ordination space. Axis 1 explained 34.5 % of the variation in the species matrix and had a positive correlation with the number of days flooded ($r^2=0.38$) and was the primary dimension that separated site 1 (dry site) from the 2 others (Fig. 2-8). The total IV of exotic vines and total shrub density were negatively associated with Axis 1 ($r^2=0.44$ and $r^2=0.19$, respectively), while the IVs of FACW/OBL shrubs and percent herbaceous cover were positively associated with this axis ($r^2=0.40$ and $r^2=0.34$, respectively; Fig. 2-9). The two species most strongly associated with Axis 1 were both shrubs; *Cornus foemina* (FACW) and *Lindera benzoin* (FAC) displayed positive ($r^2=0.34$) and negative ($r^2=0.59$) associations with Axis 1, respectively. The negative association between Axis 1 and shrub density was probably due to the influence of *Lindera benzoin*, which achieved high densities at the “dry” site (Site 1). Axis 3 was positively correlated with *Celtis laevigata* seedlings ($r^2=0.20$), distance from forest edge ($r^2=0.20$), and total seedling density ($r^2=0.20$; Fig. 2-8).

Axis 2 was positively associated with percent vine cover ($r^2 = 0.21$) and the IV of exotic shrubs ($r^2 = 0.45$; Fig. 2-10), but not with any measured environmental variables.

The position of the three dominant shrub species in ordination space, particularly the strong negative and positive associations of *Lindera benzoin* (FAC) and *Cornus foemina* (FACW) with Axis 1, suggests that the shrub community is strongly indicative of current hydrologic conditions. *Lonicera maackii*, the exotic shrub species, did not relate strongly with Axis 1. As shown in Appendix Fig. 10, stem density of *L. maackii* was generally highest at values of Axis 1 near zero. This may indicate a preference of *L. maackii* for areas with intermediate flooding intensity, such as those at Site 2, where this species achieved the highest mean density.

Shrub Distribution and Hydrology

NMS results indicate that total shrub density responded negatively to increased flooding. However, this relationship appeared to vary by species, with *Lindera benzoin*, *Lonicera maackii* and *Cornus foemina* occupying different regions of an apparent hydrologic gradient. To directly examine the relationship between shrub density and days of flooding and differences in this relationship by species, I generated scatter plots and correlation coefficients for relationships between: 1) total shrub stem density vs. days flooded (Appendix Figure 11) and 2) shrub stem density (by species) vs. days flooded (Fig. 2-11). Correlation data are given in Table 2-11. Total shrub stem density was not significantly correlated with the number of flooded days ($p=0.38$). Considering the U-shaped distribution of data points in Appendix Fig. 11, this appears to be due entirely to the influence of *Cornus foemina* which increased in density with the number of days flooded ($r^2=0.13$, $p=0.007$). The stem density of all other species decreased with the number of days flooded ($p\leq 0.05$). Of the four shrubs, *Lindera benzoin* persisted in the most narrow range of hydrologic conditions, and did not occur in transects with more than 28 days of flooding. It should be noted, however, that this species only occurred at one site, which had the most limited range of flooded days; thus its absence from transects with longer flooding durations may be limited by site factors, such as dispersal or other edaphic conditions. *L. maackii* and *Rubus* spp. had similar relationships with days flooded; they were found in transects with a relatively high number of flooded days, but did not increase in density with this factor. For clarity, it should be noted that “days flooded” is a property of the transect, and not a measure of how long an individual plant

experienced flooding, because plants at higher elevations will experience fewer days of flooding than those at lower elevations, within a transect.

Because the invasive species *Lonicera maackii* was a species of special concern, I further examined the rank elevation of *L. maackii* individuals within parallel transects, and its relationship with the number of days flooded. If areas of raised elevation, in flooded areas, created safe sites for the establishment of *L. maackii*, it was expected that the rank elevation of plants in transects would increase with the number of flooded days. As seen in Fig. 2-12, plants in transects with ~0-4 total days of flooding occupied the full range of relative elevations within their respective transects. Individuals in transects flooded for approximately 5 days or more were constrained to increasingly higher relative elevations as the number of days flooded increased. Mature *L. maackii* plant stems (>2.0 m tall) persisted into a transect experiencing up to 43 days of flooding (during the water level monitoring period) by occupying the highest recorded elevation within that transect (Site 3-N1-30m). The number of flooding days in each transect where *L. maackii* was found, along with the relative elevations, stem numbers, and heights of individual plants are listed in Appendix Table 15.

Discussion

The three most important tree species encountered in research sites were *Fraxinus pennsylvanica* (FACW), *Acer rubrum* (FAC), and *Celtis laevigata* (FACW). *A. rubrum* was the dominant adult species at all three sites. The second most important adult tree

species in the intermediate and dry sites were *C. laevigata* and *F. pennsylvanica*. *F. pennsylvanica* was extremely important across sites, and had the highest densities and/or importance values of any species in both the sapling and seedling layers, across sites. The sapling and seedling layers at the two drier sites indicate a growing importance of *Celtis laevigata*, a relatively short-lived, fast-growing species (Burns and Honkala 1990). This species is intolerant of flooding, particularly in the seedling stage; thus, this species reflects the hydrology of the two drier sites. Adult trees had higher species richness towards the forest edges, with most of the species unique to the edge being facultative upland species.

Findings from the NMS ordination suggest that the shrub community were most indicative of community differences among these three wetlands, and that these differences are primarily related to differences in hydrology. Importance values of shrubs at each site, and the location of these shrubs in ordination space, show that each site is associated with a different shrub species. *L. benzoin* (a native FAC shrub) and *C. foemina* (a native FACW shrub) were associated with the driest and wettest sites, respectively, while *L. maackii* (an invasive, exotic species) was associated with the intermediate site. *L. maackii* density at the two driest sites was significantly higher than at the wet site.

It was surprising that *L. maackii* had higher importance values and similar stem densities at the intermediate, rather than dry site. The majority of studies on *L. maackii* invasion in North America have been conducted in upland systems and I expected this species to be clearly associated with the driest habitat. This study shows that *L. maackii* has the ability to invade and gain dominance in wetland habitats. The association of *L.*

maackii with relatively higher elevations in areas subjected to greater flooding indicates that microtopography is an important factor in facilitating invasion.

Interestingly, the intermediate and dry sites had similar densities of *L. maackii*, but differed in important ways. The driest site had a dense native shrub layer (dominated by *L. benzoin*) that persisted alongside *L. maackii* throughout the forest edge and interior. This is contrary to findings from other studies that have found a negative correlation between *L. maackii* and the diversity or species richness of other plant species. This offers some evidence that *L. maackii*, under certain circumstances, may add to the native shrub community, rather than replace it. Since the stem size class structure of *L. maackii* did not appear to be different between the intermediate and dry site, there is no evidence of a more recent, less established invasion at the dry site. One clue to the coexistence of *L. benzoin* and *L. maackii* at this site may lie in the forest canopy. Since this study sought out to minimize confounding effects of light availability from sources other than the forest edge, I chose transect locations with relatively closed canopies. Studies have shown that *L. benzoin* has maximum stem growth at 25% full sun photosynthetic photon flux density (PPFD), and that *L. maackii* has highest efficiency at a higher level of light availability (near 100%). Thus, *L. maackii* is likely to outcompete *L. benzoin* in the presence of light-creating disturbances, where it can use increased light availability to achieve higher growth rates. Since we avoided large gaps, I may have encountered environmental conditions that supported a stable coexistence between *L. benzoin* and *L. maackii*. This could potentially be disrupted by the future creation of canopy gaps.

The importance of canopy gaps are particularly important to consider in the context of: 1) global climate change, where changing frequency of storms with damaging

winds may affect the forest canopy (Peterson 2000), and 2) Emerald ash borer infestation, which affects *Fraxinus* species such as *F. pennsylvanica*, a dominant species in these wetlands. According to recent estimates, Emerald ash borer (EAB) infestations can kill a healthy ash stand with close to 100% mortality within 6 years (USFS 2007). Healthy trees die within approximately 4 years of infestation. Saplings are also attacked by this beetle and can be killed in a single year (Poland and McCullough 2006), and may not be able to replace dead ash adults quickly via gap-filling. While I have not assessed the impact of EAB on my study sites, it is hard to imagine a scenario where it does not fundamentally alter the environment of these forests in many different ways (i.e. increased canopy openness, increased temperatures, and decreased evapotranspiration resulting from loss of a dominant species), with resulting shifts in plant community structure.

While the driest site had the greatest species richness and diversity in most vegetation layers, many of the species unique to this site (particularly in the adult tree and shrub layers) were exotic species or FAC/FACU species. In other words, the greater number of species at the dry site did not come primarily from a greater number of native woody wetland species. This site also had the highest percent cover of the invasive woody vine, *Lonicera japonica*, which was the most important vine species at this site. There were no exotic, woody plant species that were found only at the wettest site. The susceptibility of the dry site to invasion may be encouraged by its residential setting, but is likely permitted by drier conditions. Although wetland systems have been cited as being particularly prone to the incursion of exotic, invasive plant species (Zedler and

Kercher 2005), my study suggests that wetland hydrology offers some degree of protection from invasive, woody species.

Wetland managers should be mindful of *L. maackii* and other woody invaders when implementing restoration strategies. Microtopography in wetland forests is important because it facilitates the establishment of native species that require safe sites for germination in wetland areas (Battaglia et al. 2000, Blood and Titus 2010). Thus, the creation of microtopography (i.e. “pits and mounds”) may be a goal of wetland restoration and management (Pietrzykowski et al. 2015, Kangas et al. 2016). However, my results suggest that the results of these efforts must be monitored closely, particularly in areas with relatively open canopy conditions, which may encourage the growth and spread of exotic species, such as *L. maackii*, that can take advantage of light-creating and topographical disturbances.

There is some evidence to suggest that *L. maackii*, once established in wetlands, may alter the environment to its benefit. A recent study by Boyce et al. (2012) suggests that evapotranspiration by *L. maackii* may cause a net soil water loss, thus drying the soil. In the context of wetland systems, this represents a potential positive feedback loop, whereby water losses via *L. maackii* evapotranspiration contribute to altered wetland hydrology, further facilitating the establishment and spread of this invasive species.

Conclusions

This field study sampled plant communities over a range of hydrologic conditions and varying distance from the forest edge in three forested wetlands. The shrub community was most indicative of differences in hydrology between sites. Based on

results from this study and others (Swab et al. 2008), the invasive shrub *Lonicera maackii* can be expected to be more problematic in wetlands that have undergone hydrologic modifications, resulting in drier conditions. Because survival in wetland soils requires specialized adaptations, it is likely that wet conditions provide resistance to woody invaders from upland systems. However, the availability of more elevated “safe sites” (sensu Grubb 1977) may facilitate the colonization of wetland sites. *Fraxinus pennsylvanica* was a major component of the tree canopy at all study sites, and the losses of this species due to Emerald ash borer infestation are likely to have lasting consequences on plant community structure and composition in these forested wetlands.

Table 2-1. Characteristics of the three research sites chosen for study, including area, soil type, soil flooding/ponding characteristics, and drainage class, according to the NRCS SSURGO dataset. All information, besides size, was verified by NRCS personnel in the field.

Site Numbers and Names	Area (Ha)	Soil Map Unit	Flooding or Ponding Class	Approx. Elevation (feet)	Drainage Class	Coordinates
Site 2 Intermediate Site (Evangel)	15.1	Zipp silty clay	Ponded	451	Poor	38° 8'52.57"N 85°42'36.01"W
Site 1 Dry Site (Max Sawyer)	28.5	Melvin silt loam	Frequently flooded	456	Poor	38° 7'26.48"N 85°41'58.86"W
Site 3 Wet Site (Trinity)	31.1	Zipp silty clay	Ponded	459	Very Poor	38° 7'24.58"N 85°44'2.27"W

Table 2-2. Data used in ranking sites by wetness. Means at the scale of edge-to-interior transect (N=4 per site), parallel transect, and site. Each edge-to-interior transect consisted of five parallel transects spaced at 1, 5, 10, 30 and 60 meters.

		Site 1: Dry Site		Site 2: Intermediate Site		Site 3: Wet Site	
Edge-to-Interior Transect	Parallel Transect (m from edge)	Days Flooded SE		Days Flooded SE		Days Flooded SE	
N1	1	.	.	10.3	3.4	0.0	0.0
N1	5	.	.	0.4	0.2	12.2	1.4
N1	10	.	.	10.7	0.4	33.3	7.7
N1	30	.	.	1.4	1.4	42.5	11.4
N1	60	.	.	3.0	1.3	36.5	1.4
Mean				5.2	2.2	24.9	8.1
N2	1	0.0	0.0	14.9	4.3	40.9	6.1
N2	5	0.0	0.0	10.9	5.1	55.0	1.6
N2	10	0.8	0.5	17.9	1.6	52.5	4.1
N2	30	28.1	11.3	33.5	14.1	47.6	2.8
N2	60	10.3	7.5	71.9	4.9	23.8	1.9
Mean		7.8	5.4	29.8	11.2	44.0	5.6
S1	1	0.0	0.0	32.6	6.2	2.6	1.1
S1	5	9.7	9.6	8.2	1.7	4.5	1.1
S1	10	0.0	0.0	15.3	4.2	6.2	0.5
S1	30	0.0	0.0	17.3	5.2	8.7	1.1
S1	60	0.9	0.7	34.4	4.1	2.2	0.4
Mean		2.1	1.9	21.6	5.1	4.8	1.2
S2	1	1.5	1.5	31.5	4.9	83.2	0.5
S2	5	4.1	1.8	5.4	1.2	84.5	0.4
S2	10	1.1	0.5	21.4	4.5	84.3	0.6
S2	30	0.6	0.6	33.9	3.6	84.2	0.5
S2	60	1.2	1.2	22.3	3.5	82.6	1.3
Mean		1.7	0.6	22.9	5.0	83.7	0.4
SITE MEAN (±SE)		3.9	1.9	19.9	3.7	39.4	7.6

Table 2-3. Summary of measured environmental variables at the perpendicular transect level (N=4, within each site). Each edge-to-interior transect consisted of five parallel transects spaced at 1, 5, 10, 30 and 60 meters.

Site	Edge-to-Interior Transect	N	Days Flooded ±SE		% Herb Cover ±SE	% Bare Soil ±SE		% Leaf Litter ±SE		%CWD ±SE		% Canopy Closure ±SE		% LAI ±SE		
1	N1	5	.	.	10	3	18	10	75	11	3	2	88	1	4.60	0.16
1	N2	5	7.8	5.4	16	4	35	17	61	15	9	5	85	2	4.62	0.12
1	S1	5	2.1	1.9	22	10	21	16	77	16	1	1	92	0	4.09	0.15
1	S2	5	1.7	0.6	6	2	13	4	82	4	1	1	94	1	4.38	0.11
SITE MEAN		4	3.9	1.7	13.4	3.5	21.9	4.7	73.7	4.6	3.5	1.7	89.6	2.0	4.42	0.12
2	N1	5	5.2	2.2	41	12	6	2	85	7	3	1	95	1	2.51	0.18
2	N2	5	29.8	11.2	72	6	9	3	87	4	6	5	88	2	2.63	0.17
2	S1	5	21.6	5.1	60	13	3	1	93	2	6	2	89	1	3.02	0.35
2	S2	5	22.9	5.0	69	14	10	4	87	5	0	0	92	1	2.88	0.22
SITE MEAN		4	19.9	5.2	60.3	7.1	7.1	1.7	88.0	1.6	3.8	1.4	91.1	1.6	2.76	0.12
3	N1	5	24.9	8.1	51	15	6	3	93	3	1	1	90	2	4.13	0.38
3	N2	5	44.0	5.6	61	11	3	0	98	0	0	0	89	3	3.89	0.11
3	S1	5	4.8	1.2	60	9	24	13	75	13	2	1	92	1	2.93	0.41
3	S2	5	83.7	0.4	54	17	73	9	23	9	5	3	85	2	4.24	0.21
SITE MEAN		4	39.4	16.8	56.4	2.5	26.2	16.1	72.3	17.0	1.8	1.0	89.0	1.5	3.80	0.30

Table 2-4. Pearson correlations between environmental variables at the landscape scale (i.e. data for all transects at all sites included). Bold cells indicate pairs of variables with p-values <0.05. Top values in each cell are values for the correlation coefficient r , middle values are p-values and bottom values indicate the sample size, n .

	Distance from Edge	Days Flooded	% Herb Cover	% Bare Soil	% Leaf Litter	% CWD	% Canopy Closure	LAI
Distance from Edge	1.0000	0.1160	-0.2107	0.0045	-0.0103	-0.0231	0.1039	0.0582
		0.3992	0.1062	0.9730	0.9377	0.8607	0.4295	0.6590
	60	55	60	60	60	60	60	60
Days Flooded		1.0000	0.3060	0.3542	-0.3274	-0.0026	-0.3662	0.1163
			0.0231	0.0080	0.0147	0.9852	0.0060	0.3978
		55	55	55	55	55	55	55
% Herb Cover			1.0000	-0.0550	0.1242	-0.1817	-0.2136	-0.6284
				0.6763	0.3443	0.1647	0.1013	<.0001
			60	60	60	60	60	60
% Bare Soil				1.0000	-0.9753	0.0534	-0.2422	0.2465
					<.0001	0.6851	0.0622	0.0576
				60	60	60	60	60
% Leaf Litter					1.0000	-0.1585	0.2187	-0.2394
						0.2266	0.0932	0.0654
					60	60	60	60
% CWD						1.0000	-0.1318	0.0956
							0.3153	0.4673
						60	60	60
% Canopy Closure							1.0000	-0.1260
								0.3374
							60	60
LAI								1.0000
								60

Table 2-5. Mean density, IV and basal area \pm SE for the adult trees stratum (>2.5 cm dbh) at each of the three research sites. This could not be determined for species identified to genus level only. N=8 12 x 12 m plots at each site. Species are organized alphabetically in groups first by those occurring at the wet, then intermediate, and lastly at the dry sites. WIS = Wetland Indicator Status (see Appendix Table 16 for categories). Values in bold show the species with the highest IV and density at each site .

Species	WIS Code	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site					
		Mean (stems/Ha) \pm SE		Mean IV \pm SE		Mean Basal area (m ² /Ha) \pm SE		Mean (stems/Ha) \pm SE		Mean IV \pm SE		Mean Basal area (m ² /Ha) \pm SE		Mean (stems/Ha) \pm SE		Mean IV \pm SE		Mean Basal area (m ² /Ha) \pm SE	
<i>Acer rubrum</i>	FAC	833	315	35.1	6.5	11.4	2.6	356	74	31.8	4.1	18.4	4.5	590	156	40.6	4.9	20.9	3.7
<i>Acer saccharinum</i>	FACW	26	18	0.9	0.7	0.2	0.1	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0
<i>Celtis laevigata</i>	FACW	286	197	12.3	8.1	2.8	1.9	530	131	24.2	5.0	4.4	1.2	35	19	3.2	2.7	1.3	1.3
<i>Diospyros virginiana</i>	FAC	26	18	0.5	0.4	0.0	0.0	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0
<i>Fraxinus pennsylvanica</i>	FACW	503	162	20.9	4.4	7.0	1.8	208	73	14.7	4.5	7.2	2.8	313	114	23.0	6.2	10.4	2.9
<i>Liquidambar styraciflua</i>	FAC	43	22	5.4	3.7	3.1	2.7	0	0	0.0	0.0	0.0	0.0	130	59	8.6	4.9	5.8	5.2
<i>Nyssa sylvatica</i>	FAC	69	69	3.3	3.3	0.4	0.4	0	0	0.0	0.0	0.0	0.0	17	17	1.1	1.1	0.6	0.6
<i>Populus deltoides</i>	FAC	26	18	1.1	0.7	0.3	0.2	61	36	7.6	5.1	5.7	4.6	17	11	1.0	0.8	0.5	0.5
<i>Quercus bicolor</i>	FACW	26	18	2.4	2.0	0.9	0.9	9	9	0.2	0.2	0.0	0.0	0	0	0.0	0.0	0.0	0.0
<i>Quercus palustris</i>	FACW	200	142	9.9	4.6	3.7	2.0	43	22	4.8	3.8	5.2	5.0	17	11	1.3	0.9	0.2	0.2
<i>Salix nigra</i>	OBL	26	26	1.9	1.9	0.5	0.5	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0
<i>Ulmus rubra</i>	FAC	122	31	6.3	1.7	2.2	1.1	226	93	11.3	4.4	2.8	1.4	122	52	6.1	3.6	0.6	0.3
<i>Acer negundo</i>	FAC	0	0	0.0	0.0	0.0	0.0	17	11	0.7	0.5	0.1	0.1	0	0	0.0	0.0	0.0	0.0
<i>Platanus occidentalis</i>	FACW	0	0	0.0	0.0	0.0	0.0	9	9	2.5	2.5	1.5	1.5	104	37	9.6	5.2	4.2	1.9
<i>Quercus lyrata</i>	OBL	0	0	0.0	0.0	0.0	0.0	9	9	2.1	2.1	0.9	0.9	0	0	0.0	0.0	0.0	0.0
<i>Carya sp.</i>	-	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	9	9	0.2	0.2	0.0	0.0
<i>Cornus florida</i>	FACU	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	9	9	0.2	0.2	0.0	0.0

Species	WIS Code	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site					
		Mean (stems/Ha) ±SE		Mean IV ±SE		Mean Basal area (m ² /Ha) ±SE		Mean (stems/Ha) ±SE		Mean IV ±SE		Mean Basal area (m ² /Ha) ±SE		Mean (stems/Ha) ±SE		Mean IV ±SE		Mean Basal area (m ² /Ha) ±SE	
<i>Fagus grandifolia</i>	FACU	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	9	9	0.2	0.2	0.0	0.0
<i>Juniperus virginiana</i>	FACU	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	17	17	0.6	0.6	0.3	0.3
<i>Liriodendron tulipifera</i>	FACU	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	52	34	2.6	1.7	1.6	1.1
<i>Ulmus americana</i>	FACW	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.0	0.0	17	11	1.6	1.0	0.9	0.6
TOTAL		2188		100		32.5	4.1	1467		100		46.2	5.4	1458		100		47.1	5.1

Table 2-6. Mean species richness (number of species) and Shannon-Weiner diversity values (H) for all vegetation layers, averaged at the site level over all parallel transects (16 m²/transect) or adult sampling plots (144 m²/plot). Values in bold indicate which site had the highest values of richness or H occurring within each vegetation layer.

Layer	Site	N	Mean Richness ±SE		Mean H ±SE	
Adult tree	1: Dry Site	8	5.75	1.01	1.12	0.14
Adult tree	2: Intermediate Site	8	4.75	0.41	1.08	0.10
Adult tree	3: Wet Site	8	5.25	0.56	1.27	0.11
Sapling	1: Dry Site	20	3.65	0.44	1.08	0.09
Sapling	2: Intermediate Site	20	2.75	0.32	0.73	0.10
Sapling	3: Wet Site	20	3.40	0.42	0.82	0.11
Tree Seedling	1: Dry Site	20	2.25	0.30	0.60	0.12
Tree Seedling	2: Intermediate Site	20	1.85	0.27	0.44	0.10
Tree Seedling	3: Wet Site	20	2.1	0.27	0.43	0.10
Shrubs	1: Dry Site	20	7.25	0.68	0.79	0.08
Shrubs	2: Intermediate Site	20	2.30	0.52	0.21	0.07
Shrubs	3: Wet Site	20	3.35	0.80	0.31	0.08
Vines	1: Dry Site	20	4.75	0.35	0.99	0.10
Vines	2: Intermediate Site	20	3.25	0.32	0.52	0.08
Vines	3: Wet Site	20	2.35	0.32	0.42	0.09

Table 2-7. Tree sapling (<2.5 cm dbh, >1 m in height) abundance summaries by species for each forested wetland site. Abundance data are given as mean frequency across transects within site, sapling density, and IV (\pm SE) at each site. Species are organized alphabetically in groups first by those occurring at the wet, then intermediate, and lastly at the dry sites. WIS = Wetland Indicator Status (see Appendix Table 16 for categories). Values in bold show the species with the highest IV and density at each site.

Species Name	WIS	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site					
		Freq. \pm SE		Density (stems/Ha) \pm SE		IV \pm SE		Freq. \pm SE		Density (stems/Ha) \pm SE		IV \pm SE		Freq. \pm SE		Density (stems/Ha) \pm SE		IV \pm SE	
<i>Acer rubrum</i>	FAC	0.33	0.08	1406	368	22.7	6.4	0.06	0.03	375	281	4.0	1.9	0.08	0.04	281	190	4.7	2.5
<i>Acer saccharinum</i>	FACW	0.01	0.01	31	31	0.2	0.2	0.01	0.01	31	31	0.2	0.2	0.01	0.01	31	31	0.3	0.3
<i>Celtis laevigata</i>	FACW	0.11	0.06	438	198	6.1	3.2	0.41	0.08	2500	596	37.0	6.7	0.19	0.06	563	186	15.0	4.7
<i>Crataegus spp.</i>		0.01	0.01	31	31	0.3	0.3	0.01	0.01	31	31	0.7	0.7	0.00	0.00	0	0	0.0	0.0
<i>Fraxinus pennsylvanica</i>	FACW	0.44	0.08	5844	2083	35.1	6.4	0.28	0.08	4063	2079	18.5	4.6	0.29	0.06	1250	339	22.4	3.4
<i>Liquidambar styraciflua</i>	FAC	0.13	0.07	1469	855	3.7	2.1	0.00	0.00	0	0	0.0	0.0	0.15	0.06	469	226	10.6	4.1
<i>Liriodendron tulipifera</i>	FACU	0.03	0.02	63	43	0.4	0.3	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0
Unidentified		0.01	0.01	31	31	0.4	0.4	0.00	0.00	0	0	0.0	0.0	0.04	0.02	94	51	1.5	1.0
<i>Nyssa sylvatica</i>	FAC	0.13	0.07	1094	689	3.2	1.8	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0
<i>Quercus bicolor</i>	FACW	0.03	0.02	63	43	0.6	0.4	0.03	0.02	63	43	1.4	1.0	0.01	0.01	31	31	1.3	1.3
<i>Quercus michauxii</i>	FACW	0.03	0.02	63	43	5.2	5.0	0.00	0.00	0	0	0.0	0.0	0.06	0.03	156	77	3.5	1.6
<i>Quercus palustris</i>	FACW	0.29	0.06	969	254	14.0	3.4	0.20	0.06	875	322	11.0	2.9	0.13	0.04	375	160	9.1	3.1
<i>Ulmus rubra</i>	FAC	0.18	0.06	594	220	8.0	3.0	0.20	0.07	625	227	14.8	5.6	0.20	0.05	688	181	14.8	3.8
<i>Diospyros virginiana</i>	FAC	0.00	0.00	0	0	0.0	0.0	0.01	0.01	31	31	0.9	0.9	0.01	0.01	31	31	0.3	0.3
<i>Salix nigra</i>	OBL	0.00	0.00	0	0	0.0	0.0	0.01	0.01	125	125	1.5	1.5	0.00	0.00	0	0	0.0	0.0
<i>Asimina triloba</i>	FAC	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.08	0.04	469	283	7.4	4.0
<i>Carya spp.</i>		0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.03	0.02	63	43	1.3	0.9
<i>Platanus occidentalis</i>	FACW	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.01	0.01	31	31	1.7	1.7
<i>Prunus spp.</i>		0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.01	0.01	31	31	0.8	0.8
<i>Sassafras albidum</i>	FACU	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.01	0.01	31	31	0.3	0.3
SUM		12094 \pm3273						8719 \pm2656						4594 \pm4593					
		100						90						95					

Table 2-8. Tree seedling (<0.3 m tall) abundance summaries by research site. Abundance data are given as mean frequency, density, and IV (\pm SE) at each site. Species are organized alphabetically in groups first by those occurring at the wet, then intermediate, and lastly at the dry sites. WIS = Wetland Indicator Status (see Appendix Table 16 for categories). Values in bold show the species with the highest IV and density at each site.

Species	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site						Across Site Means					
	Mean Freq.	\pm SE	Mean Density (stems/ha)	\pm SE	Mean IV	\pm SE	Mean Freq.	\pm SE	Mean Density (stems/ha)	\pm SE	Mean IV	\pm SE	Mean Freq.	\pm SE	Mean Density (stems/ha)	\pm SE	Mean IV	\pm SE	Mean Freq.	\pm SE	Mean Density (stems/ha)	\pm SE	Mean IV	\pm SE
<i>Acer spp.</i>	0.03	0.02	63	43	3.8	2.7	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.01	0.01	21	21	1.3	1.3
<i>Celtis laevigata</i>	0.01	0.01	31	31	2.1	2.1	0.13	0.03	625	198	24.7	7.2	0.1	0.0	719	199	24.5	7.2	0.09	0.04	458	215	17.1	7.5
<i>Fraxinus pennsylvanica</i>	0.19	0.02	5188	1518	47.8	7.8	0.14	0.03	4688	2290	32.6	7.5	0.1	0.0	1188	471	25.9	7.5	0.15	0.02	3688	1258	35.4	6.5
<i>Liquidambar styraciflua</i>	0.05	0.02	313	154	4.5	2.2	0.00	0.00	0	0	0.0	0.0	0.1	0.0	281	147	7.5	3.6	0.03	0.02	198	99	4.0	2.2
<i>Nyssa sylvatica</i>	0.05	0.02	125	57	11.5	6.8	0.00	0.00	0	0	0.0	0.0	0.0	0.0	0	0	0.0	0.0	0.02	0.02	42	42	3.8	3.8
<i>Quercus palustris</i>	0.15	0.03	1188	505	20.2	5.3	0.11	0.03	375	105	19.5	6.2	0.1	0.0	188	102	7.0	3.7	0.10	0.03	583	307	15.6	4.3
<i>Ulmus rubra</i>	0.05	0.02	250	139	5.2	2.8	0.05	0.02	281	190	4.7	2.3	0.1	0.0	156	62	9.9	5.3	0.05	0.00	229	38	6.6	1.7
<i>Diospyros virginiana</i>	0.00	0.00	0	0	0.0	0.0	0.03	0.02	63	43	1.9	1.4	0.0	0.0	31	31	1.0	1.0	0.01	0.01	31	18	1.0	0.6
<i>Prunus spp.</i>	0.00	0.00	0	0	0.0	0.0	0.01	0.01	31	31	1.7	1.7	0.0	0.0	31	31	5.0	5.0	0.01	0.00	21	10	2.2	1.5
<i>Asimina triloba</i>	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.0	0.0	31	31	1.0	1.0	0.00	0.00	10	10	0.3	0.3
<i>Carya sp.</i>	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.0	0.0	63	43	4.4	3.0	0.01	0.01	21	21	1.5	1.5
<i>Liriodendron tulipifera</i>	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.0	0.0	31	31	0.8	0.8	0.00	0.00	10	10	0.3	0.3
<i>Quercus michauxii</i>	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.0	0.0	94	51	3.8	2.1	0.01	0.01	31	31	1.3	1.3
<i>Rosaceae</i>	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.0	0.0	31	31	1.0	1.0	0.00	0.00	10	10	0.3	0.3
Unidentified	0.00	0.00	0	0	0.0	0.0	0.00	0.00	0	0	0.0	0.0	0.0	0.0	63	43	3.1	2.2	0.01	0.01	21	21	1.0	1.0
SUM			7156	1855	95			6063	2431	85					2906	644	95			5375	2899			

Table 2-9. Shrub abundance summaries by research site. Abundance data are given as mean frequency, stem density, and IV (\pm SE) at each site. Species sorted alphabetically by name by those occurring in Site 3, 2, and 1, in order. WIS = Wetland Indicator Status (see Appendix Table 16 for categories). Values in bold show the species with the highest IV and density at each site.

Species	WIS	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site					
		Freq. \pm SE		IV \pm SE		Density (stems/Ha) \pm SE		Freq. \pm SE		IV \pm SE		Density (stems/Ha) \pm SE		Freq. \pm SE		IV \pm SE		Density (stems/Ha) \pm SE	
<i>Aralia spinosa</i>	FAC	0.01	0.01	0.5	0.5	94	94	0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0
<i>Cephalanthus occidentalis</i>	OBL	0.08	0.03	6.5	3.3	281	124	0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0
<i>Cornus foemina</i>	FACW	0.29	0.07	40.1	8.7	6031	2842	0.15	0.06	21.0	8.0	3375	2260	0.08	0.04	3.3	1.8	1031	605
<i>Lonicera maackii</i>	NI	0.10	0.04	12.6	5.7	813	458	0.31	0.07	43.1	9.5	4844	1256	0.39	0.07	18.8	3.7	4406	1186
<i>Rosa spp.</i>	-	0.01	0.01	1.0	1.0	156	156	0.00	0.00	0.0	0.0	0	0	0.04	0.03	2.8	2.4	1031	881
<i>Rubus spp.</i>	-	0.10	0.06	6.5	3.7	1938	1224	0.11	0.05	16.0	7.3	1156	558	0.39	0.08	21.7	5.6	4969	1393
<i>Sambucus canadensis</i>	FAC	0.01	0.01	0.4	0.4	31	31	0.00	0.00	0.0	0.0	0	0	0.08	0.03	2.2	1.0	281	160
<i>Symphoricarpos orbiculatus</i>	FACU	0.01	0.01	0.9	0.9	31	31	0.00	0.00	0.0	0.0	0	0	0.01	0.01	0.2	0.2	31	31
<i>Euonymus alatus</i>	NI	0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0	0.03	0.02	1.3	0.9	313	233
<i>Euonymus americanus</i>	FAC	0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0	0.01	0.01	0.4	0.4	94	94
<i>Lindera benzoin</i>	FAC	0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0	0.71	0.08	41.8	5.3	11844	2271
<i>Prunus sp.</i>	-	0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0	0.01	0.01	0.4	0.4	31	31
Unidentified		0.00	0.00	0.0	0.0	0	0	0.00	0.00	0.0	0.0	0	0	0.04	0.02	2.2	1.3	344	210
SUM				68.4		9375				80.0		9375				95.0		24375	

Table 2-10. Vine abundance summaries by research site. Abundance data are given as mean frequency, percent cover, and IV (\pm SE) at each site. Species are sorted alphabetically by name. WIS = Wetland Indicator Status (see Appendix Table 16 for categories). Values in bold show the species with the highest IV and percent cover at each site.

Species	WIS	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site					
		Freq.	Std. Error	% Cover	Std. Error	IV	Std. Error	Freq.	Std. Error	% Cover	Std. Error	IV	Std. Error	Freq.	Std. Error	% Cover	Std. Error	IV	Std. Error
<i>Campsis radicans</i>	FAC	0.28	0.08	3.3	1.3	22.5	7.8	0.21	0.07	1.3	0.6	7.5	3.4	0.15	0.06	1.0	0.6	3.9	1.5
<i>Euonymus fortunei</i>	NI	0.01	0.01	0.0	0.0	0.5	0.5	0.03	0.03	0.5	0.5	0.9	0.9	0.11	0.06	3.6	3.2	3.5	2.4
<i>Lonicera japonica</i>	NI	0.23	0.07	3.4	2.0	10.5	3.5	0.31	0.08	5.5	2.7	8.4	2.3	0.79	0.07	19.6	3.7	37.9	4.2
<i>Menispermum canadensis</i>	FACU	0.00	0.00	0.0	0.0	0.0	0.0	0.03	0.03	0.2	0.2	0.5	0.5	0.09	0.04	0.4	0.2	2.4	1.3
<i>Parthenocissus quinifolia</i>	FACU	0.16	0.06	0.6	0.2	5.6	2.2	0.31	0.09	4.5	2.1	9.3	2.6	0.46	0.09	1.3	0.3	9.9	2.4
<i>Smilax spp.</i>	-	0.01	0.01	0.0	0.0	0.2	0.2	0.03	0.02	0.1	0.0	0.8	0.6	0.28	0.05	2.0	0.9	8.4	1.9
<i>Toxicodendron radicans</i>	FAC	0.59	0.09	15.9	5.0	49.0	7.5	0.83	0.06	40.9	6.6	57.5	5.5	0.65	0.07	9.4	3.1	26.1	4.6
<i>Vitaceae</i>	-	0.08	0.03	0.2	0.1	6.7	5.0	0.26	0.06	1.6	0.9	10.1	3.1	0.28	0.06	2.2	0.9	7.9	2.1
TOTAL		1.35		23.59		95.00		2.00		54.53		95.00		2.80		39.47		100.00	

Table 2-11. Summary of species, environmental variables and biotic variables associated with axes from NMS ordination of woody vegetation at all sites. Species having the highest negative and positive r^2 values with each axis are shown. Environmental and biotic variables with $r^2 \geq 0.15$ for each axis are shown. The + or - indicates the direction of the correlation.

	% Variance Explained	Species	r	r^2	Environmental Variable	r	r^2	Biotic Variable	r	r^2
Axis 1	34.50%	(-) <i>Lindera benzoin</i>	-0.765	0.586	(+) Days Flooded	0.613	0.376	(-) Exotic Vine IV	-0.665	0.442
		(+) <i>Cornus foemina</i>	0.585	0.342				(-) Shrub Density	-0.432	0.187
								(+) FACW/OBL Shrub IV	0.634	0.402
								(+) % Herb Cover	0.582	0.339
Axis 2	18.50%	(+) <i>Lonicera maackii</i>	0.674	0.454	-			(+) Exotic Shrub IV	0.668	0.447
		(-) <i>Fraxinus pennsylvanica</i> (saplings)	-0.498	0.248				(+) % Vine Cover	0.453	0.205
Axis 3	19.20%	(+) <i>Celtis laevigata</i> (seedlings)	0.446	0.199	(+) Distance From Edge	0.45	0.203	(+) Seedling Density	0.443	0.196
		(-) <i>Rubus</i> spp.	-0.629	0.395						

Table 2-12. Pearson correlation coefficients, r^2 , and p-values for relationships between number of flooded days and shrub stem density by total stem density and density of individual species. Data includes 55 transects from all three sites where the number of flooded days was estimated.

Species	n	r	r^2	p-value
Total Stems	55	-0.12	0.01	0.3737
<i>Cornus foemina</i>	55	0.36	0.13	0.0072
<i>Lindera benzoin</i>	55	-0.34	0.12	0.0107
<i>Lonicera maackii</i>	55	-0.29	0.09	0.0307
<i>Rubus</i> sp.	55	-0.28	0.08	0.041

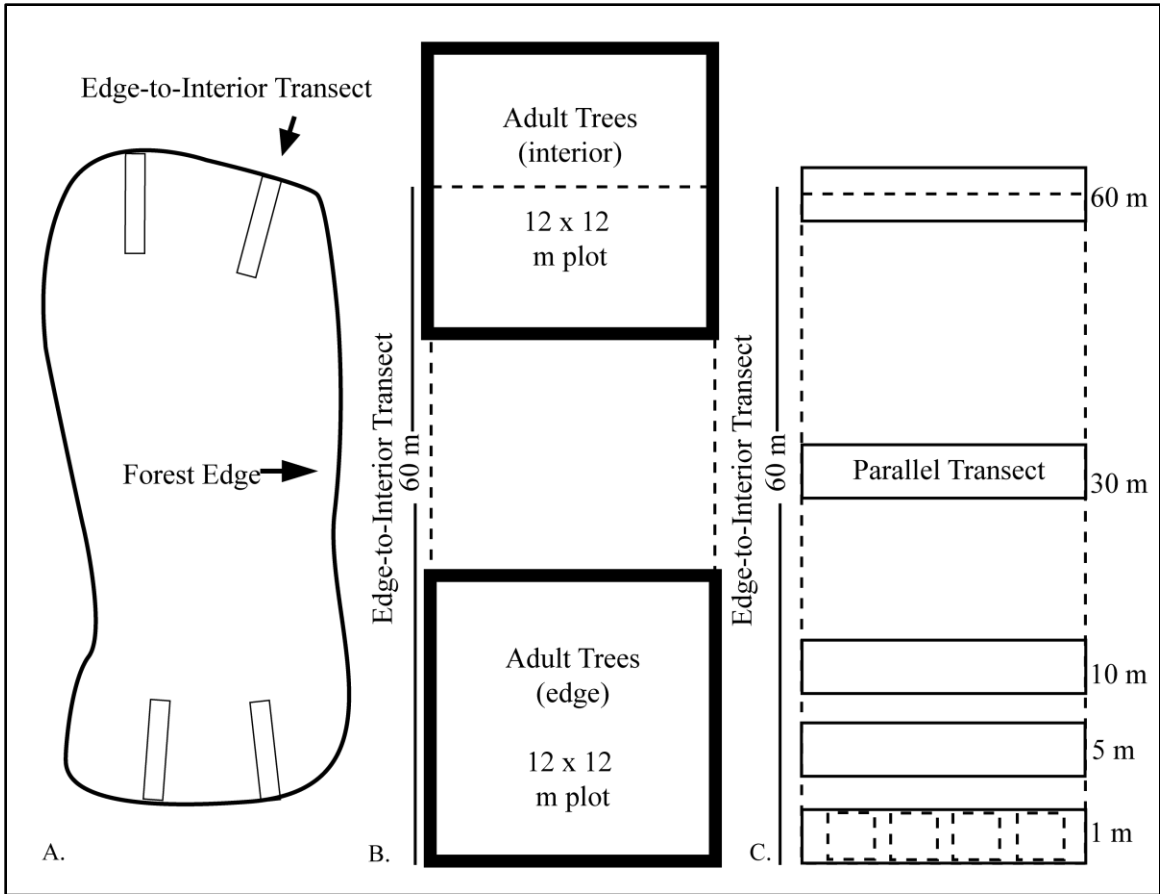


Figure 2-1. Layout and dimensions of sampling units. A. An outline of an irregularly shaped forest patch with a hypothetical placement of edge-to-interior transects. B. An edge-to-interior transect (large dashed rectangle), with the placement of adult tree sampling plots. C. An edge-to-interior transect containing five 12 x 2 m parallel transects at 1, 5, 10, 30 and 60 m from the forest edge. Parallel transects contained four 2 x 2 m quadrats for collecting plant, ground cover and elevation data. B and C both depict the same edge-to-interior transect, but featuring different sampling areas.

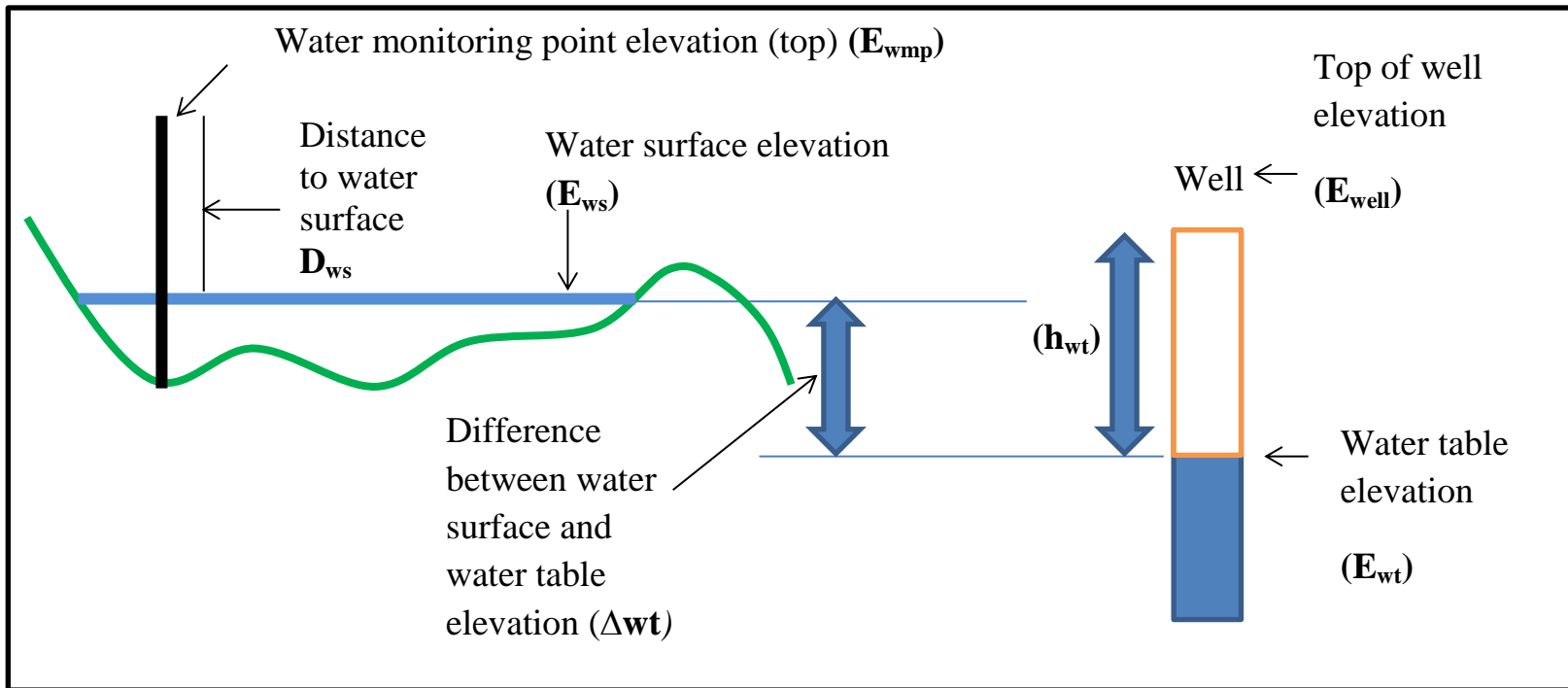


Figure 2-2. Visual aid explaining terms used in quantifying site hydrology. Definitions of terms used are: E_{wmp} is the elevation of the top of the water monitoring point, E_{ws} = elevation of the water surface, E_{wt} = elevation of the water table, Δwt = distance between the water surface elevation and the water table elevation, E_{well} is the elevation of the top of the groundwater monitoring well, D_{ws} distance between water surface and top of water monitoring point, and h_{wt} = difference between the elevation of the water table and the top of the well.

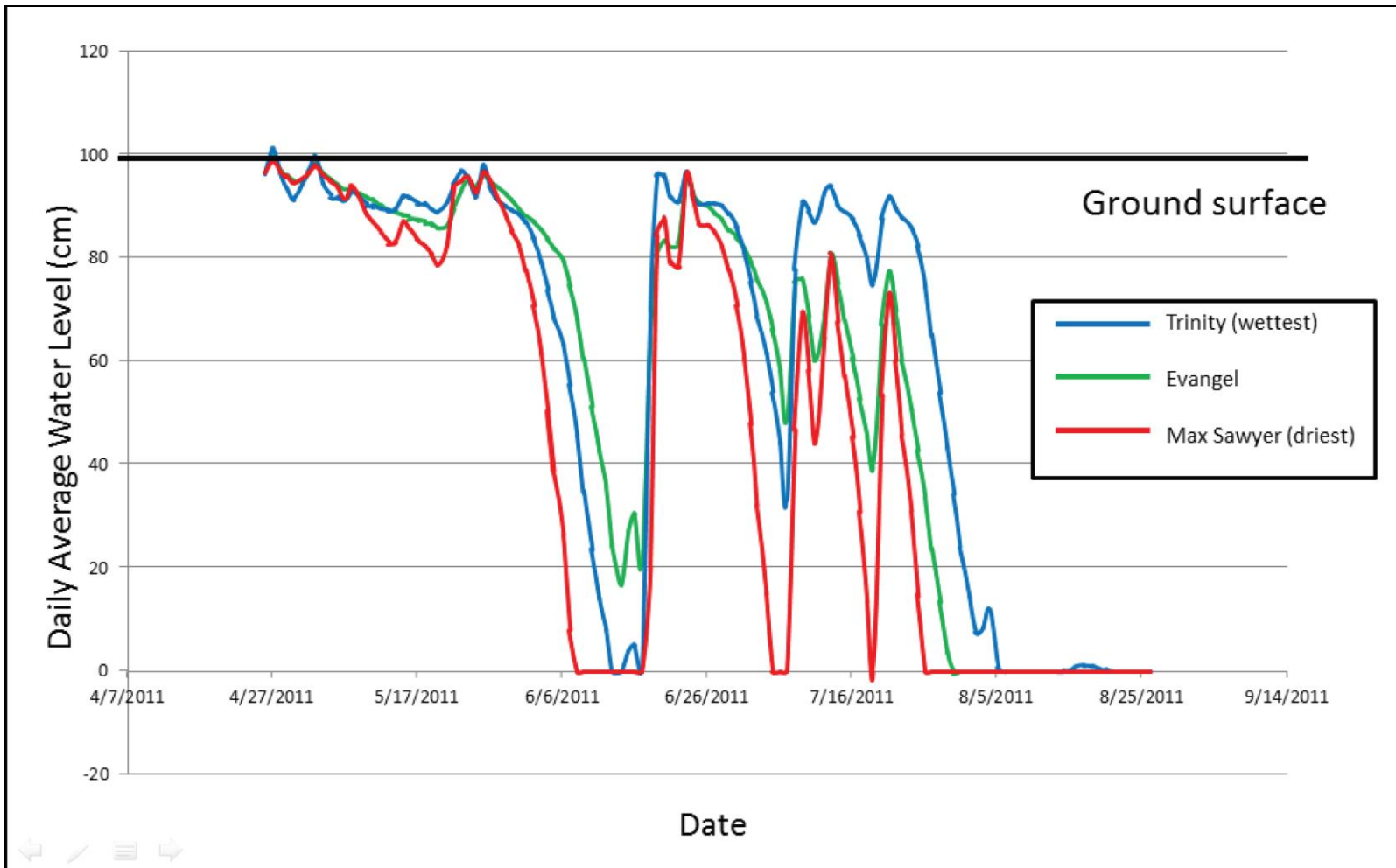


Figure 2-3. Hydrographs depicting water levels in water monitoring wells in each of the 3 research sites, relative to the ground surface (100 cm).

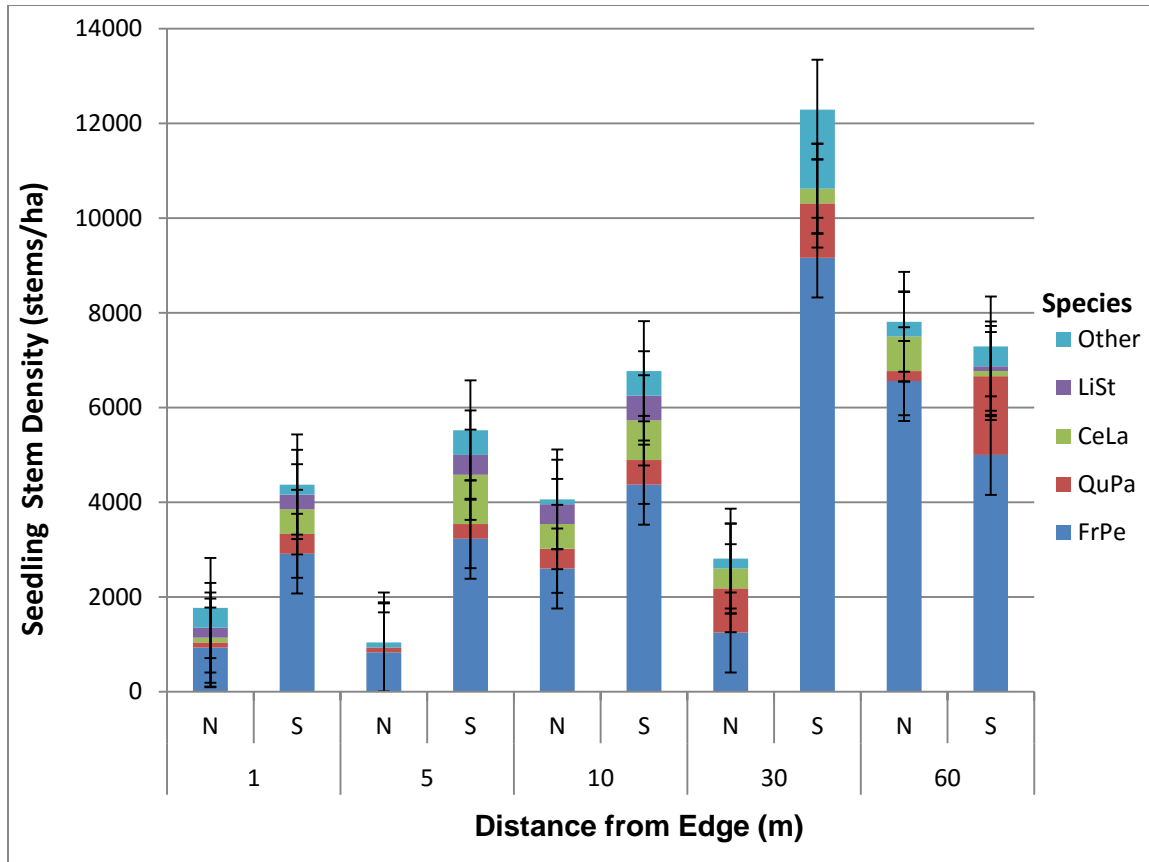


Figure 2-4. Seedling density in north and south-facing edges at varying distance from the edge. Bars are color coded (see legend) to show density of the most abundant species. Species shown are *Fraxinus pennsylvanica* (FrPe), *Quercus palustris* (QuPa), *Celtis laevigata* (CeLa) and *Liquidambar styraciflua* (LiSt). The density of all other tree seedlings combined is included in the “Other” category.

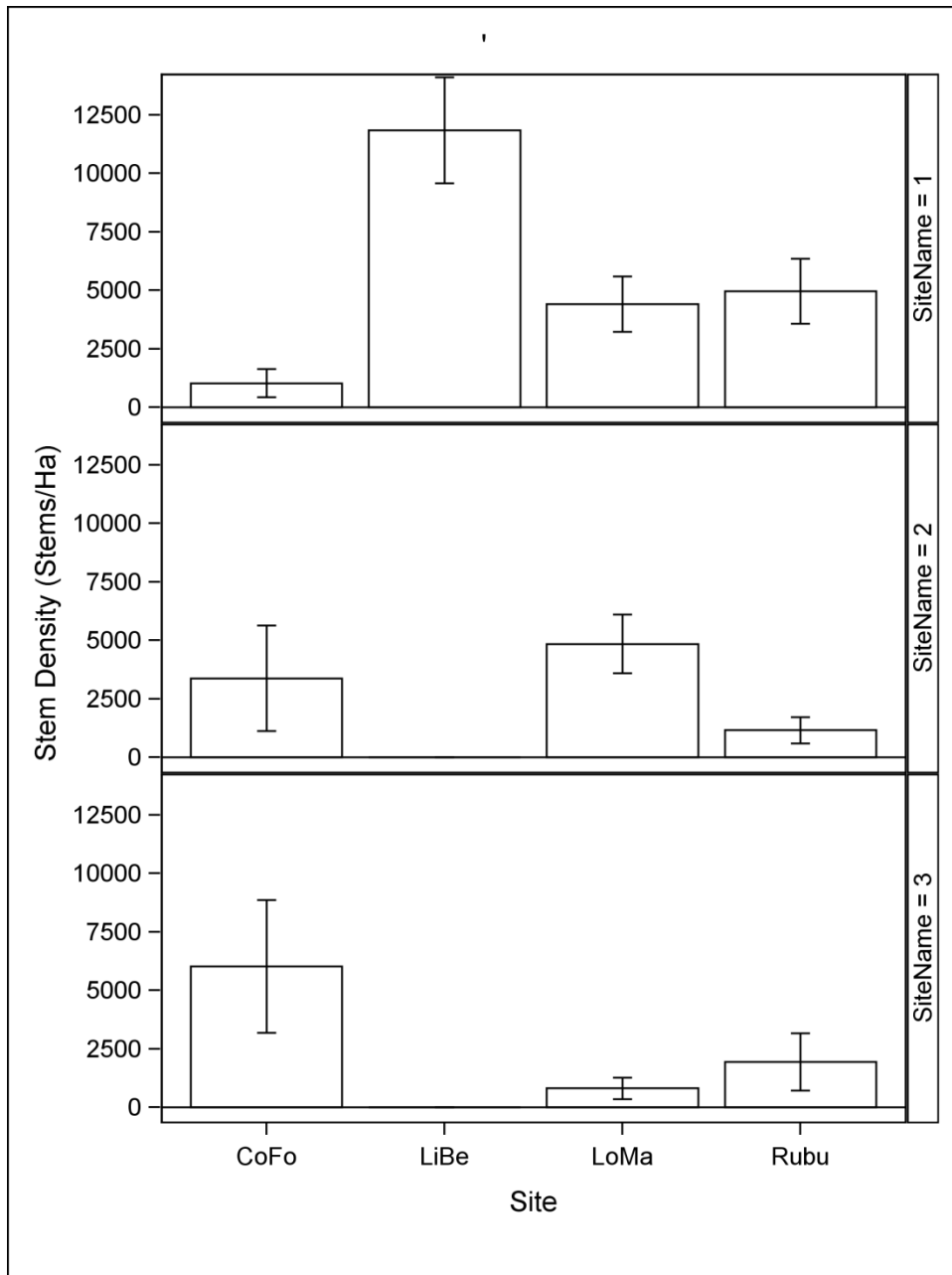


Figure 2-5. Mean stem density of four shrub species at each site. Mean values were calculated by pooling shrub data from all parallel transects (n=20) within each site. Species codes are: CoFo=*Cornus foemina* (FACW), LiBe=*Lindera benzoin* (FAC), LoMa=*Lonicera maackii*, Rubu=*Rubus* spp. Sites 1, 2 and 3 are the dry, intermediate and wet sites, respectively. Error bars are $\pm 1SE$.

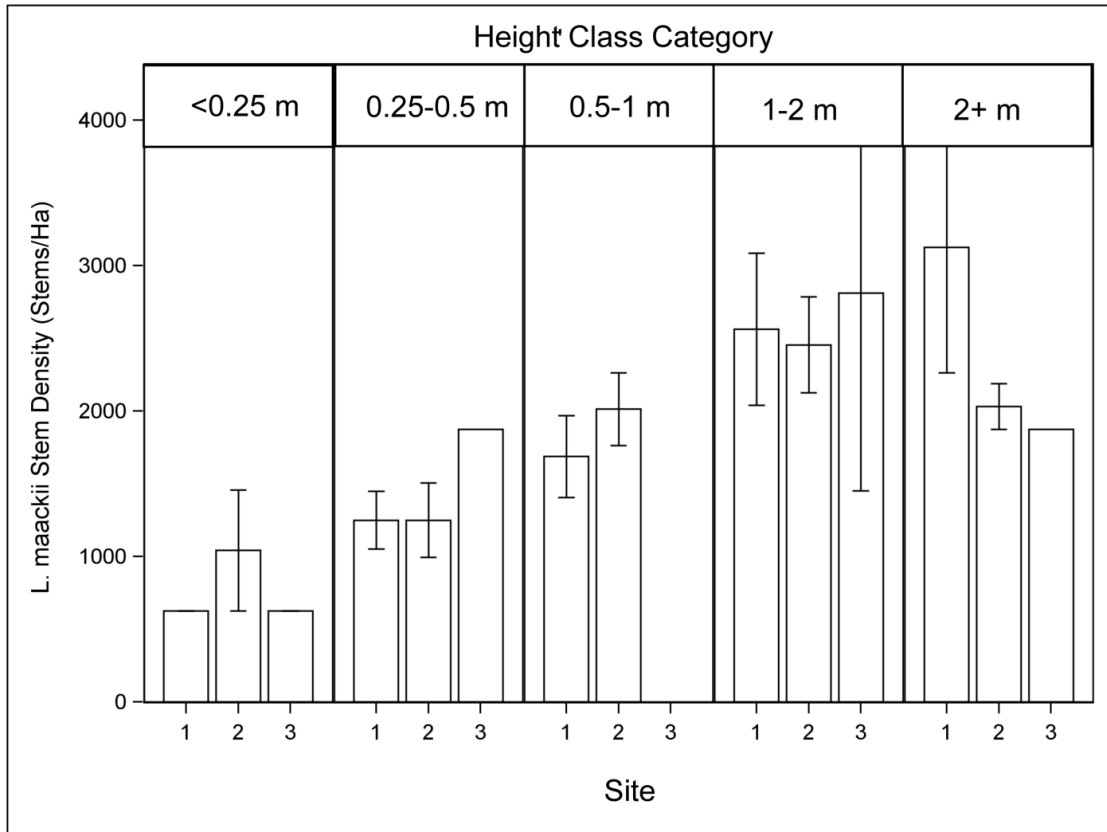


Figure 2-6. Density of *Lonicera maackii* stems in different height class categories at each site. Site 1 = dry site, Site 2 = intermediate site, and Site 3 = wet site. Error bars are ± 1 SE.

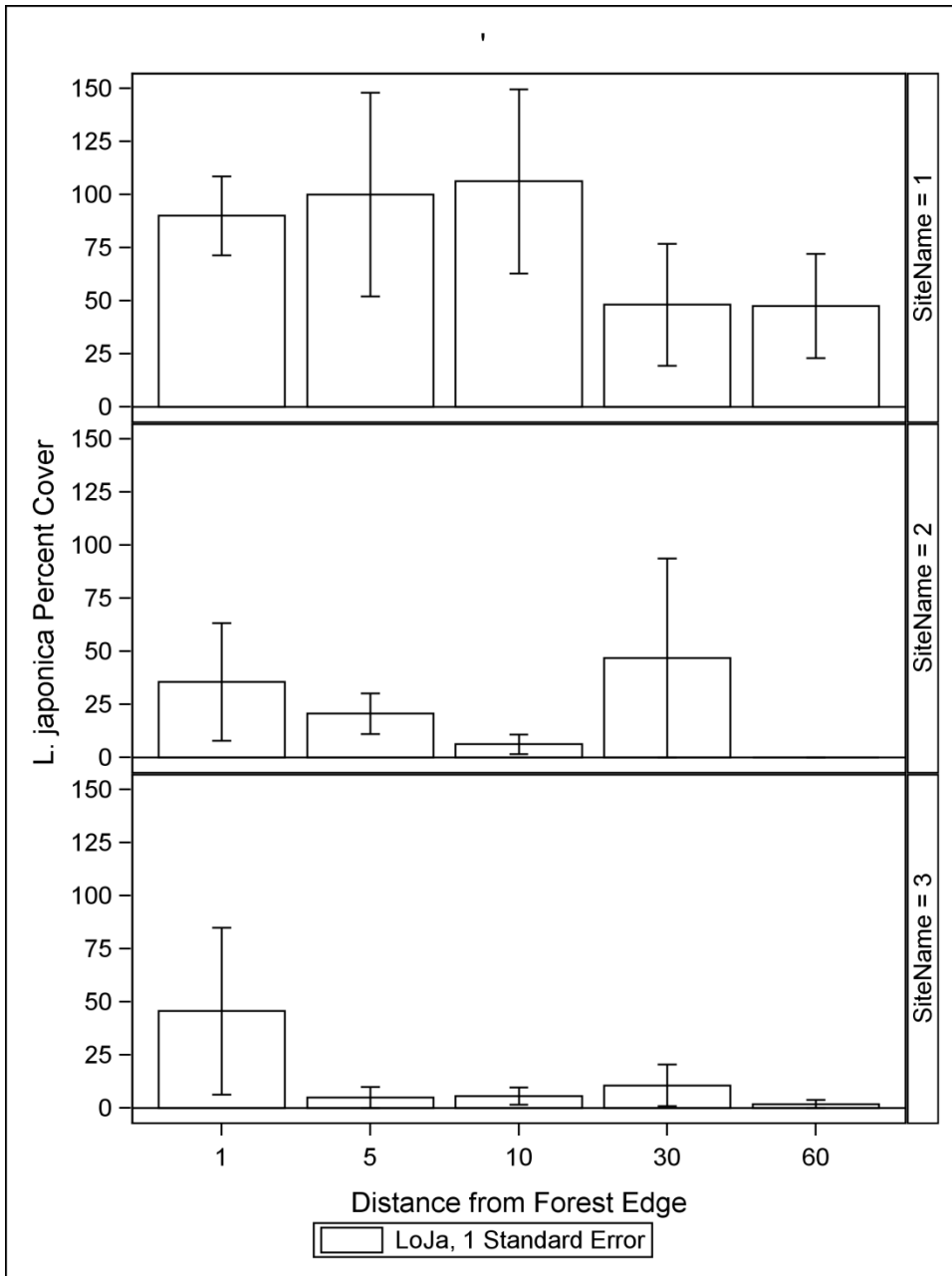


Figure 2-7. Total percent cover of *Lonicera japonica* vines with distance from the forest edge at all three research sites. Each bar represents the mean percent cover of *L. japonica* at four transects per site, corresponding to 1, 5, 10, 30 or 60 meters from the forest edge. Sites 1, 2 and 3 refer to the dry, intermediate, and wet sites, respectively. Error bars are ± 1 SE.

NMS - Woody Vegetation - All Sites

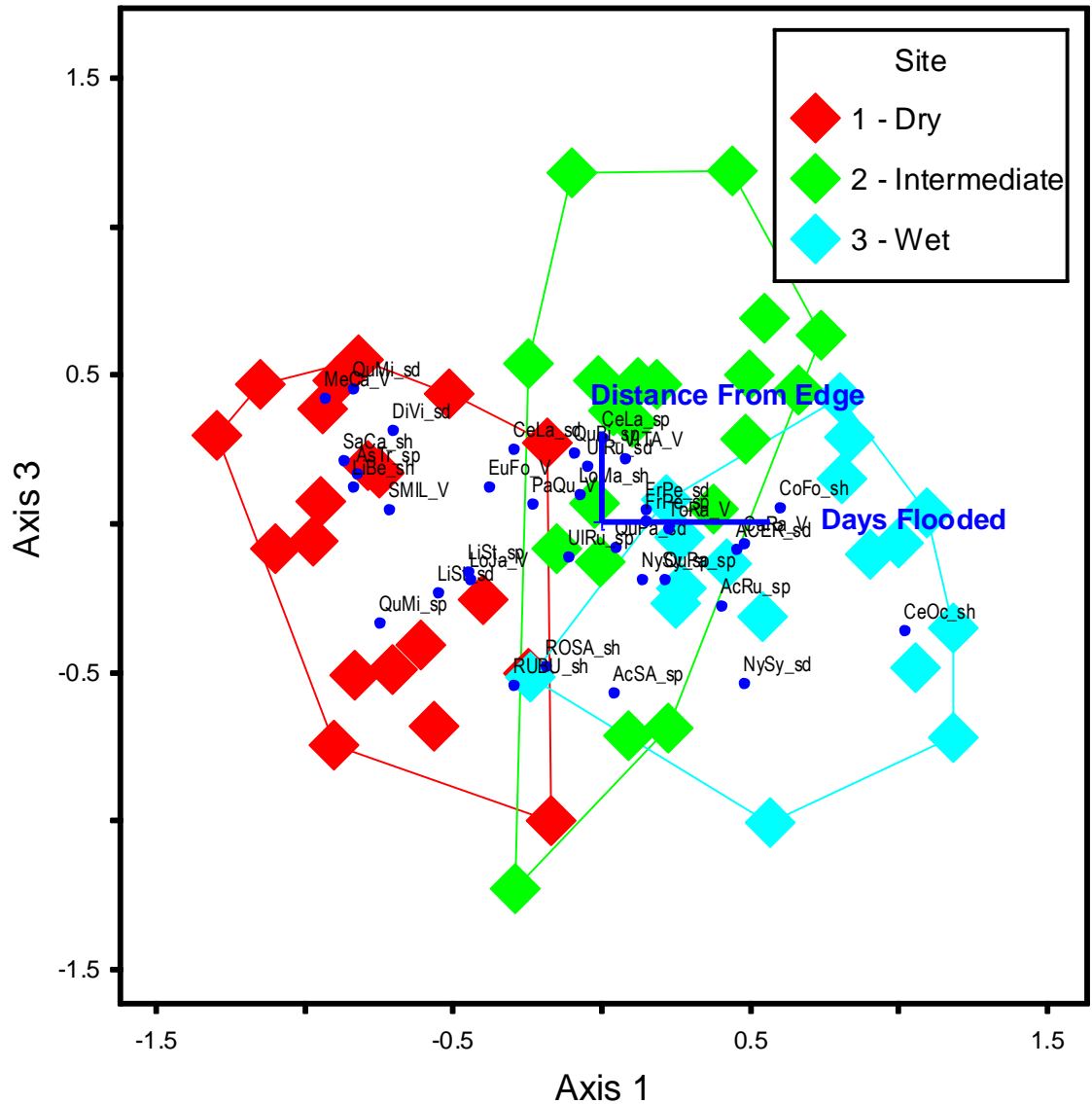


Figure 2-8. Biplot of NMS ordination based on woody plant species Importance Values (IVs) in all sampling units (parallel transects) from all three study sites. Environmental variables most strongly correlated with either axis (r^2 values of 0.15 or greater) are depicted in dark blue lines and letters; dark blue lines indicate the positive direction of the correlation. Axis 1 and 3 explained 34.5% and 19.2% of the variation in the IV matrix, respectively. IVs were computed separately for seedlings and saplings, and therefore are displayed as different “species” in the ordination plot. Vegetation layers are coded as follows: sh = shrub, V = vine, sp=sapling, sd=tree seedling. Abbreviations for species are given in Appendix Table 2.

NMS - All Sites - Woody Vegetation

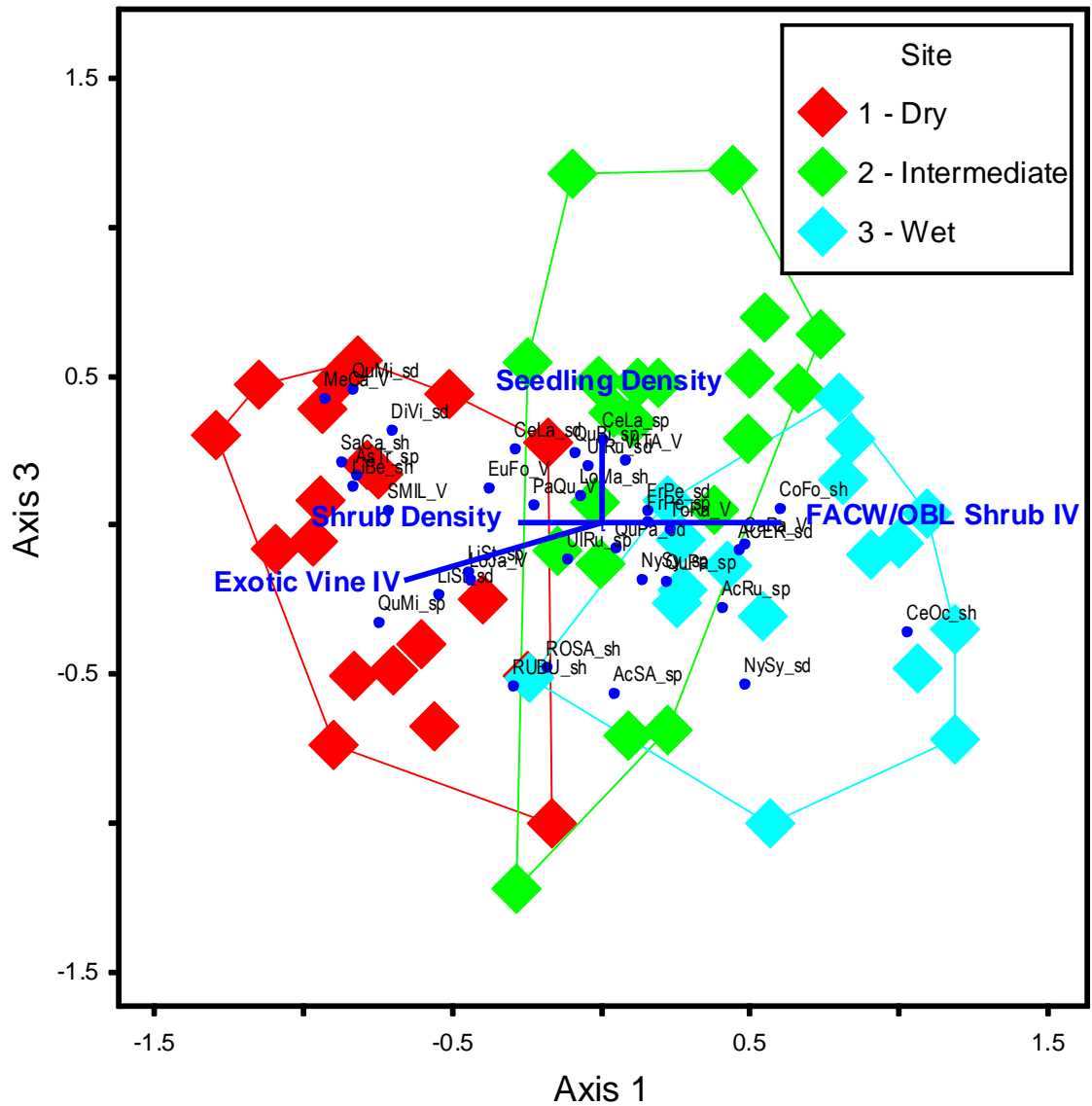


Figure 2-9. Biplot of NMS ordination based on woody plant species IVs in all sampling units (parallel transects) from all three study sites. Biotic variables most strongly correlated with either axis (r^2 values of 0.15 or greater) are depicted in dark blue; dark blue lines indicate the positive direction of the correlation. Axis 1 and 3 explained 34.5% and 19.2% of variation in the IV matrix, respectively. IVs were computed separately for seedlings and saplings, and therefore are displayed as different “species” in the ordination plot. Vegetation layers are coded as follows: sh = shrub, V = vine, sp=sapling, sd=tree seedling. Abbreviations for species are given in Appendix Table 2.

NMS - All Sites - Woody Vegetation

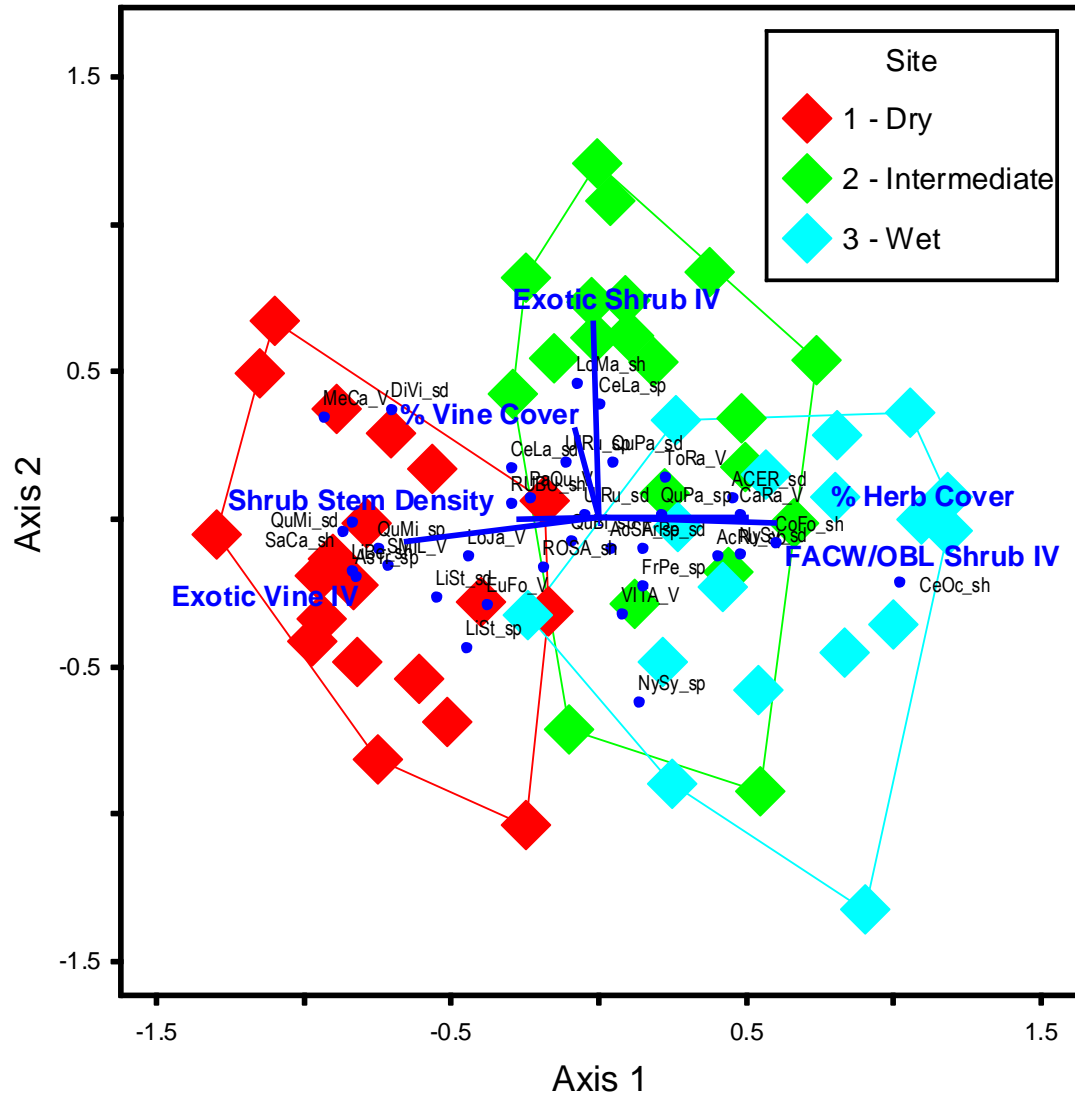


Figure 2-10. Biplot of NMS ordination based on woody plant species IVs in all sampling units (parallel transects) from all three study sites. Biotic summary variables most strongly correlated with either axis (r^2 values of 0.15 or greater) are depicted in dark blue; dark blue lines indicate the direction of the correlation. Axis 1 and 2 explained 34.5% and 18.5% of variation in the IV matrix, respectively. IVs were computed separately for seedlings and saplings, and therefore are displayed as different “species” in the ordination plot. Vegetation layers are coded as follows: sh = shrub, V = vine, p=sapling, sd=tree seedling. Abbreviations for species are given in Appendix Table 2.

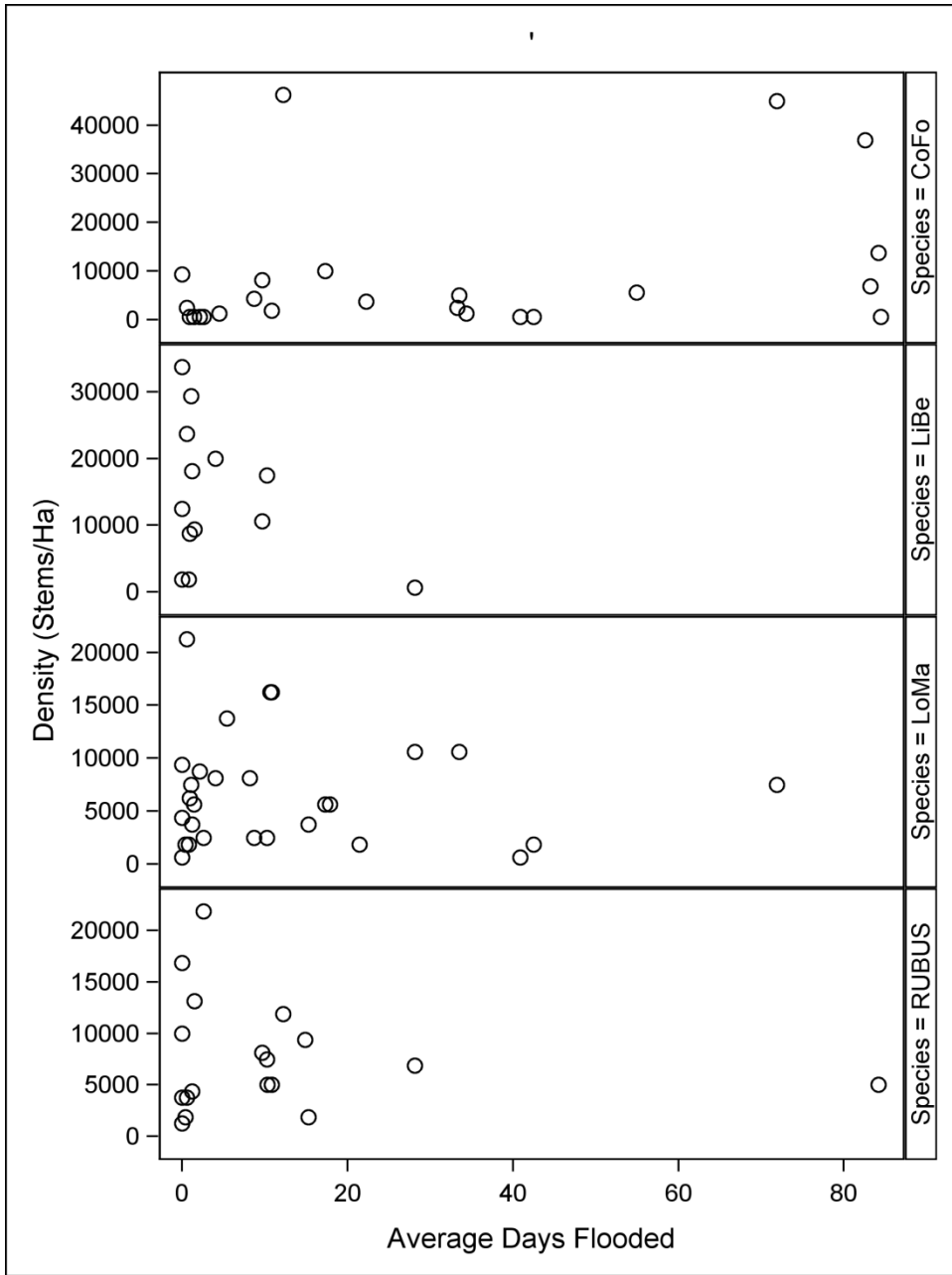


Figure 2-11. Stem density of four dominant shrub species as it relates to the number of days flooded in transects. CoFo=*Cornus foemina* (FACW), LoMa=*Lonicera maackii*, Rubus=*Rubus* spp., LiBe=*Lindera benzoin* (FAC).

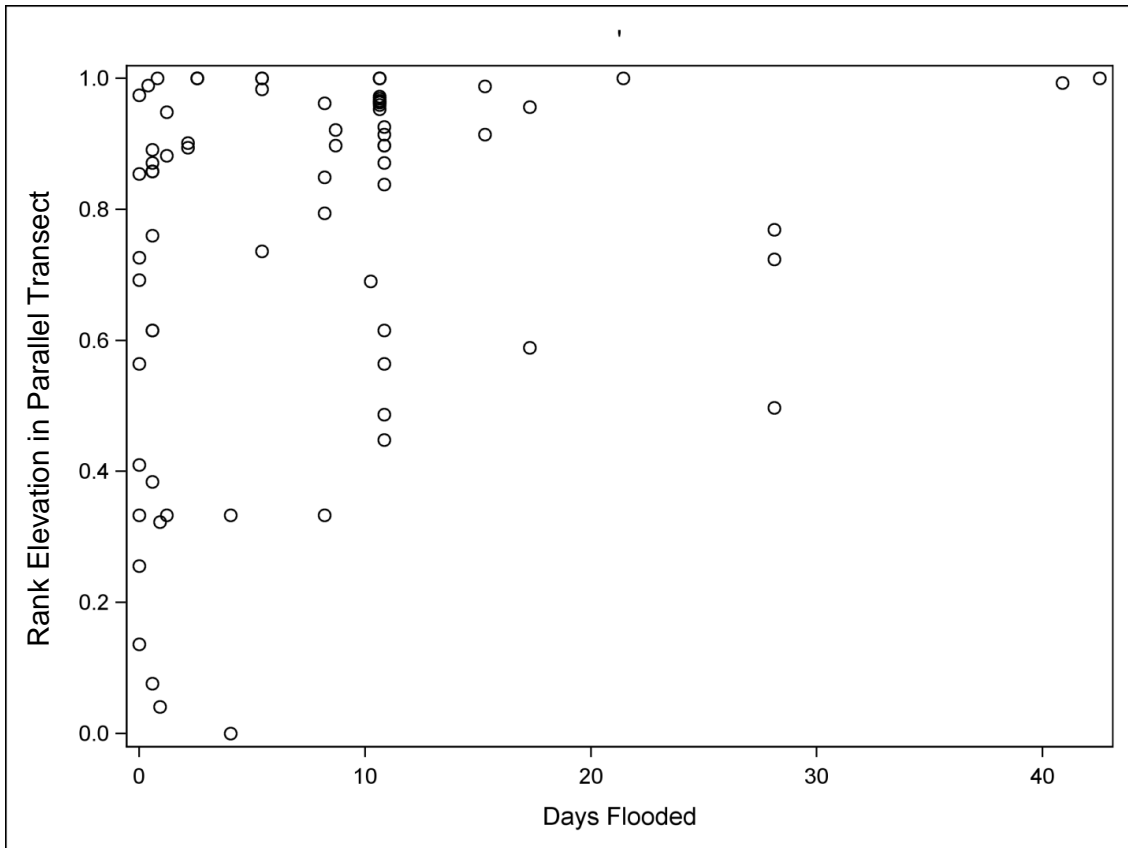


Figure 2-12. Factor –ceiling distribution of the number of days flooded vs. the rank elevation (a measure of the relative elevation of plants in a transect) of all *Lonicera maackii* individuals sampled. Each point represents an individual plant. Data across all sites is shown. The distribution reveals that *L. maackii* was restricted to increasingly higher elevation microsites within transects as days flooded per year increased

CHAPTER III

EFFECTS OF FLOODING DURATION, FLOODING DEPTH AND LIGHT ON THE GROWTH AND SURVIVAL OF *LONICERA MAACKII* IN AN EXPERIMENTAL MESOCOSM

Introduction

The success of invasive species has been described as being dependent on the match between “opportunity and opportunist” (Zedler and Kercher 2004), in which opportunities are determined by particular disturbance patterns. Wetland hydrology—the frequency, timing, depth and duration of water level fluctuations in a wetland—may create opportunities, or barriers, for the establishment of invasive plant species, depending on plant life history traits. Gradients of flood duration and flood depth are the most important factors limiting the distribution of individual species in bottomland hardwood forests (Kozlowski 2002). Therefore, forested wetlands are dominated by woody vegetation that has physiologically evolved to withstand the anaerobic conditions associated with water-logged wetland soils, either through tolerance or avoidance of stress (Mitsch 2000). However, even hydrophytic woody species are impeded by flood-related stresses at early life history stage, and successful establishment of woody seedlings depends largely on the availability of unflooded soil.

Such “safe sites” are created due to both wetland drawdown and variations in wetland microtopography. Microtopography interacts with wetland hydrology to create spatial and temporal heterogeneity in inundation patterns, increasing the diversity of wetland microsites, and providing refugia for the colonization of plant species with different requirements and physiological limitations. Thus, since microtopography expands the range of available regeneration niches (*sensu* Harper 1966), certain plant invaders may be able to colonize both upland and wetland ecosystems.

The same disturbances that create microtopography may be accompanied by changes in light availability. For instance, natural tree fall creates tip-up mounds accompanied by canopy gaps and logged wetland forests undergo dramatic changes in microtopography due to heavy equipment operations (Anderson et al. 2007). Thus, a number of studies have examined the interaction between light availability and microtopography on various measures of plant success and plant community composition and structure (Battaglia et al. 2000).

In this chapter, I examine the potential of wetland microtopography and light availability to impact the growth and survival of *Lonicera maackii* seedlings. The extent and impact of *Lonicera* spp. invasion in North American forests is a growing concern that has received considerable attention in recent years. *L. maackii*, in particular, has been cited as an invader of serious concern, with the potential to reduce species diversity (Hartman & McCarthy, 2008) and limit recruitment of native species (Ens & French, 2008). In its native range, this exotic shrub occupies riparian habitat, which may be thought of as lying somewhere between the wetland and upland continuum. Studies concerning this species in eastern North America have largely been restricted to upland

forests, but several recent papers have studied its occurrence in bottomland hardwood forests (Predick and Turner 2008, Swab et al. 2008, Mills et al. 2009, Pennington et al. 2010, Boyce et al. 2012). However, it appears to be less successful in bottomland than upland habitats (Gayek and Quigley 2001). Abiotic factors that are likely to be important in facilitating or restricting the recruitment and success of *L. maackii* in wetland forests include inundation duration, water depth, and light levels.

The importance of light availability to *L. maackii* has been implicated in a number of studies. Studies from upland forest systems indicate that successful invasion of *Lonicera maackii* is associated with high light microhabitats such as forest edges and canopy gaps (Luken and Goessling 1995, Luken et al. 1995, Hutchinson and Vankat 1997). Its success may be due, in part, to its ability to take advantage of light-creating disturbances to a greater degree than native shrub species (Luken et al. 1997). Hidayati et al. (2000) demonstrated that higher percentages of *L. maackii* germinated in light than dark treatments, though the effects of partial shade were not examined. But despite being fairly shade intolerant (Luken et al. 1995), it has an extended leaf phenology that allows it to persist in the forest understory after canopy closure (McEwan et al. 2009).

In contrast to light requirements and tolerances, little appears to be known about the flood tolerance of *L. maackii*—a factor which most certainly restricts its potential habitat within wetland areas. The wetland indicator status of *L. maackii* has not been evaluated for its introduced range (NRCS 2016). However, in its native range, *L. maackii* occupies riparian habitat, which may be thought of as lying somewhere between the wetland and upland continuum. Two studies (Gayek and Quigley 2001, Swab et al. 2008) suggest a relationship between elevation and abundance of this woody, invasive

shrub *L. maackii*. According to both papers, which examined the distributional patterns of honeysuckle along upland-bottomland elevation gradients in Ohio, USA, *L. maackii* is less successful at low elevations. This was anecdotally attributed to a dense herbaceous understory in Gayek and Quigley (2001), which was thought to be a potential limitation to *Lonicera* sp. recruitment. However, Swab et al. (2008) did not identify dense herbaceous layers in their bottomland areas, and excluded competition with herbaceous vegetation in their bottomland areas as a possible driving mechanism for limited *Lonicera* sp. Recruitment there, and hydrology was proposed as the most probable driving factor for these observed trends. These studies strongly imply that flooding limits *L. maackii* germination, growth and/or survival.

The aforementioned studies suggest that wetland hydrology influences the distributional patterns of *Lonicera maackii*, but to my knowledge no published studies have used controlled experiments to determine the flood tolerance threshold for *L. maackii*. The importance of light availability on the success and distribution of *L. maackii* is better documented. However, no studies to my knowledge, have simultaneously attempted understand the combined main effects (and any interaction) of flooding and high vs. low light environments on any measure of *L. maackii* success. In this study, I manipulated light availability, flooding duration, and flooding depth in a fully crossed mesocosm experiment with the following goals: 1) to determine the main effects of light and flooding treatment variables on the growth and survival of *L. maackii* seedlings, 2) to identify any significant interactions between light, flooding depth and flooding duration treatments, and 3) to identify thresholds of flooding that appear to severely impede the growth and survival of *L. maackii*.

Methods

Experimental Design

We examined the effects of light and flooding characteristics expected to affect the growth and survival of *L. maackii* seedlings using a split-split plot design. The three manipulated, explanatory variables were: simulated canopy closure (2 levels), flooding depth (4 levels) and flooding duration (3 levels). Levels of explanatory variables at the plot, split-plot and split-split plot level are summarized in Fig. 3-1. Response variables were: change in plant height, change in leaf number, aboveground biomass (ABG), belowground biomass (BGB), root-shoot ratio (RSR) and days survived (see *Experimental Timelines and Protocols*).

Plant materials, selection and maintenance

First year seedlings were obtained from a naturalized population of *L. maackii* in a mesic upland forest (Cherokee Park) in Louisville, Kentucky. Seedlings were identified as such by presence of cotyledons or lack of woody stem tissue. The risk of accidentally collecting non-target species was minimized by ensuring that no other *Lonicera* species were present in the collection area. Seedlings of similar size (~3-6 cm) were transplanted into small peat pots using a common soilless potting mix (Fafard® Complete Potting Mix with slow-release fertilizer), and allowed to acclimate to their containers for approximately two weeks in an outdoor setting (part-sun/part-shade). At this point, seedlings were transplanted into larger plastic pots (9 cm by 9 cm by 13 cm depth) with a mix of 6 parts field soil to 1 part peat moss. The field soil was obtained from a nearby stand of bottomland hardwood forest in southwest Jefferson County, Kentucky, from the

Zipp soil map unit, which is characterized as a poorly drained silty clay loam (NRCS 2005). Seedlings were allowed to acclimate for an additional two weeks in the larger containers before the start of the experiment.

Size differences in seedlings were apparent after this acclimation period. In order to minimize the risk of confounding initial seedling height with experimental treatments, the following measures were taken. The initial height (one day prior to the beginning of the experiment) of each seedling was determined by measuring from the stem base to the apical meristem. Seedlings with signs of disease or extensive insect damage were discarded. The largest 144 seedlings (ranging from 10.1-21.2 cm in height) were sorted into six height classes with equal numbers of seedlings.

Each of the 24 treatment groups (2 light levels x 4 flood depth levels x 3 flood duration treatments= 24 treatment groups) was assigned one seedling from each of the 6 height classes (24 treatment groups x 6 seedlings= 144 seedlings). The six seedlings in each of the 24 treatment groups was randomly assigned to one of 6 experimental tanks. Thus each experimental tank received one seedling from each treatment group (6 tanks x 24 treatment groups=144 seedlings), and initial seedling size did not differ significantly among treatment groups or blocks.

Experimental timeline and protocols

Each of the six experimental units consisted of a single plastic tank measuring 70 x 45 x 20 cm (~63 L capacity). Tanks were arranged in a single row on top of a leveled wood riser (Fig. 3-2A) and filled with water to a depth of approximately 15 cm from the city water supply, a height sufficient to achieve the intended flooding depths. Overflow

holes were drilled just above this to prevent overflowing. To prevent a water temperature gradient from forming on different sides of the tank, a small submersible pump was placed centrally in each tank to circulate water. Each half of the tank was assigned one of two possible treatments, 80% or 30% canopy closure. This was manipulated by use of a shade cloth suspended on a cubical PVC frame (Figure. 3-2C).

Potted seedlings were subjected to three levels of flood duration (3 day, 10 day and 17 day) within each level of canopy closure. Potted seedlings assigned to a common flood duration (within each canopy closure level) were housed in a single crate made of galvanized steel mesh. Flooding depth was manipulated within the crates by creating PVC risers of 4 different heights (0 cm or no PVC, 5 cm, 10 cm, or 16 cm) such that potted seedlings were held at different heights relative to the tank water level: 1) *Upland* treatments entirely above water, 2) *moist* soil treatments with soil surface 5 cm above water, 3) *saturated* treatments with soil surface even with water, and 4) *inundated* treatments with soil surface 5 cm below water. Upland treatments served as controls and were never under water. The placement of the risers within each crate was randomized to avoid confounding flooding depth with any potential shading effects (e.g. a tall riser next to a short one could potentially cause shading to the seedling). Fig. 3-3 summarizes the structure of a single experimental tank, with the hierarchically manipulated treatments.

The experiment was initiated by placing seedlings assigned to each treatment group in water filled tanks, as described previously. Flood duration was manipulated by raising the appropriate crate above the water line using plastic risers after the specified interval (3 days, 10 days or 17 days after the initiation of the experiment). For example, on day 3, all 3-day flood duration treatments were moved above the water line in each

enclosure, and remained at this position for the remainder of the experiment. Fig. 3-4 illustrates the position of flooding depth treatments before and after crates were removed from the water. After the 17-day flood duration treatments were removed from the water, the tanks were emptied, and the crates were housed in the empty tank. During the final recovery period, plants were allowed to grow in the enclosures for an additional 23 days after all the flooding treatments were completed. The experiment lasted a total of 40 days from June 6 to August 15, 2010.

Plant heights (as measured from the stem base to the apical meristem) were recorded at days 0 (initial plant height), and at days 3, 10 and 17, when flood duration treatments were manipulated, and again at day 40 (conclusion of experiment). Additionally, counts of all leaves greater than 1 mm in length were made. Not all plants survived the 40 days of the experiment, and plants were regularly monitored for mortality, insect damage, and signs of stress at regular watering periods. At the end of the experiment the aboveground and belowground portions of each seedling were separated. Roots were cleaned by soaking them in water for several minutes, then gently rinsing them. However, heavy clay content of the soil often formed hard nodules that were difficult to remove from the plant without the loss of some root material. Aboveground portions (stems and leaves) and cleaned roots were oven dried at 55 °C for several days and weighed. Stems and leaves were weighed separately. Final aboveground biomass (AGB) of seedlings was calculated as the sum of oven-dried stem and leaf weights for each seedling, and final belowground biomass (BGB) was simply the oven-dried weight of the dried roots. The root-shoot ratio (RSR) of each plant was also calculated by dividing the root mass by the shoot mass for each individual.

During the experimental period, the local area experienced record-breaking summer heat with little rainfall. Therefore, water was checked daily and added as needed to maintain water levels at 15 cm and/or to maintain the temperatures under 30 °C. Ambient air temperature inside a single experimental enclosure was measured continuously throughout the study period with a Onset HOBO temperature data logger. Soil temperatures were measured in the 17 day flooding duration crates in Tanks 1 and 6 on eight dates near the beginning of the experiment. Near the end of the flooding treatments, on July 23rd 2010, the daily soil temperature fluctuations were measured by recording soil temperatures in 17-day flooding duration crates, for all tanks, at 4 time periods (9 am, 1 pm, 3 pm and 5 pm) on a single day. All these treatments were flooded according to their assigned flooding depths during this time.

The percentage of photosynthetic photon flux density (% PPFD) reaching plants on either side (80% or 30% shade) of the enclosures was estimated on two days near the beginning and end of the experiment. A LI-COR LI-250 photometer was used to take readings of photosynthetic photon flux density (PPFD in $\mu\text{mol m}^{-2} \text{s}^{-1}$, a measurement of photosynthetically active radiation, in the 400-700 nm wavelength range) under the open sky above each enclosure, and under each side of all 6 enclosures. These readings were taken at four times (9 am, 11 am, 1 pm, 3 pm and 5 pm) on July 23rd, 2010. The effectiveness of shade cloth in reducing incident PPFD in enclosures was estimated by calculating % PPFD as $\frac{P_a}{P_o} \times 100$, where P_a and P_o are the measurements of PPFD above and inside of the enclosures, respectively. Mean % PPFD at each time period was calculated by averaging % PPFD across tanks (n=6) for 80% or 30% shade treatments at

each time period. These values were then averaged within each light treatment to estimate mean % PPFDF for each light treatment over the course of an entire day.

Throughout the experiment, seedlings that were at least partially in water (moist, saturated and inundated treatments) did not receive additional water. Upland treatments, and other treatments that had been raised out of the water, received supplemental water. Upland plants were initially watered to 50% soil moisture by weight (100% soil moisture being equivalent to the soil water holding capacity). These plants were weighted approximately 3 times each week. When soil moisture dropped below 30% (by weight), water was added to achieve 50% soil moisture. After moist, saturated and inundated treatments had been removed from the water (at 3, 10 and 17 days), they were watered identically to upland treatments for the remainder of the experiment.

There were several rainfall events during the experiment. During some of these, rainfall was prevented from entering enclosures by covering them with clear plastic sheets. However, eight rainfall events resulted in rain entering the enclosures. The different types of shade cloth used on either side of the enclosures made it likely that rainfall would differ between 30% and 80% shade treatments. To correct for this effect, two plastic cups were attached at opposite ends on each side of every enclosure (2 cups/side x 2 sides/enclosure = 4 cups/enclosure). After a rain event, the amount of water in each cup was weighed, and the average amount of rainfall on each side of the enclosure calculated. To calculate rainfall in units of mass per ground surface area (R_{sa} in units of g/cm^2), we used the formula $R_{sa} = \frac{R_m}{A}$, where R_m was the average amount (in g) of event rainfall in cups on each side of an enclosure, and A was the surface area of the mouth of the collection cup (in cm^2). The side of the enclosure with less rainfall was

determined to have a deficit, which was the difference in R_{sa} between the two sides of each enclosure ($\Delta R_{sa} = |R_{sa_1} - R_{sa_2}|$). The deficit of rainfall per pot (ΔR_{pot} in g/pot) was calculated as $\Delta R_{pot} = \Delta R_{sa} * A$. The calculated ΔR_{pot} was added to each upland or raised treatment on the side of the enclosure with the deficit of rainfall.

Later in the experiment, after all treatments had been raised out of the water, it was observed that pot weights could vary more within enclosure sides, than between enclosure sides, after rainfall events. These differences were possibly due to sustained effects of previous flooding treatments, differences in evapotranspiration between plants, and effects of the experimental structures themselves. For instance, water tended to pool on the surface of the 80% shade cloth, and drip selectively on certain pots. After this was discovered (on the 24th day of the experiment) we changed how we dealt with correction for rainfall. Instead of focusing on the differences in rainfall between sides, we focused on minimizing the variability in pot weights within each side of the enclosure. This made sense, because all plants had been removed from standing water at this point and we thus expected the weights of pots to be more similar. To achieve this correction, we weighed all pots, and calculated the mean pot weight for each side of enclosures. Pots that fell 30g or more below the mean pot weight (per light or shade treatment of each tank), were watered up to the mean pot weight. This reduced the variance and range of pot weights immediately following rainfall events.

Statistical Analyses

Vertical Growth

Growth curve analysis was used to test the hypothesis that the seedling growth response (rate of increase in plant height) is affected by light, flooding duration and flooding depth treatments, and to test for interactions in these effects. This was accomplished by constructing a linear mixed model with repeated measures and was implemented with the MIXED procedure in SAS 9.4.

To examine the effects of explanatory variables on vertical plant growth, the change in plant height over time was modeled as the continuous response variable (R) using Equation 1, where H_i equals the plant height at day I and H_o equals the initial plant height at the beginning of the experiment.

$$R = H_i - H_o \quad \text{Equation 1}$$

The explanatory variables were *number of days*, *light* (shade cloth treatment), *flooding duration*, *flooding depth*, *block*, and *plant ID*. Number of days was modeled as a continuous variable, where values of the response variable were calculated for 0, 3, 7, 10 and 40 days. Light was modeled as a fixed factor with two levels: simulated open canopy (30% shade cloth) and simulated closed canopy (80% shade cloth). Flooding duration was modeled as a continuous variable with possible values of 3, 10 and 17 days. Flooding depth was modeled as a continuous variable with possible values of 0, 1, 2, and 3, which correspond, respectively, to the ranked flooding depths of *upland (no flooding)*, *moist*, *saturated* and *inundated* described previously. The variable, *block*, was treated as a random effect with values 1-6, each corresponding to a replicate experimental tank.

Finally, a unique identifier for each seedling, *plant ID*, was modeled as the subject effect in a repeated measures design, using autoregressive-1 (AR(1)) covariance structure. This covariance structure is commonly used with repeated-measures time series data to handle autocorrelation of within-subjects error terms.

To make the analysis sensitive to a wide range of possible effects, a polynomial model was used. Terms up to degree two for *number of days*, degree two in *flooding depth* and *flooding duration* (combined), and one degree in *light* were included in the initial model to allow detection of any significant non-linear responses. Thus, no term exceeded degree 5.

The full, initial model is described below (Equation 2), where $R_{(t,u,v,w)}$ is the change in plant height over time (from Equation 1) modeled as a polynomial function of time (t), flooding depth (u), flooding duration (v) and light treatments (w), and $b_i(u,v,w)$ is the coefficient of t raised to the i th degree. Since t was modelled up to degree two, coefficients for t and t^2 ($b_1(u,v,w)$ and $b_2(u,v,w)$, respectively) were modelled as defined in Equation 3 and Equation 4; subscripts indicate the polynomial degree of factors u , v , and w in each term for flooding depth, flooding duration and light treatment, respectively. For instance, $b_{1,0,0,0}$ (in Equation 2) denotes the coefficient of t when the degree of $u=0$, $v=0$ and $w=0$ (e.g. main effects of *ndays*). Main effects of flooding duration, flooding depth and light were not included, because these variables can only affect the response variable as number of days increases.

$$R_{(t,u,v,w)} = b_1(u,v,w)*t + b_2(u,v,w)*t^2$$

Equation 2

$$b_1(u,v,w) = b_{1,0,0,0} + b_{1,1,0,0}u + b_{1,0,1,0}v + b_{1,0,0,1}w + b_{1,1,1,0}uv + b_{1,2,0,0}u^2 + b_{1,0,2,0}v^2 + b_{1,1,0,1}uw + b_{1,0,1,1}vw + b_{1,1,1,1}uvw + b_{1,2,0,1}u^2w + b_{1,0,2,1}v^2w$$

Equation 3

$$b_2(u,v,w) = b_{2,0,0,0} + b_{2,1,0,0}u + b_{2,0,1,0}v + b_{2,0,0,1}w + b_{2,1,1,0}uv + b_{2,2,0,0}u^2 + b_{2,0,2,0}v^2 + b_{2,1,0,1}uw + b_{2,0,1,1}vw + b_{2,1,1,1}uvw + b_{2,2,0,1}u^2w + b_{2,0,2,1}v^2w$$

Equation 4

Runs of the full model produced residuals that were highly skewed to the right. Additionally, plots of residuals vs. predicted values revealed a dramatically wedge-shaped pattern, indicating heteroscedasticity. Using a transform of the response variable was found to produce normally distributed residuals and satisfied the assumptions of homogeneity of variance when residuals were plotted against explanatory variables. This transform is shown in Equation 5, where Δh is the plant height on a given day minus the plant height at day 0. Since some values of Δh were negative, and the natural log is not defined for negative values (which occurred if the seedling became necrotic), a value of 3 was added to Δh before taking the natural log, and then $\ln(3)$ subtracted from this value.

$$R = \ln(\Delta h + 3) - \ln(3)$$

Equation 5

By definition, this transform results in a *response* value of 0 for all plants when *number of days* = 0. Therefore, an intercept of zero was set, and only values of 3, 10, 17

and 40 were used for *number of days*. Positive *response* values when *number of days*=3, 7, 10 or 40 indicate positive growth, and negative values indicate negative growth (e.g. dieback).

Backward elimination using Akaike's Information Criterion (AIC) was used to reduce the number of terms and produce a more parsimonious model. Terms of the highest degree were sequentially removed one at a time from the model and AIC computed. A term was omitted from the model if its removal lowered AIC by 2 or more units. If the removal of a term increased AIC or decreased AIC by less than 2 units, it was retained in a reduced model. This reduced model was then subject to one more round of backward elimination using the same elimination criteria, resulting in a final reduced model.

Leaf Number Response

A nearly identical procedure was used to develop a model testing the effects of the same suite of explanatory variables on the increase in leaf number over time. Similar to plant height, leaf number is a continuous variable that was measured where number of days=0, 3, 10 17, or 40 days). The initial, full model was identical to that shown in Equation 2, where the variable $R_{(t,u,v,w)}$ takes the values shown in Equation 6. Here, Δn is the number of leaves at day 3, 10, 17 or 40 minus the number of leaves at day 0 (i.e. the change in leaf number). In order to produce normally distributed model residuals, and meet the assumptions of equal variance, Δn was transformed, and a constant (40) was used to avoid taking the natural log of a negative number. The "unstructured" variance structure (UN) was used in place of AR(1).

$$R = \ln(\Delta n + 40) - \ln(40)$$

Equation 6

Backward elimination of terms to produce a simplified model of the leaf number response was performed as described previously for the vertical growth model using AIC as the elimination criterion.

Biomass Data

The effects of light, flooding depth and flooding duration on AGB were modeled with a mixed-linear model using the PROC MIXED procedure in SAS 9.4. Seedlings that died before the end of the experiment were omitted from this analysis; failure to promptly remove seedlings from the field after death made biomass data from these treatments unusable. The inundated treatments were most impacted by these omissions, and therefore biomass data from all inundated seedlings was omitted from the analysis due to the large imbalance in sample size this created. Fixed effects of light and flooding variables included all one-, two- and three-way interactions. Experimental block and initial plant height were included as random effects using the variance components covariance structure. Identical specifications were used for two additional models using BGB and RSR as response variables.

Model residuals were examined for normality and homoscedasticity and the response variables were transformed, if necessary, to improve data fit. BGB was transformed by taking the square root, and RSR by taking the natural log.

Results

Environmental Factors

Average temperatures during the study period of 2010 (June-August) were the second highest on record in Kentucky (NCEI 2016). The mean daily air temperature inside the monitored enclosure (from July 10th 2010-August 15, 2010) ranged from 21.77 °C to 33.42 °C, averaging 28.17 ± 0.35 °C. The mean daily minimum and maximum were 22.26 ± 0.04 °C and 36.25 ± 0.44 °C, respectively

Soil temperature displayed a temperature gradient that directly paralleled differences in flooding depth (see Fig. 3-5), with unflooded soils being the hottest, and inundated the coolest. The most complete record of daily soil temperature variations was made on the fourth hottest day of the experimental period (7/23/10), when ambient air temperature averaged 30.89 ± 0.59 °C (range: 25.56-37.44 °C). Based on soil temperature data collected at four time points on this day, unflooded soil temperatures showed the greatest daily temperature variation, with the mean temperature varying 8.37 °C and 6.07 °C for 30% and 80% shade treatments, respectively. The mean temperature of inundated soils fluctuated approximately 5 °C for both light treatments.

Photometer readings made the same day estimate mean % PPFD over the course of a day as $55.87 \pm 0.03\%$ and $17.94 \pm 0.01\%$ for 30% and 80% shade treatments, respectively.

Seedling Growth: Vertical Growth

No terms containing light as a factor were retained in the final model using backward elimination. Therefore all seedling data from both light treatments were pooled for subsequent analyses. The final model retained six terms relating number of days, flooding depth treatment and flooding duration to change in plant height.

Fig. 3-6 illustrates the growth curves for all treatment combinations using mean values of the observed and predicted response variable. As shown, the observed growth response closely approximates the predicted values from the model; thus the chosen regression model appears to accurately describe the plant growth response.

Table 3-1 summarizes the results of the final polynomial regression where change in plant height (transformed variable) was used as the response variable. Statistically significant p-values for coefficients of first and second order terms for number of days ($nDays$, $p < 0.0001$ and $nDays^2$, $p < 0.0001$) shows that seedlings exhibited an increase in height over time, and this response was non-linear.

Significant effects of flooding duration, flooding depth and interactions between these terms are indicated by several tests (Table 3-1). The effects of flooding depth on linear growth ($nDays * flood\ depth$) were found to be significant and negative ($p < 0.0001$). Additionally, the interaction effect of coefficients for number of days, flooding depth, and flooding duration was found to be statistically significant and negative ($nDays * flood\ depth * flood\ duration$, $p = < 0.0001$). This indicates that flooding depth and flooding duration had linear, non-additive effects on linear plant growth (change in height) over

the course of the experiment. A negative coefficient for this interaction indicates that increasing values of flood duration or flooding depth (by level), or a combination of the two, have negative effects on vertical plant growth.

The panels in Figs. 3-6 through 3-8 illustrate the effects of flooding depth at different flooding durations on the plant height response variable over the course of the experiment. At flood durations of 3 days (Fig. 3-7), treatments of all flooding depths showed a positive net increase in height over the 40 day experimental run with upland control and moist treatments maintaining higher growth rates than saturated and inundated treatments.

At longer flooding durations, the upland controls and moist treatments maintained positive growth, while the saturated and inundated treatments experienced periods of negative growth (e.g. dieback). Despite periods of negative growth within the 10 day flooding treatments, the saturated seedlings showed positive net growth over the course of the experiment, while the inundated seedlings experienced net dieback (Fig. 3-8).

Treatments with the longest flooding duration (17 days) showed the most dramatic differences in growth rate between flooding depth treatments (Fig. 3-9). Growth curves of these treatments clearly show the effects of the flooding gradient; control, moist, saturated and inundated seedlings had the highest to lowest growth rates, respectively. Seedlings subjected to moist conditions for 17 days maintained positive growth throughout the course of the experiment, intermediate between those of upland controls and seedlings saturated for 17 days.

Seedlings saturated for 17 days, similar to seedlings saturated or inundated for 10 days, experienced a period of average dieback from 10-17 days, but exhibited modest growth during the recovery period (17-41 days). In contrast, seedlings inundated for 17 days experienced net dieback from 10-17 days, and did not survive the recovery period.

Two second-order terms ($nDays*nDays*Flood\ Depth$ and $nDays*nDays*Flood\ Duration*Flood\ Depth$) were found to be significant and positive indicating that both flooding depth and the interaction between flood depth and flood duration affect the shape of the growth curve.

A significant positive effect of flood duration on plant growth ($nDays*Flood\ Duration$, $p=0.0271$) was indicated by the model, but is apparent in only one case. Plants receiving 10 days of moist “flooding” outperformed upland control which were never flooded (flood duration=0 days). This could be explained by constant moisture providing seedlings with an advantage over upland seedlings during period when temperatures were high. Considering the significant negative coefficient for the term $nDays*sublevel*duration$, it appears that the positive effects of increasing flooding duration on plant growth are overshadowed by the interaction effects between flood duration and flood depth.

The subject effect (the ID of an individual seedling) was significant ($p<0.0001$), indicating that there was variation in the plant growth response due to individual differences in seedlings ($p<0.0001$). Experimental block was not found to have a statistically significant effect on plant height response ($p=0.07$).

Seedling Growth: Leaf Number

Similar to the vertical growth model, no terms containing light were retained in the final model for change in leaf number. Therefore, all seedling data were pooled for subsequent analyses. The final model retained five terms involving interactions between number of days, flood duration and flood depth (Table 3-2).

Fig. 3-10 illustrates a close correspondence between response curves generated using observed and predicted values for change in leaf number, one indicator of good model fit. The term $nDays$, but not $nDays^2$, was retained in the model, and was highly significant ($p < 0.0001$), indicating that change in leaf number (Δ leaf number/day) followed a pattern of linear increase in the absence of other variables, as can be seen for the unflooded control treatment in Fig. 3-10 (upper left corner, $Flood\ Duration = 0$, $Flood\ Depth = 0$ (unflooded)).

As with the vertical growth models, tests of significance indicated that flood duration had significant positive effects on the change in leaf number over time ($nDays * flood\ duration$, $p < 0.0001$), but that this effect was moderated by a negative interaction with flood depth ($nDays * Flood\ Depth * Flood\ Duration$, $p < 0.0001$). Thus the effects of flooding depth on the change in leaf number over time vary with flooding duration.

Figs. 3-10 through 3-12 depict the change in leaf number over the duration of the experimental period for different flooding depths, within each flood duration. As with the response curves for vertical growth, little difference between flooding depth treatments is evident with 3 days of flooding (Fig. 3-11) and the net mean change in leaf

number was positive for treatments of all flooding depths over the course of the experiment. Differences between flooding depth treatments became apparent at flooding durations of 10 days (Fig. 3-12). There was a steady loss of leaves from days 3-17 in seedlings saturated or inundated for 10 days, while moist treatments maintained an increase in leaf number. From 17-40 days, however, these seedlings showed signs of recovery, exhibiting a slow increase in leaf number. It should be noted that 66% of seedlings subjected to 10 day inundation died before the end of the experiment (see following *Plant Survival* section); thus the estimates of change in leaf number during latter time points are based on a smaller sample size of surviving seedlings only. Similar to 10 day flooding treatments, seedlings saturated or inundated for 17 days showed a steady decline in leaf number from days 3-17, with saturated seedlings showing signs of recovery between days 17-41 (Fig. 3-13).

Plant Survival

The number of days lived for moist and saturated treatment groups remained similar to the upland control (38.6 ± 1.0 days), regardless of flood duration). However, seedlings inundated for 10 or 17 days had noticeably shorter lifespans than all other treatments (29.8 ± 2.9 and 27.2 ± 1.5 days, respectively). No seedlings inundated for 17 days survived past 17 days. Mean days lived, proportion surviving, and other statistics are summarized by all combinations of flood duration and flood depth in Table 3-3.

Biomass

Light levels appeared to be of primary importance in biomass determination and root-shoot ratio. Light treatment was a significant predictor of AGB ($p < 0.0001$; Table 3-

4), with mean AGB being higher in all 30% shade treatments, at all combinations of flood depth and duration (Fig. 3-14). AGB generally declined with increasing flood duration and depth, but this response was not monotonic, and varied with light level. For instance, while AGB generally decreased with flood duration for 80% shade treatments, moist treatments in 30% shade showed a non-monotonic response to increasing flood duration (Fig. 3-15). Thus, the relative impact of flooding variables on AGB appears to vary somewhat with light treatment, as indicated by significant p-values for the interaction terms *Flood Duration*Light* and *Flood Duration*Flood Depth*Light*.

Similarly, BGB was significantly higher in 30% shade than 80% shade treatments (Table 3-5), and this trend was evident across all combinations of flood duration and depth. However, differences between 30% and 80% shade appeared more pronounced in unflooded controls than moist or saturated treatments (Fig. 3-16), which likely accounts for the significance interaction between flood depth and light ($p=0.0234$). A significant negative interaction ($p=0.041$) between flood depth and duration indicates BGB declines with increasing values of either, or both of these variables, and that their combined effect on BGB is non-additive.

The RSR of seedlings was only related to light (Table 3-6), with significantly higher mean RSR in 30% shade than 80% shade treatments. This indicates a higher biomass allocation to belowground biomass in the higher light environment. However, this trend was not consistent across all combinations of flooding depth and duration; treatments with moist conditions for 10 or 17 days did not show this trend (Fig. 3-17). Differences in RSR between light treatments were most obvious with unflooded controls.

Neither experimental block, nor initial plant height were significant covariates in any of the models.

Discussion

The results of this study are meant to serve as a starting point for gauging the potential success or failure of *Lonicera maackii* establishment in wetland areas under a range of hydrologic conditions. Brief inundation or saturation of seedlings (3 days) did not appear to have large impacts on seedling growth curves, and did not significantly reduce the number of days lived. Inundation and saturation of seedlings for 10 to 17 days appears to have a markedly negative effect on honeysuckle seedlings as shown by slow vertical growth or dieback and loss of leaves. Seedlings exhibited some ability to recover from flooding stress, once drawdown had occurred; seedlings saturated or inundated for 10 days or saturated for 17 days exhibited a net increase in height and leaf number during days 17-40 (no seedlings flooded during this time), after previously showing decreases in these variables. Despite negative growth effects on saturated seedlings, only inundated seedlings demonstrated a significantly reduced lifespan compared to unflooded controls.

Effects of light treatments on plant growth were evident in biomass data, but not vertical stem growth or leaf number increase. The lack of significant light effect on stem growth and leaf number was unexpected, considering results from (Luken et al. 1997) in which *L. maackii* plants were grown at three light levels (1%, 25% and 100% of PPFD). In their study, *Lonicera* plants achieved maximum relative stem growth rates and had higher leaf numbers at 100% PPFD, and demonstrated the ability to acclimate and increase photosynthetic rates with greater light availability. Contrary to this, the experimental data from our study showed generally higher stem growth rates in the low light treatments. The relatively short time frame of this experiment (5.7 weeks) may explain this apparent lack of light effect on vertical growth and leaf number. In a different study by Luken et al. (1995), forest-grown seedlings were transplanted to shadehouses providing 5%, 25% and 100% of PPFD, with maximum stem growth initially associated with the 25% PPFD treatments in the first 3 weeks of the experiment. However, this pattern shifted later in the experiment, with seedlings attaining maximum stem growth in 100% PPFD treatments in weeks 3-7, as seedlings produced new leaves with higher carbon capture abilities. Our experiment lasted under 6 weeks and examined stem growth integrated over the entire experimental period, thus we may not have had ample time to see a positive growth response to enhanced light.

Both aboveground and belowground biomass were significantly higher in high light treatments, which agrees with findings from Luken et al. (1997, 1995). Thus, while light did not significantly impact vertical stem growth or leaf number over the experimental period, higher biomass and higher root-shoot ratios in high light treatments suggests that seedlings may have responded to higher light levels with more horizontal

growth and/or thicker leaves and investment in belowground resources than more shaded seedlings. However, we did not measure horizontal growth or leaf thickness, and these suggestions are speculative. Significant main effects of light on root-shoot ratio indicate that seedlings grown in the more shaded environment generally allocated more biomass aboveground. This finding is also confirmed by Luken et al. (1997), who attributed this as a “light-seeking response” by a shade-intolerant plant that contributes to its ability to overgrow slower growing species. Interactions between light and flooding variables were significant predictors of seedling biomass (ABG and BGB) and suggest that flooding characteristics may moderate the relationship between plant biomass and light. The lack of significant interactions between light and flooding variables RSR suggests that the biomass allocation of *Lonicera maackii* seedlings is similar across flooding depths and durations.

Caveats

Average temperatures during June-August of 2010 were the second warmest on record in Kentucky. Despite measures to keep soil and water temperatures at a minimum (i.e. daily refreshment of tank water and surrounding pots with reflective foil), because of the relatively small size of the pots and tanks used, soil and water temperatures were likely to exceed those encountered in a natural setting—particularly during peak daylight hours. This may have adversely affected plants in multiple ways. Heat-stress can negatively affect nearly all aspects of plant performance, including growth, development and metabolism (Hasanuzzaman et al. 2013). High microbial respiration, combined with high plant oxygen demand and lower dissolved oxygen solubility in warm, water-logged soils may also have exacerbated the anaerobic stresses typical of wetland soils. Soil

pathogens also may benefit from higher soil temperatures, increasing susceptibility to root rot. Since we have no basis for assessing how much these factors contributed to plant performance, direct extrapolation of these results to natural systems must be considered with caution.

As a result of experimental design, plants with shorter flood durations had longer recovery periods after the simulated drawdown. However, if the experimental design were altered to standardize the length of the recovery, then the experimental periods for different treatments would differ in length. Alternately, standardizing the length of recovery and timing of drawdown would cause total experimental length to vary with flooding duration and force the initiation of experimental flooding to begin on different days. This could potentially create experimental artifacts, since the seasonal timing of flooding events may influence plant growth (Robertson, Bacon, & Heagney, 2001). Since the effects of seasonal flood timing are not questions addressed by this study, we chose to synchronize flooding events, and allow recovery periods to vary in length.

Implications

The impact of *L. maackii* on regional forests appears to have broad implications on ecosystem functions and services, with no established solutions for its effective and efficient eradication on a large scale. Due to the presence of seasonally high water tables, forested wetlands appear to be less susceptible to *L. maackii* dominance than adjacent upland systems. However, as seen in the last chapter, this species is capable of invading wetland areas and establishing itself as the dominant shrub species. Considering the greater variation in regional weather patterns that are predicted to occur as a result of

climate change, the vulnerability of these systems to *L. maackii* incursion may change. Specifically, summer drought conditions may be more frequent in this region (mid-western United States) because of warmer summer temperatures and increasing variability in precipitation patterns (Field, 2007), which may potentially make a greater area of bottomland hardwood forest favorable for *Lonicera* sp. colonization. This information should be relevant to restoration practitioners who seek to recreate natural microtopography and disturbance regimes of wetland forests, while minimizing the abundance of exotic invasive species.

There is also some limited evidence to suggest that *L. maackii* may enhance stand transpiration, and thus could contribute to shortened hydroperiods in ephemeral wetland areas. In a case study comparing stand transpiration in depressional wetlands with relatively high and low basal area of *L. maackii*, (Boyce et al. (2012)) estimated that approximately 10% of stand transpiration was due to *L. maackii*. Because *L. maackii* appeared to be adding to, not replacing, the native shrub layer, they suggested that this species may actually be increasing evapotranspiration in these wetlands. This scenario has the potential to create a positive feedback loop where *L. maackii* alter wetland hydrology, creating drier conditions, and thus facilitating its spread in wetland systems.

Conclusions

The growth of *Lonicera maackii* seedlings in this study was negatively impacted by flooded (saturated or inundated) conditions in this study. This coincides with previous studies indicating that the distribution of *L. maackii* is limited by standing water and that flooding has a negative impact on *L. maackii* in at least one life stage (also see

Chapter II of this manuscript). However, seedlings exhibited some ability to recover from flooding stresses when subjected to saturation for up to 17 days or inundation up to 10 days. This was in spite of near record high air temperatures and periodically high soil temperatures. These results provide evidence for some resiliency to flooding stress ability to become established in intermittently saturated or inundated areas. Therefore, factors that may alter wetland hydrology and shorten hydroperiods can facilitate the invasion of this exotic species in wetland areas. These factors include the urban heat island effect and climate change (which may increase stand evapotranspiration (Jackson et al. 2001)), as well as direct human modification of wetland areas.

Table 3-1. Model coefficient estimates and significance values for final mixed linear model testing effects of linear and non-linear variable combinations on plant growth response (change in plant height). Coefficient estimates are not interpretable in the original scale of measurement, since they are based on transformed data.

	Effect	Estimate	Standard Error (+/-)	DF	t Value	P > t
Fixed Effects	<i>nDays*Flood</i>	-0.0010	0.0001	532	-7.79	<.0001
	<i>Depth*Flood Duration</i>					
	<i>nDays*nDays*Flood</i>	0.0003	0.0000	532	7.07	<.0001
	<i>Depth</i>					
	<i>nDays*Flood Depth</i>	-0.0131	0.0021	532	-6.23	<.0001
	<i>nDays*Flood Duration</i>	0.0008	0.0002	532	3.94	<.0001
	<i>nDays*nDays</i>	-0.0011	0.0001	532	-14.30	<.0001
	<i>nDays</i>	0.0807	0.0038	532	21.03	<.0001
		Estimate	Standard Error (+/-)		Z Value	p
Random Effects	<i>Block</i>	0.02797	0.01893		1.48	<.0001
Repeated-measures	Subject= <i>Plant Id</i>	0.7558	0.02649		28.53	<.0001

Table 3-2 Model coefficient estimates and significance values for final mixed linear model testing effects of linear and non-linear variable combinations on change in leaf number. Coefficient estimates are not interpretable in the original scale of measurement, since they are based on transformed data.

Effect		Estimate	Standard Error (+/-)	DF	t Value	p
	<i>nDays*Flood Depth*</i>	-0.0002	0.0006	530	-0.36	0.7184
	<i>Flood Depth</i>					
	<i>nDays*Flood Depth</i>	0.0004	0.0018	530	0.25	0.8044
	<i>nDays*Flood Duration</i>	0.0008	0.0002	530	4.26	<.0001
	<i>nDays</i>	0.0061	0.0008	530	7.57	<.0001
		Estimate	Standard Error (+/-)		Z Value	p
Random Effects	<i>Block</i>	0.0014	0.0010		1.46	0.0724

Table 3-3. Mean, minimum and maximum days lived for all combinations of flooding depth and flooding duration (light treatments pooled). Proportion surviving at the end of the experiment (Day 40) is also shown.

Flood Duration	Flood Depth	N	Mean Days Lived	Standard Error (+/-)	Minimum	Maximum	Proportion Surviving
0	Unflooded (Control)	36	38.6	1.0	14	40	0.94
3	Moist	12	40.0	0.0	40	40	1.00
	Saturated	12	38.4	1.6	21	40	0.92
	Inundated	12	40.0	0.0	40	40	1.00
10	Moist	12	40.0	0.0	40	40	1.00
	Saturated	12	39.8	0.3	37	40	0.92
	Inundated	12	29.8	2.9	14	40	0.33
17	Moist	12	36.5	2.4	14	40	0.83
	Saturated	12	40.0	0.0	40	40	1.00
	Inundated	12	27.2	1.5	21	37	0.00

Table 3-4. Model coefficient estimates and significance values for mixed linear model testing effects of fixed (main and interaction effects) and random effects on aboveground biomass of seedlings, as measured at the end of the experiment. Significant p-values are in bold.

	Parameter	Light	Estimate	Standard Error (+/)	DF	t Value	p
Fixed Effects	Intercept		0.1337	0.1192	92.4	1.12	0.2651
	<i>Light</i>	Light	0.3389	0.0651	88.4	5.20	<.0001
		Shade	
	<i>Flood Depth</i>		-0.0199	0.04967	88.2	-0.40	0.6903
	<i>Flood Duration</i>		0.0075	0.0095	88.1	0.78	0.4372
	<i>Flood Duration*Light</i>	Light	0.0418	0.0144	88.6	2.90	0.0047
		Shade	0
	<i>Flood Depth*Light</i>	Light	-0.0832	0.0723	88.4	-1.15	0.2525
		Shade	0
	<i>Flood Depth*Flood Duration</i>		-0.0113	0.0068	88.1	-1.67	0.0976
	<i>Light*Flood Duration*Flood Depth</i>	Light	-0.0225	0.0099	88.4	-2.28	0.0251
		Shade	0
			Estimate	Standard Error (+/-)		Z Value	p
Random Effects	<i>Block</i>		0.003288	0.003515		0.94	0.1748
	<i>Initial Plant Height</i>		0.002789	0.004000		0.70	0.2428

Table 3-5. Model coefficient estimates and significance values for mixed linear model testing effects of fixed (main and interaction effects) and random effects on belowground biomass of seedlings, as measured at the end of the experiment. Significant p-values are in bold.

	Parameter	Light	Estimate	Standard Error (+/-)	DF	t Value	p	
Fixed Effects	Intercept		-2.1277	0.2237	5	-9.51	0.0002	
	<i>Light</i>	Light	0.6536	0.1257	87	5.20	<.0001	
		Shade	0	
	<i>Flood Depth</i>		0.1196	0.0959	87	1.25	0.2156	
	<i>Flood Duration</i>		0.0219	0.0184	87	1.19	0.2383	
	<i>Flood Duration*Light</i>	Light	-0.0244	0.0290	87	-0.84	0.4020	
		Shade	0	
	<i>Flood Depth*Light</i>	Light	-0.3222	0.1396	87	-2.31	0.0234	
		Shade	0	
	<i>Flood Depth*Flood Duration</i>			-0.0270	0.0131	87	-2.07	0.0413
		<i>Light*Flood Duration*Flood Depth</i>	Light	0.0257	0.0194	87	1.32	0.1887
		Shade	0	
			Estimate	Standard Error (+/-)		Z Value	p	
Random Effects	<i>Block</i>		0.003260	0.0074		0.44	0.3306	
	<i>Initial Plant Height</i>		0.003891	0.0057		0.68	0.2477	

Table 3-6. Model coefficient estimates and significance values for mixed linear model testing effects of fixed (main and interaction effects) and random effects on the root-shoot ratio of seedlings, as measured at the end of the experiment. Significant p-values are in bold.

	Parameter	Light	Estimate	Standard Error (+/)	DF	t Value		
Fixed Effects	Intercept		-1.2244	0.1578	3.01	-7.76	0.0044	
	<i>Light</i>	Light	0.3419	0.1087	89.5	3.15	0.0022	
		Shade	0	
	<i>Flood Duration</i>		0.0125	0.0162	89.3	0.77	0.4404	
	<i>Flood Depth</i>		0.1231	0.0840	89.4	1.47	0.1463	
	<i>Flood Duration*Light</i>	Light	-0.0314	0.0243	90.5	-1.30	0.1984	
		Shade	0	
	<i>Flood Depth*Light</i>	Light	-0.2236	0.1217	89.6	-1.84	0.0696	
		Shade	0	
	<i>Flood Duration*Flood Depth</i>		-0.0133	0.0114	89.4	-1.17	0.2470	
	<i>Flood Duration*Flood Depth*Light</i>	Light	0.0277	0.0166	89.9	1.67	0.0992	
		Shade	0	
				Estimate	Standard Error (+/-)		Z Value	p
	Random Effects	<i>Block</i>		0.00219	0.0055		0.40	0.3454
<i>Initial Height</i>			0.0001	0.0004		0.40	0.3454	

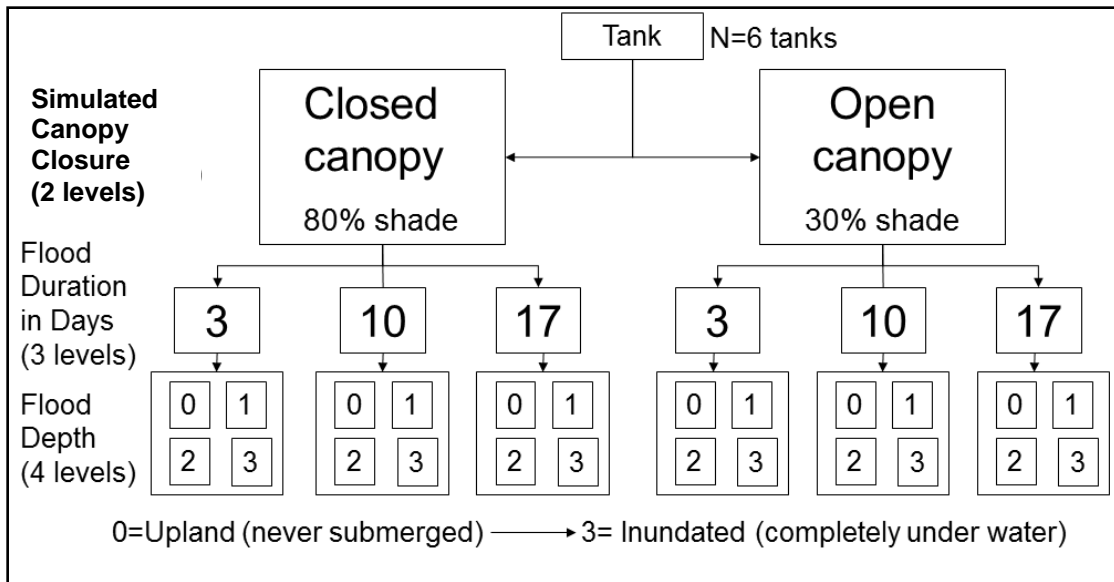


Figure 3-1. Graphical summary of split-split plot experimental design, showing nested structure of variables. Four levels of flood depth are nested within three levels of flood duration, which are both nested within two levels of simulated canopy closure. Each one of six tanks contained all these treatments.



Figure 3-2. Outdoor mesocosm construction. A. The six experimental tanks arranged on a level, wooden riser. B. Seedlings arranged within a single experimental tank, without surrounding shade cloth enclosure. Metal crates on each side of the tank (three per side) correspond to the three different flooding durations, each containing four seedlings (one of each flooding depth). C. A completed mesocosm with a shade cloth enclosure. Each shade cloth enclosure bisected the tank into two light treatments (30% and 80% shade).

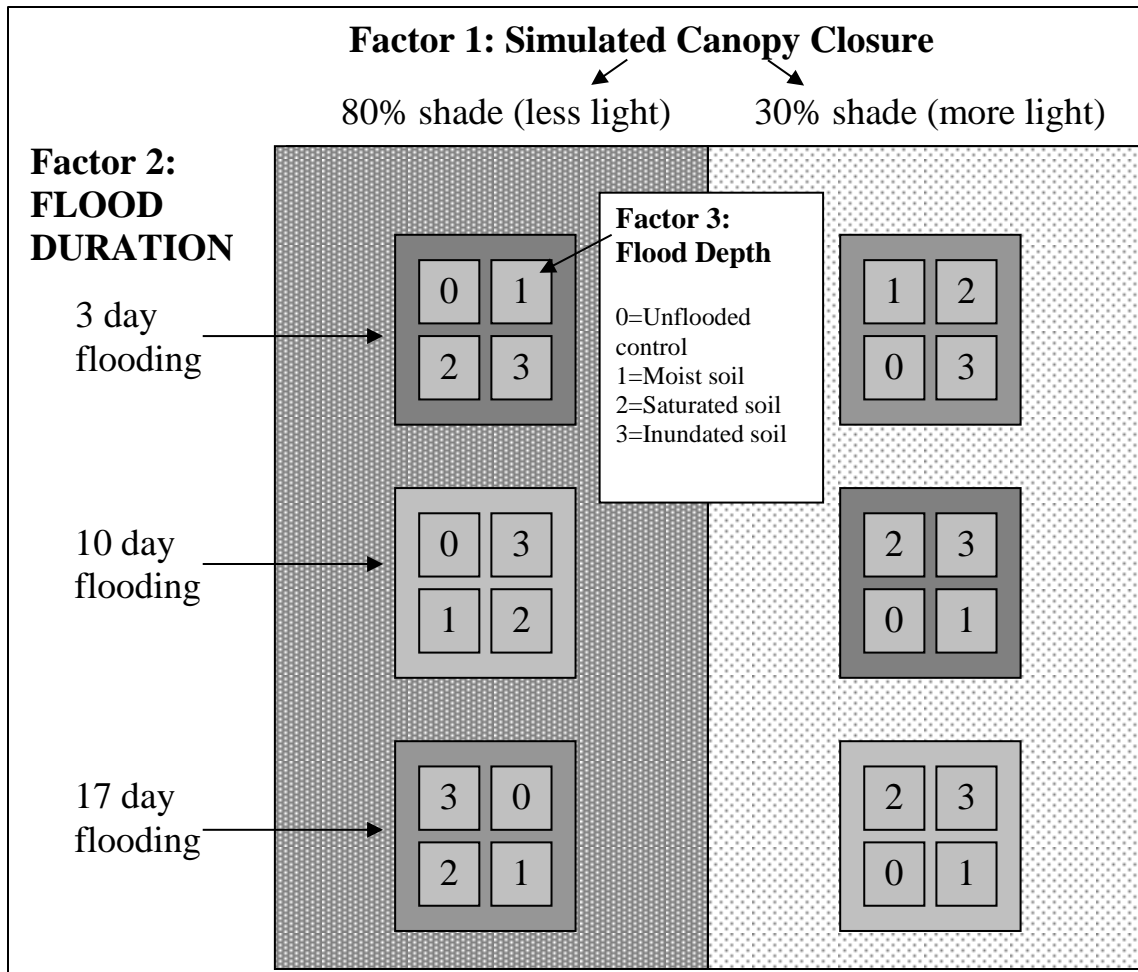


Figure 3-3. Graphical summary of split-split plot design for each experimental tank (n=6). This should be interpreted as a top-down view.

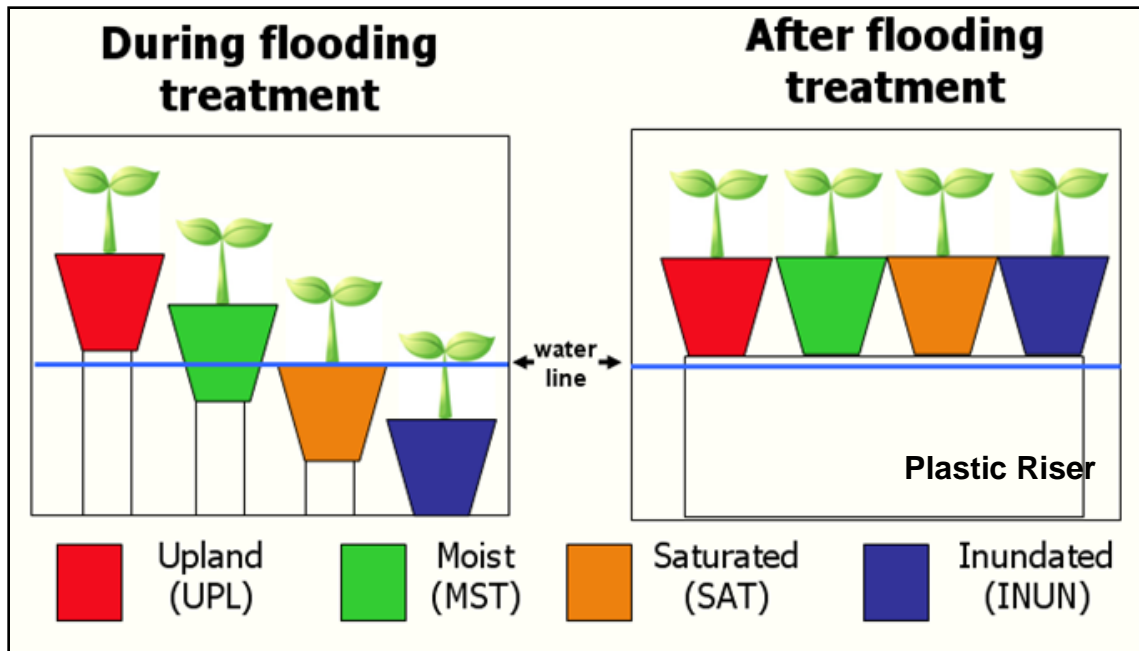


Figure 3-4. Graphical explanation showing flood depth and flood duration manipulations. The box on the left depicts the relative position of flooding depth treatments within a given crate. Crates were assigned one of three flood durations (3, 10 or 17 days) on each side (30% or 80% shade) of a tank enclosure. After the period of assigned flood duration had lapsed for a given crate, it was held above the water line on a plastic riser, with all pots sitting on the bottom of the crate.

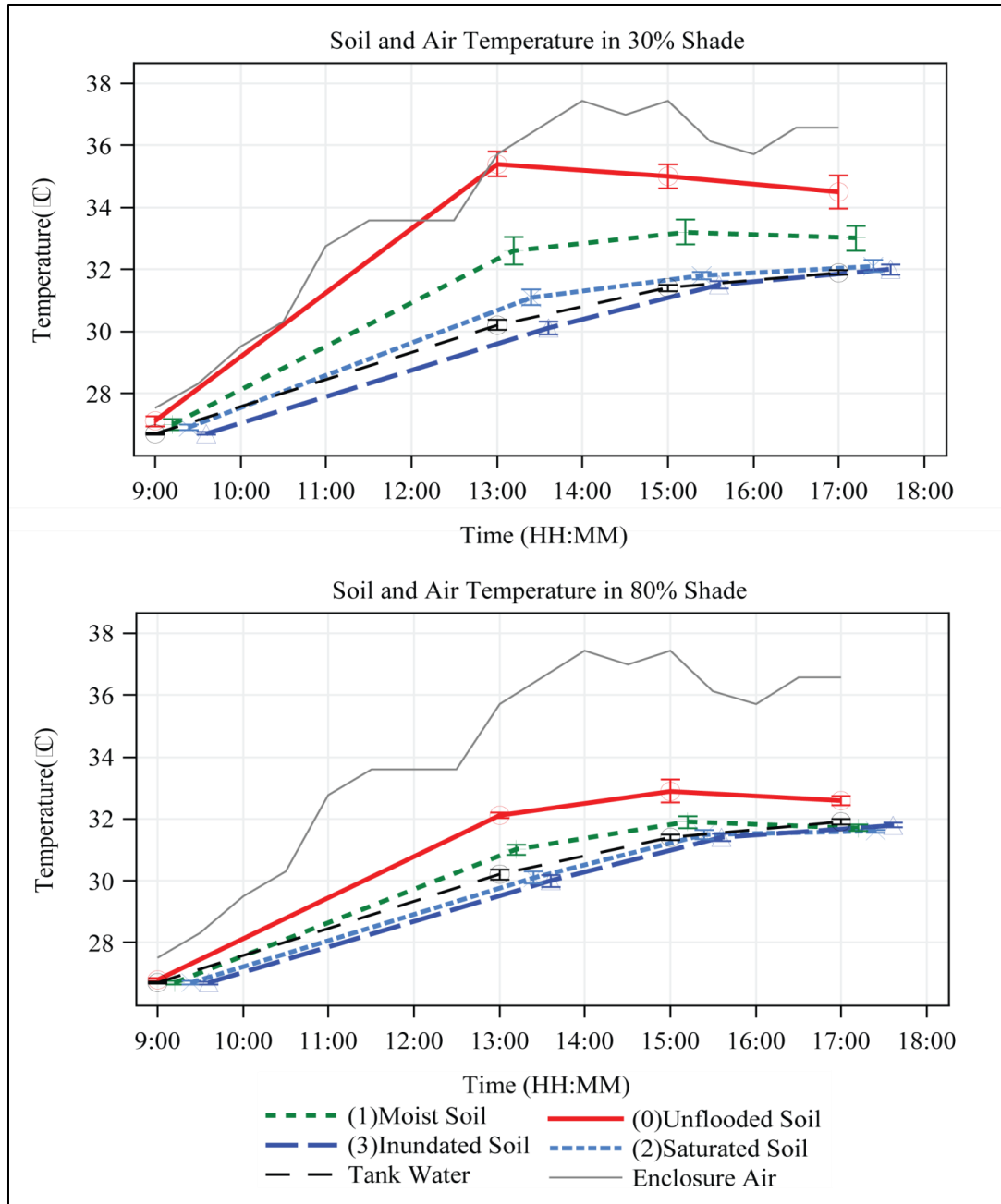


Figure 3-5. Daily changes in temperature for soil, water and air in enclosures, as measured on July 23rd, 2010. Panels show mean temperature curves for 30% and 80% shade treatments in the top and bottom panels, respectively. Enclosure air temperature was gathered from a single data logger placed at the center of the enclosure (i.e. at the boundary of the two light treatments) in tank 3 only. The same data for enclosure air temperature and water temperature is shown in both panels, to serve as a reference. Error bars are \pm one standard error. Soil temperatures are means based on measurements 17 day flooding treatments within each light treatment, in each tank ($n=6$ for each data point). Water temperature data is identical in the top and bottom panels, and is the mean water temperature based on measurements in each tank ($n=6$ for each data point).

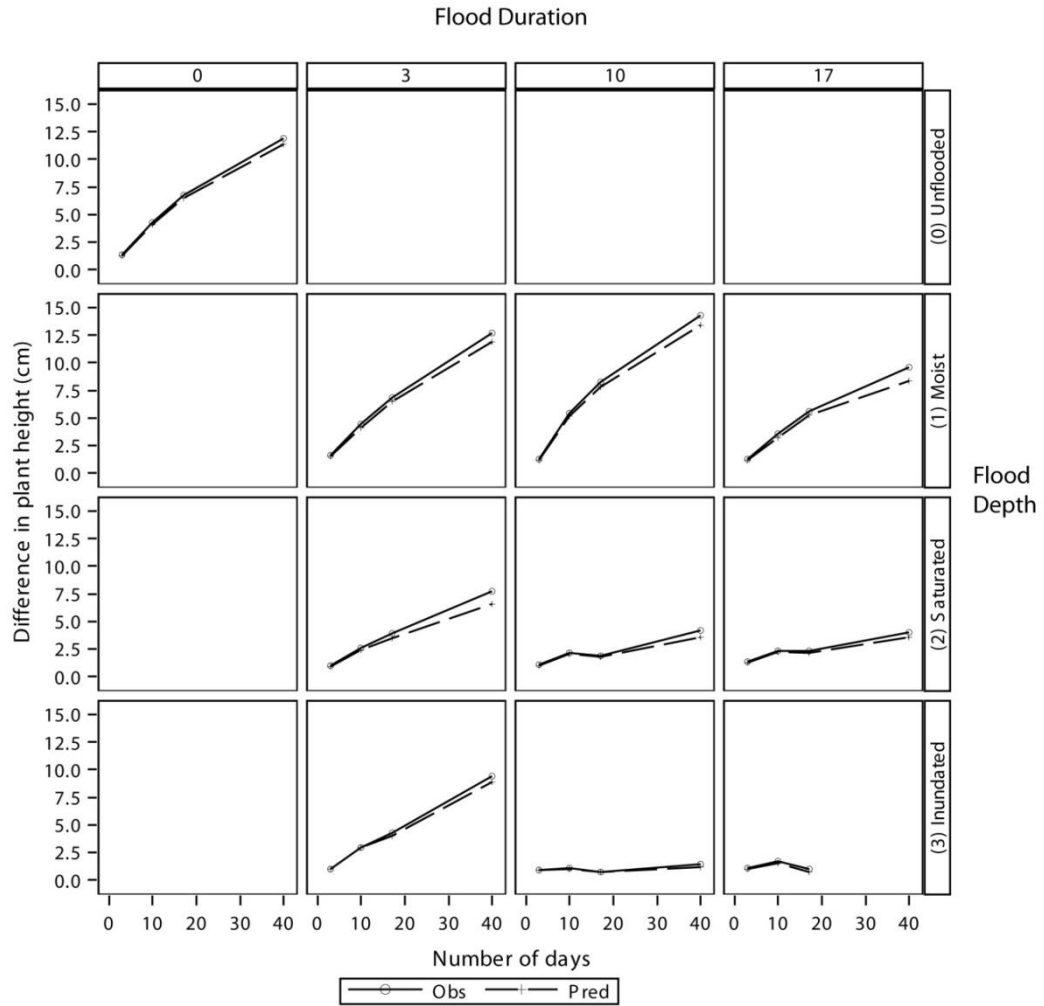


Figure 3-6. Mean observed (solid line) vs. predicted (dashed line) growth curves for seedlings over the full 40 days of the experiment. Each cell depicts the mean growth for treatments belonging to each combination of flooding depth and flooding duration. Flooding depth increases from top to bottom (see right vertical axis) and flooding duration increases from left to right (see top horizontal axis).

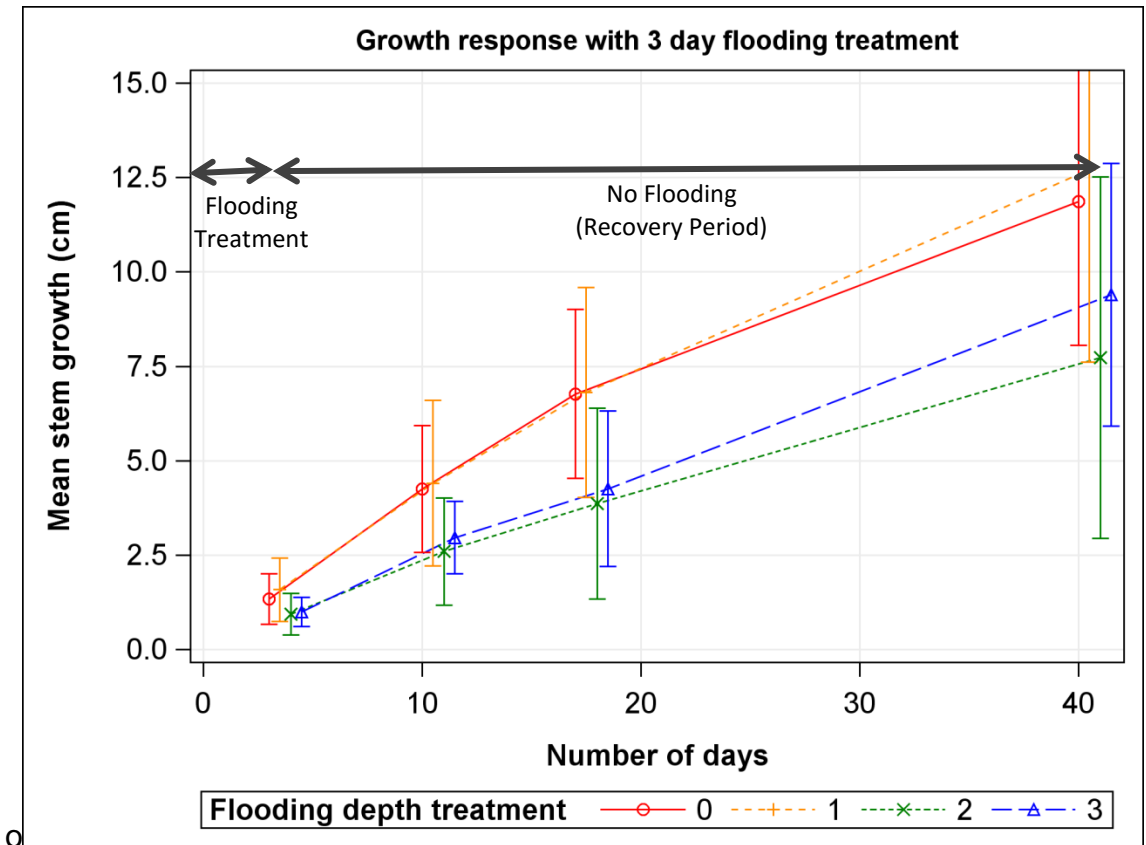


Figure 3-7. Stem growth response of seedlings subjected to moist (1 in +), saturated (2 in x), and inundated (3 in Δ) flooding conditions for 3 days. The growth response of upland controls (never flooded) are also shown in red (0 in red circle) as a reference. Graph depicts the growth response of the seedlings over the entire duration of the study. Error bars are +/- 1 standard deviation. Dates for each treatment are staggered a day or two on graph to permit outcomes on each sampling date to be discerned more easily. But all dates were: 3, 10, 17 and 40 after initial submergence treatment on day zero.

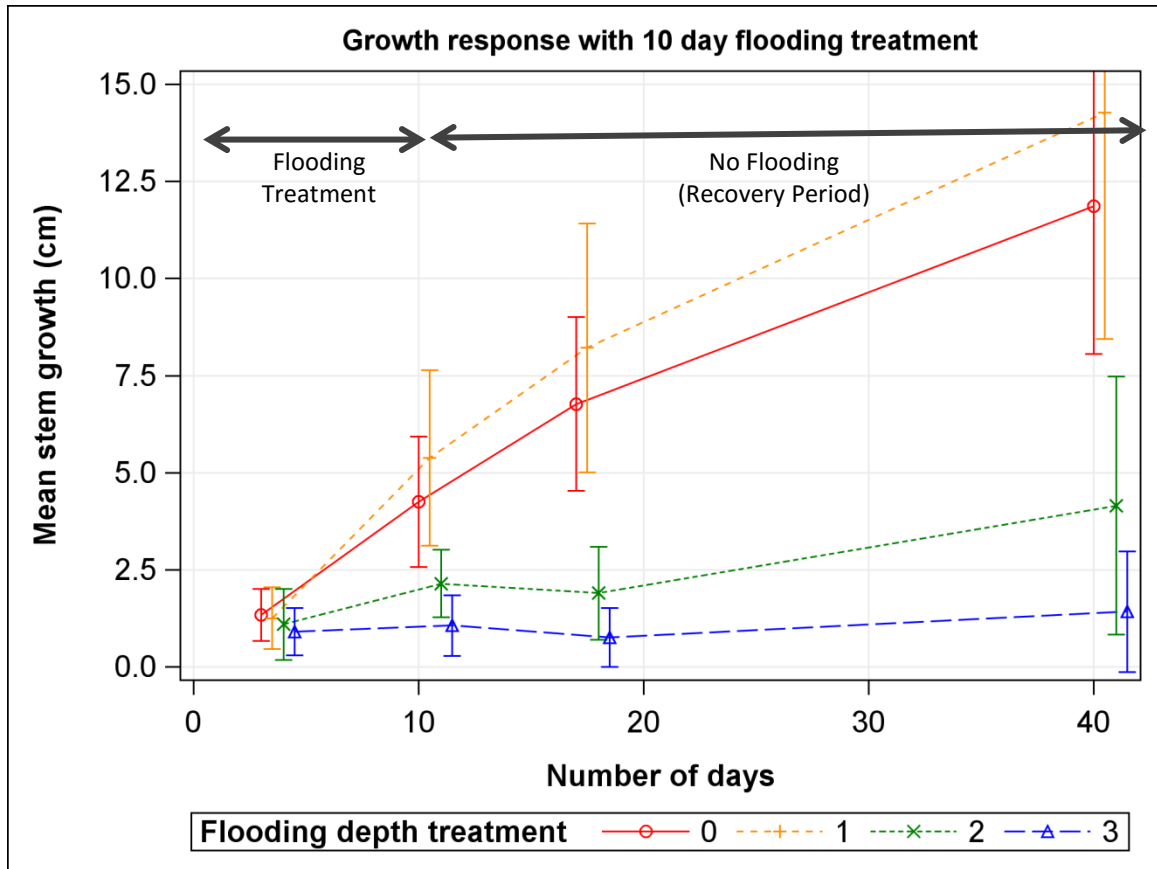


Figure 3-8. Stem growth response of seedlings subjected to moist (1 in +), saturated (2 in x), and inundated (3 in Δ) flooding conditions for 10 days. The growth response of upland controls (never flooded) are also shown in red. Graph depicts the growth response of the seedlings for the duration of the 40-day study. Error bars are +/- 1 standard deviation. Dates for each treatment are staggered a day or two on graph to permit outcomes on each sampling date to be discerned more easily, but all dates were: 3, 10, 17 and 40 after initial submergence treatment on day zero.

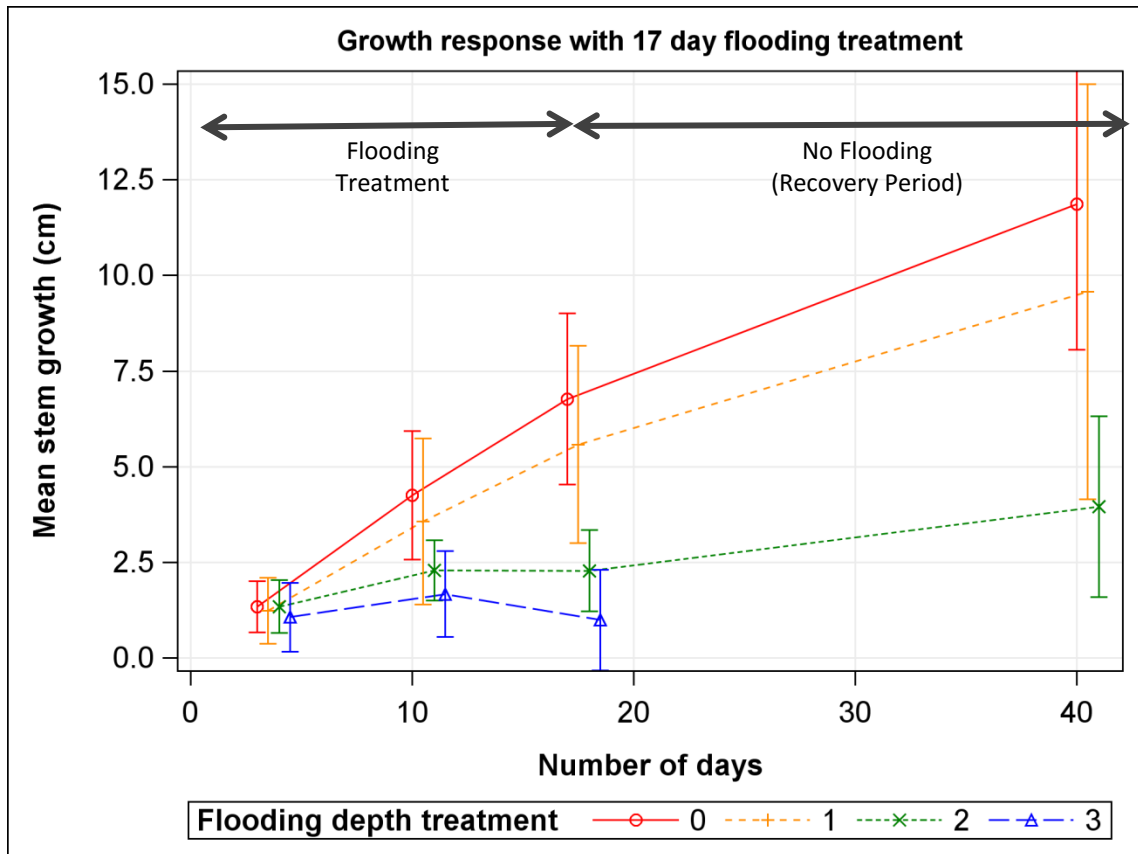


Figure 3-9 Stem growth response of seedlings subjected to moist (1 in +), saturated (2 in x), and inundated (3 in Δ) flooding conditions for 17 days. The growth response of upland controls (never flooded) are also shown in red. Graph depicts the growth response of the seedlings for the duration of the study. Error bars are +/- 1 standard deviation. Dates for each treatment are staggered a day or two on graph to permit outcomes on each sampling date to be discerned more easily. But all dates were: 3 , 10, 17 and 40 after initial submergence treatment on day zero.

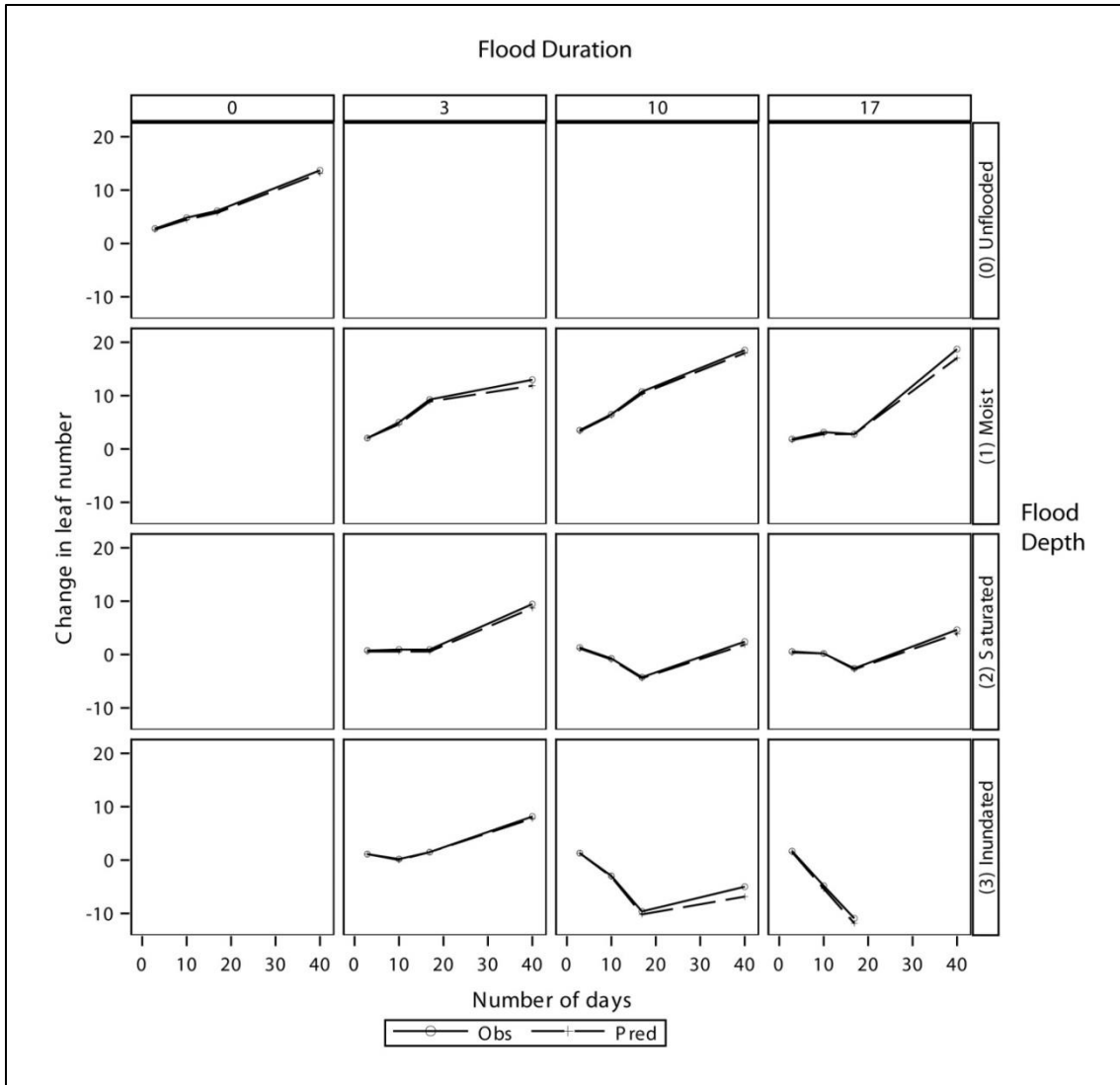


Figure 3-10. Mean observed (solid line) vs. predicted (dashed line) curves for change in seedling leaf number over the full 40 days of the experiment. Each cell depicts the mean change in leaf number for treatments belonging to each combination of flooding depth and flooding duration. Flooding depth increases from top to bottom (see right vertical axis) and flooding duration increases from left to right (see top horizontal axis).

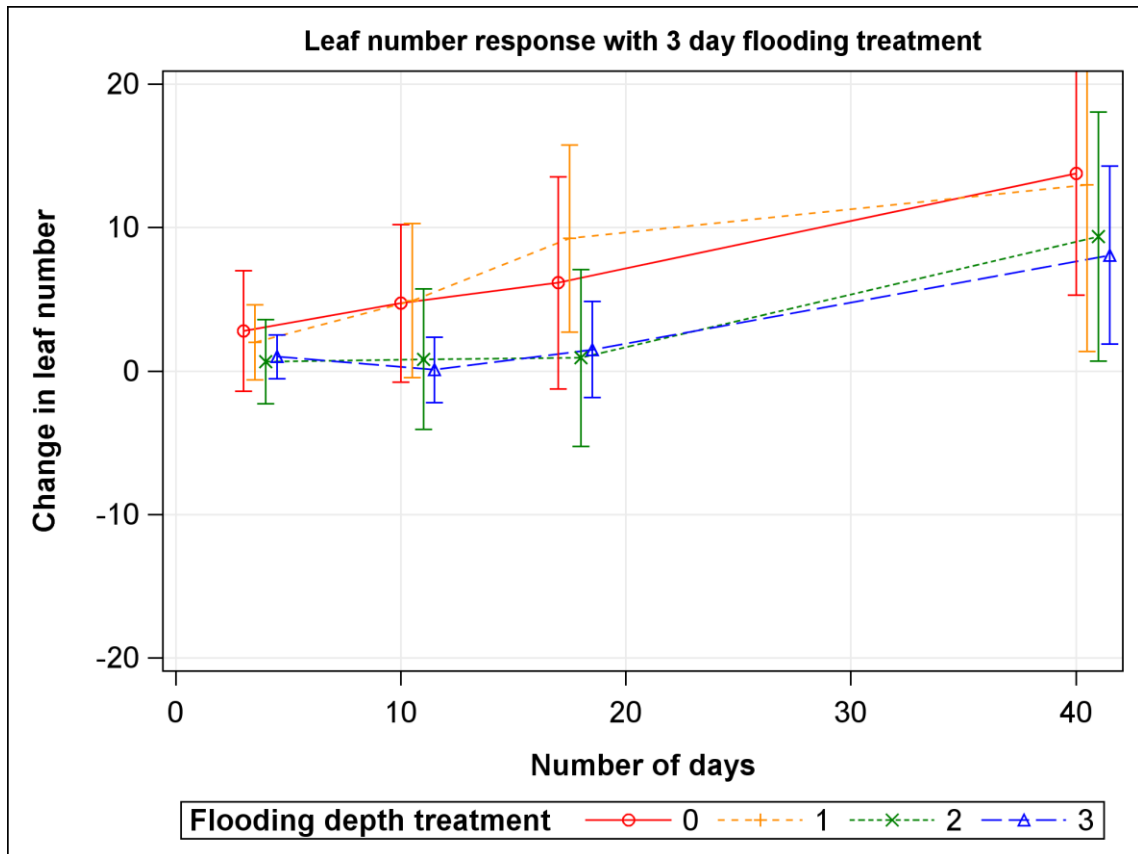


Figure 3-11. Change in leaf number for seedlings subjected to moist (1 in +), saturated (2 in x), and inundated (3 in Δ) flooding conditions for 3 days. The growth response of upland controls (never flooded) are also shown in red. Graph depicts the growth response of the seedlings for the duration of the study. Error bars are +/- 1 standard deviation. Dates for each treatment are staggered a day or two on graph to permit outcomes on each sampling date to be discerned more easily. But all dates were: 3, 10, 17 and 40 after initial submergence treatment on day zero.

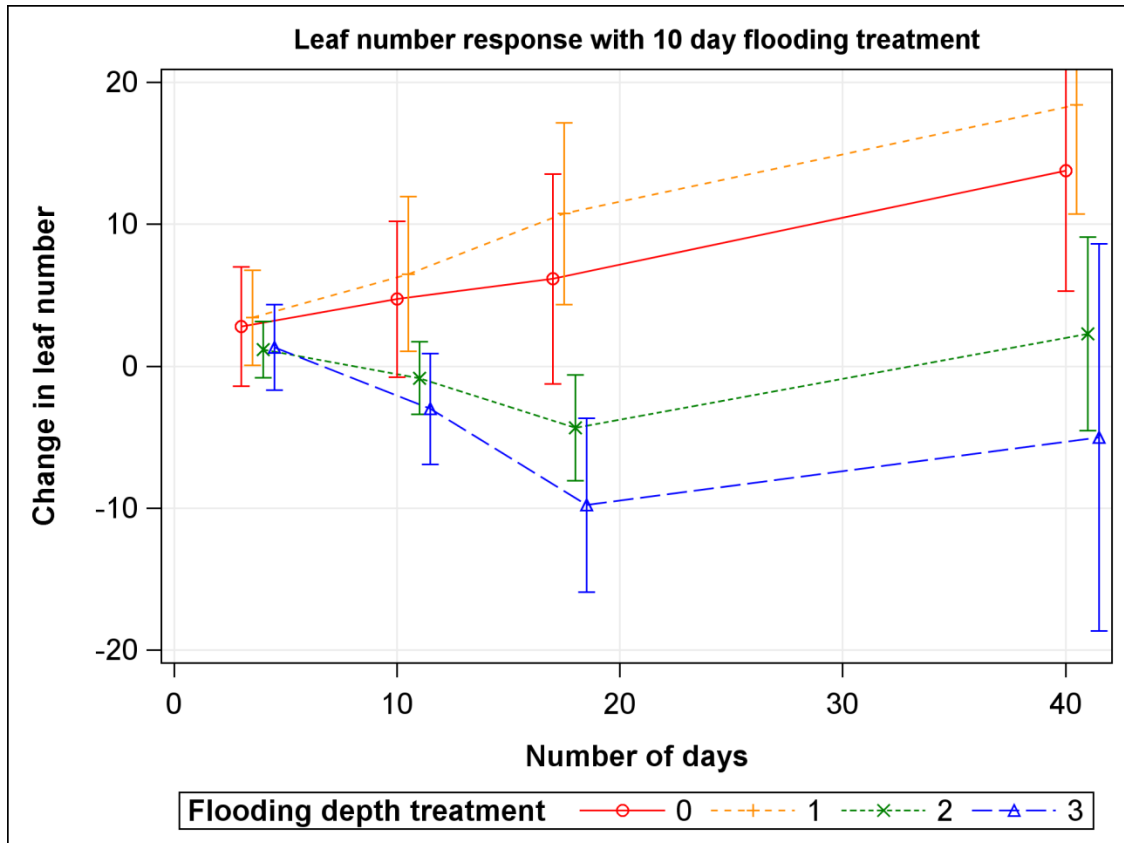


Figure 3-12. Change in leaf number for seedlings subjected to moist (1 in +), saturated (2 in x), and inundated (3 in Δ) flooding conditions for 10 days. The growth response of upland controls (never flooded) are also shown in red. Graph depicts the growth response of the seedlings for the duration of the study. Error bars are +/- 1 standard deviation. Dates for each treatment are staggered a day or two on graph to permit outcomes on each sampling date to be discerned more easily. But all dates were: 3, 10, 17 and 40 after initial submergence treatment on day zero.

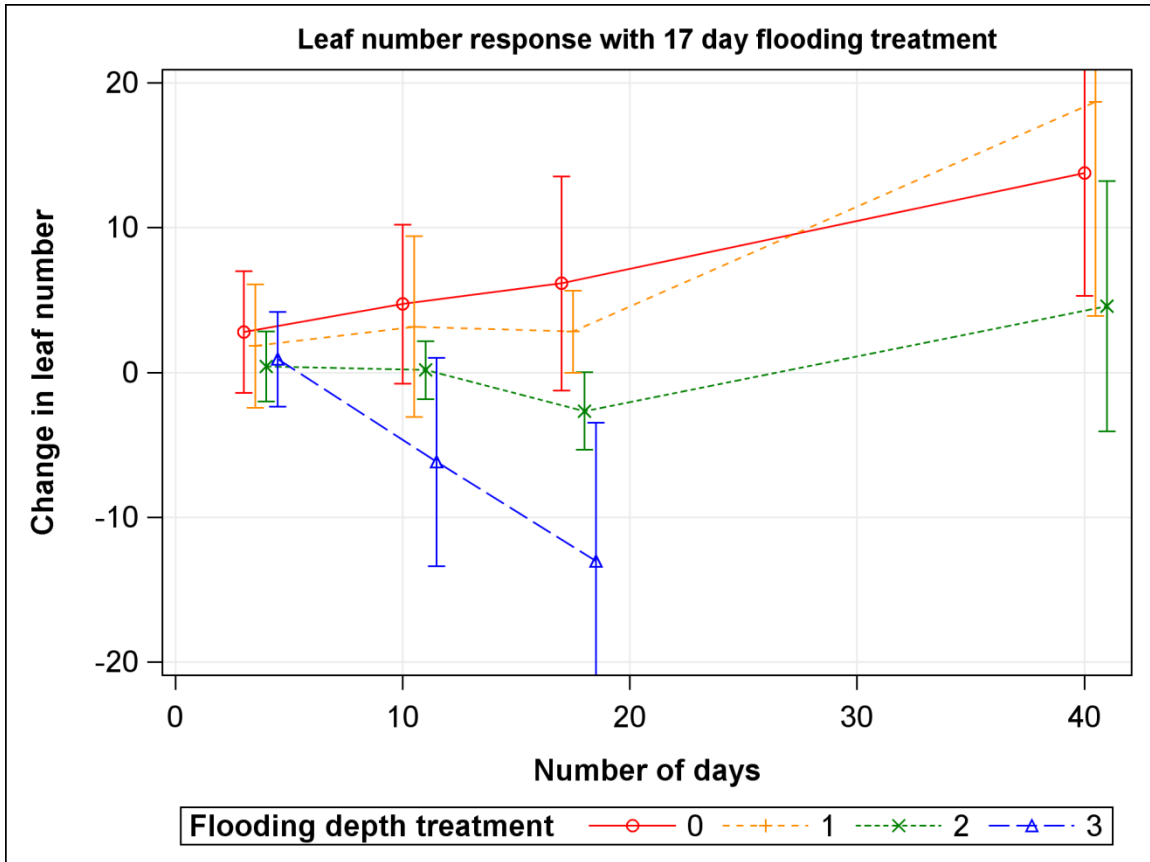


Figure 3-13. Change in leaf number for seedlings subjected to moist (1 in +), saturated (2 in x), and inundated (3 in Δ) flooding conditions for 17 days. The growth response of upland controls (never flooded) are also shown in red. Graph depicts the growth response of the seedlings for the duration of the study. Error bars are +/- 1 standard deviation. Dates for each treatment are staggered a day or two on graph to permit outcomes on each sampling date to be discerned more easily. But all dates were: , 10, 17 and 40 after initial submergence treatment on day zero.

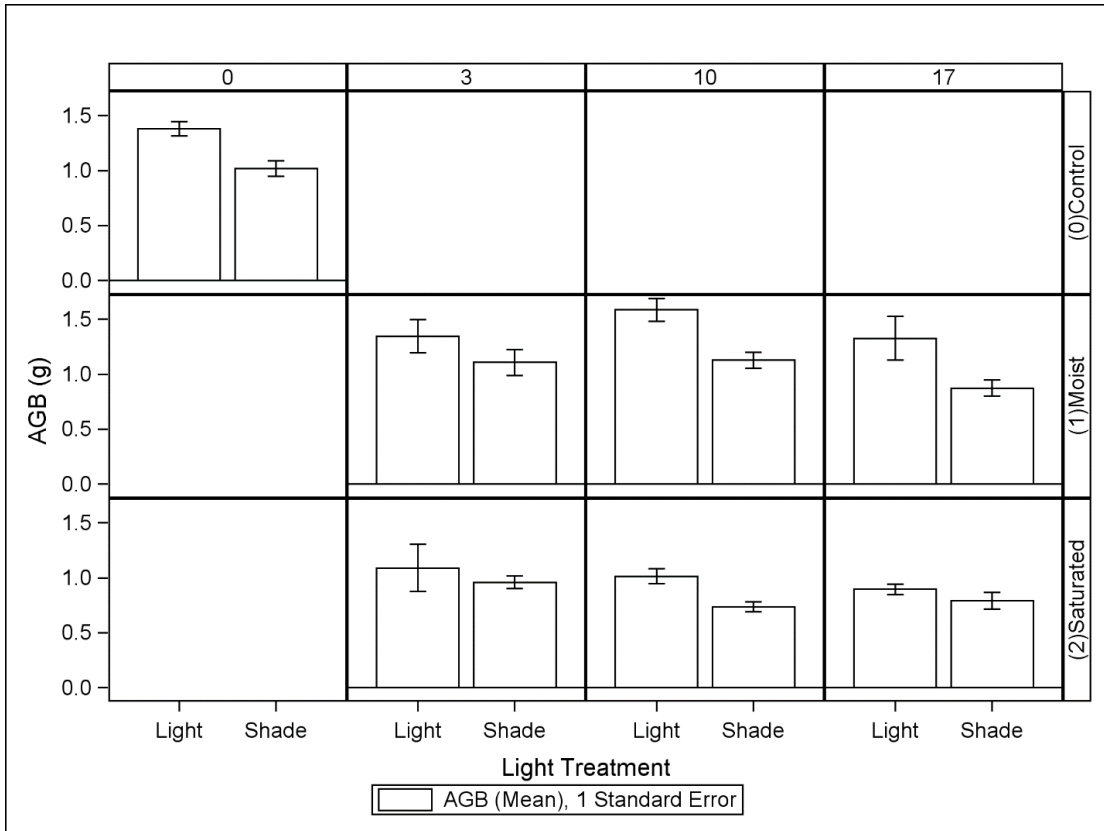


Figure 3-14. Mean aboveground biomass (AGB) for all combinations of light, flood depth and flood duration. “Light” and “Shade” treatments are 30% shade and %80 shade, respectively. Error bars are ± 1 standard error.

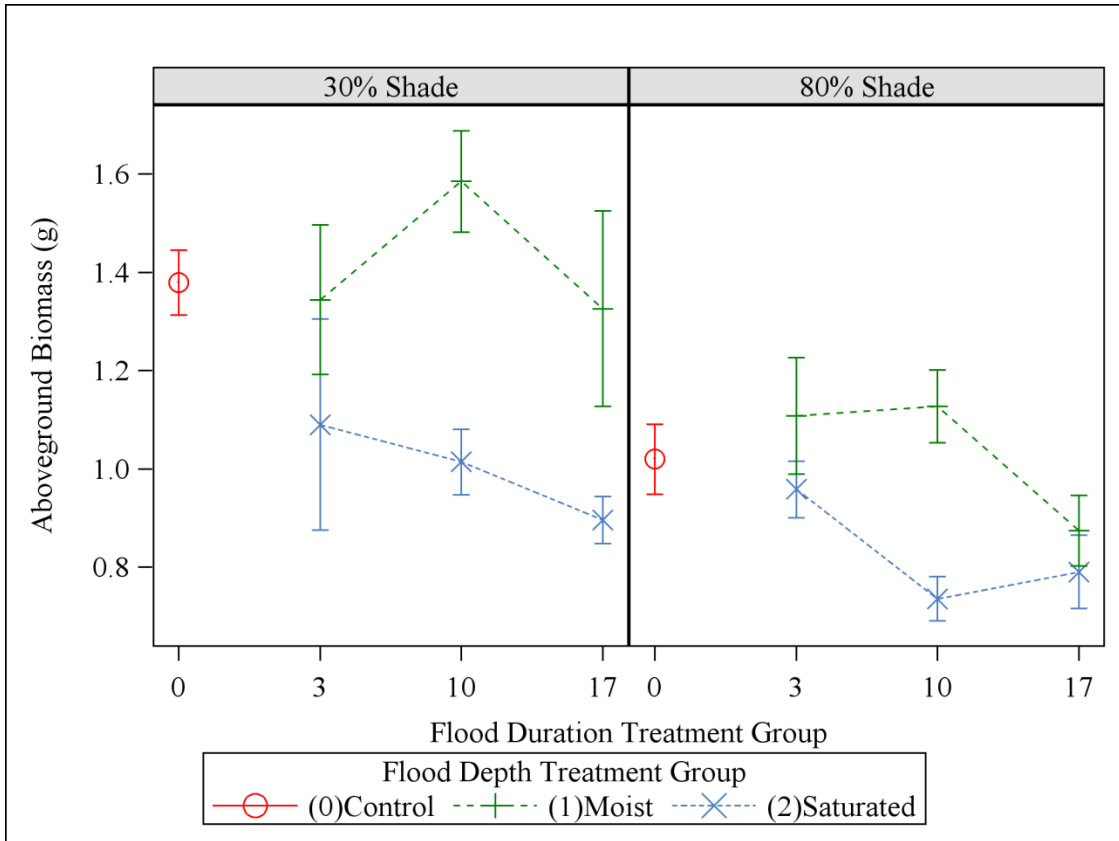


Figure 3-15. Interaction plot showing mean aboveground biomass for all combinations of light, flood depth and flood duration on Day 40, for surviving seedlings only. Error bars are ± 1 standard error.

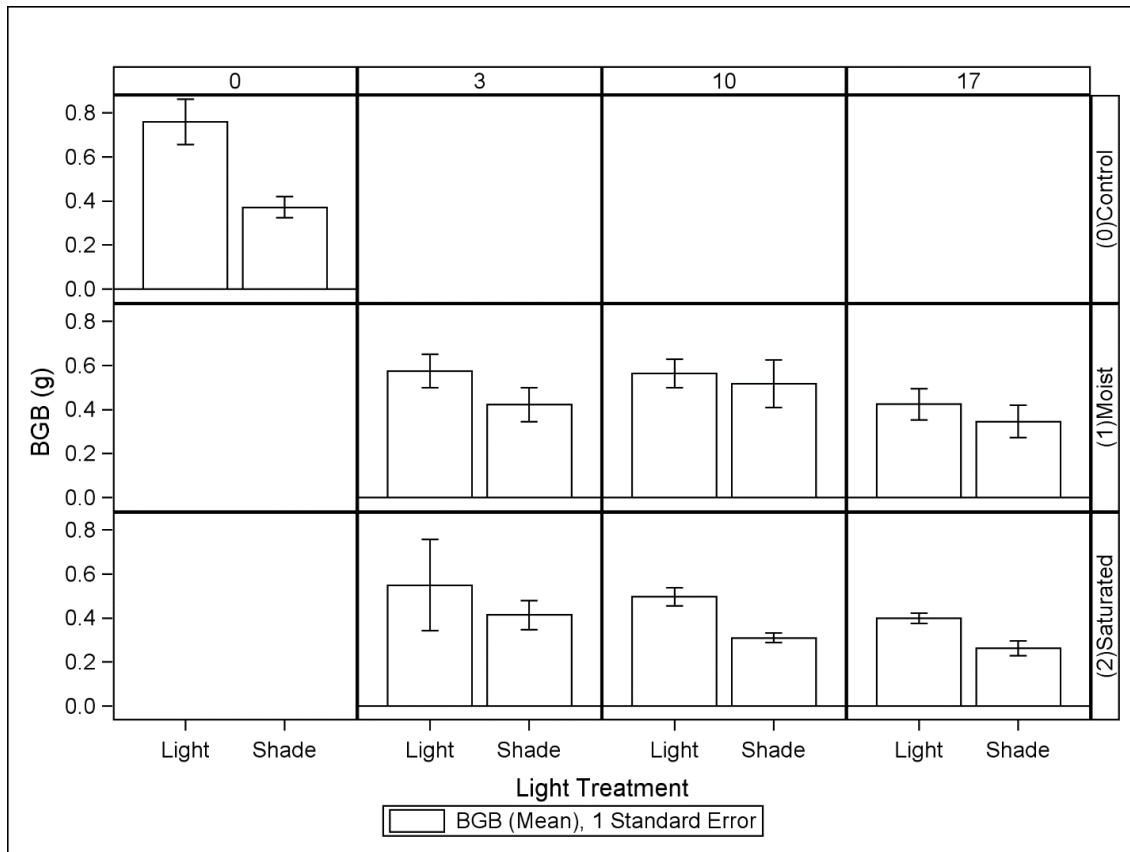


Figure 3-16. Mean belowground biomass (BGB) for all combinations of light, flood depth and flood duration, on Day 40 for surviving seedlings only. “Light” and “Shade” treatments are 30% shade and 80% shade, respectively. Error bars are ± 1 standard error.

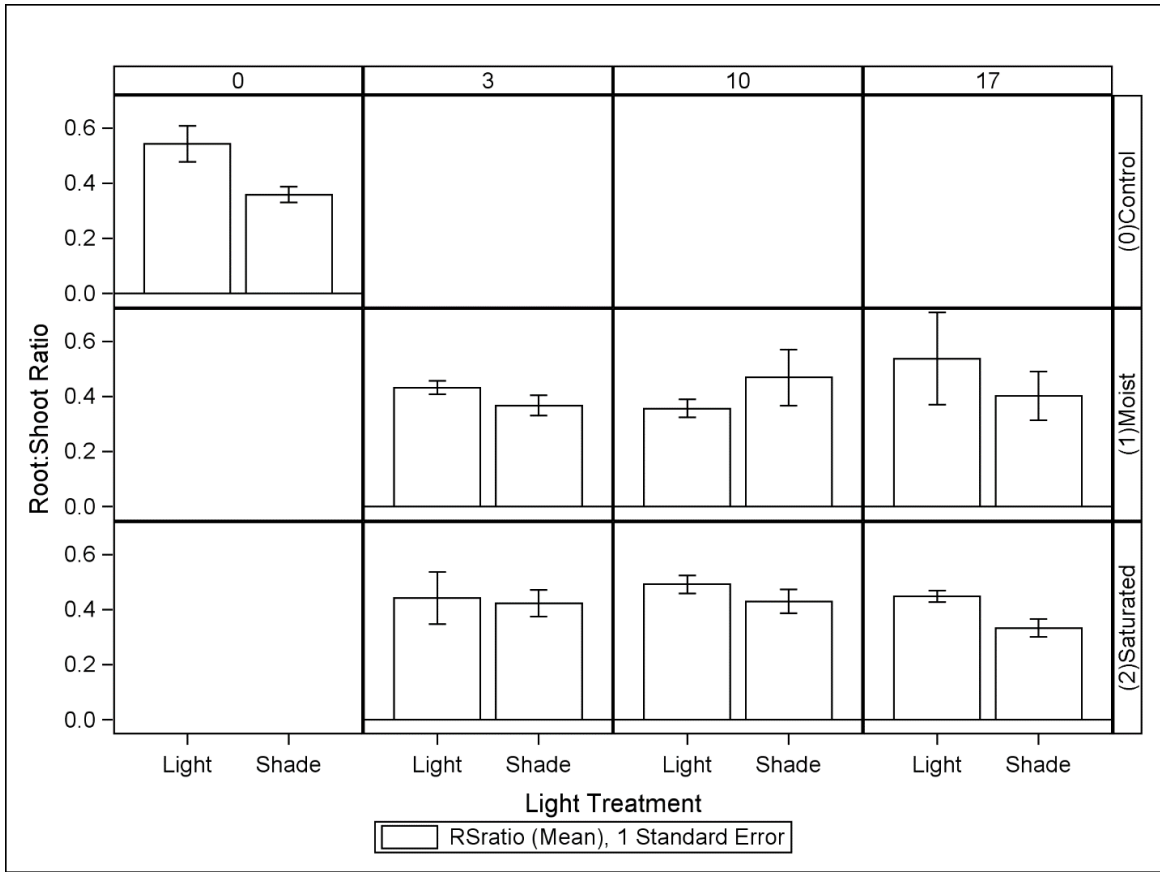


Figure 3-17. Mean root-shoot ratio (RSR) for all combinations of light, flood depth and flood duration on Day 40 for surviving seedlings only. “Light” and “Shade” treatments are 30% shade and %80 shade, respectively. Error bars are ± 1 standard error.

CHAPTER IV

EFFECTS OF SIMULATED FLOODING ON GERMINATION OF *LONICERA* *MAACKII* SEEDS

Introduction

Gleasonian models of plant community development emphasize how species distributions are controlled by environmental gradients. Within this framework, the environmental sieve model describes how plant species distributions are limited by the availability of favorable abiotic conditions that may change through time and space (Vandervalk 1981). For instance, the anoxic stresses of wetland soils act as an ecological filter that limit successful seedling establishment to particular windows in time and space (Middleton 2000). To establish a successfully reproducing population in any habitat, a species must pass through this filter at each critical life stage.

Several recent studies, including the second chapter of this dissertation, show that the non-native invasive shrub species *Lonicera maackii* has an established presence in riparian, floodplain and bottomland hardwood forests in the United States (Predick and Turner 2008, Boyce et al. 2012, White 2014). Suitable habitat within these systems appears to be limited by the availability of drier, higher elevation sites (Swab et al. 2008). However, it is not known what life stages are most sensitive to the effects of flooding that limit the presence of *L. maackii* in bottomland hardwood forests. Because plant

requirements and tolerances can change with ontogeny (Blood and Titus 2010), examining the role of biotic and abiotic stressors at multiple life stages is critical in delimiting the fundamental niche of plant species (Anderson et al. 2009).

Chapter III demonstrated that the growth of *Lonicera maackii* seedlings is negatively impacted by durations of saturation or inundation of 10 days or more. However, to some extent, they show the potential to survive and recover from the stresses of ephemeral saturated and inundated conditions. This chapter examines the potential of waterlogged conditions to impact another critical life history stage of *L. maackii*, seed germination.

Studies from upland systems show viable *L. maackii* seeds are dispersed by both birds (Bartuszevige and Gorchoy 2006) and deer (Vellend 2002). Undoubtedly, these dispersal mechanisms are also important in wetland systems, but the occurrence of this species in floodplains suggests hydrochory could be another means of dispersal. The fleshy red fruits of *Lonicera maackii* mature in late fall, and it is possible that they may be distributed onto floodplains during winter flooding in riparian systems. In depressional wetlands, seeds and fruits may be washed in from adjacent higher-elevation sites, or deposited through zoochory.

While some plants, such as *Fraxinus pennsylvanica*, have demonstrated the ability to germinate underwater (Schmiedel and Tackenberg 2013), many woody species rely on dispersal to higher elevation microsites, or drawdown, for successful germination in wetlands (Middleton 2000, Blood and Titus 2010). Seeds distributed by hydrochory are generally concentrated along drift lines in bottomland hardwood forests (Nilsson et al.

2010). These features mark the interface between areas of inundation and higher elevation microsites. Dispersal into these areas is advantageous, as higher elevation microsites are generally more conducive to seed germination for most woody species (Middleton 2000). Thus, while the ability of seeds to germinate under flooded conditions is not generally a prerequisite to wetland establishment, it is advantageous for seeds to remain viable under waterlogged conditions. As a first step in understanding the degree to which flooding restricts the germination potential of *Lonicera maackii*, this study examines its potential seed germination under various flooding scenarios by quantifying the ability of *Lonicera maackii* seeds to germinate under various conditions of simulated flooding.

Methods

The germination assay consisted of two consecutively applied manipulations intended to mimic different temporal flooding regimes, one during a seed stratification period and the other as a post-stratification event (or treatment). This transition was intended to mimic natural changes in hydrology that may occur in wetland soils (e.g. drawdown or flooding), and therefore assess the potential impact of these inundation fluctuations on *L. maackii* seed germination.

Seed Sources and Viability Testing

Seed material was obtained from *L. maackii* plants from a single wetland site in Jefferson County, Kentucky, USA. Mature fruits were collected on a single date in October 2011. These were briefly stored in a refrigerator for 2 days. Seeds were then separated from the fruit pulp in distilled water using a homemade macerator constructed

by covering the blades of a conventional kitchen blender with rubber tubing. Recovered seeds were allowed to dry on paper towels until visibly dry (1-2 days), transferred to paper envelopes, and then placed in dry, cold storage in plastic containers until the beginning of the experiment.

Just prior to the initiation of the experiment (February 2012), samples of the stored seeds were tested for viability using a 1% tetrazolium (TZ) solution (10 seeds/Petri dish, n=5) using established protocols for *Lonicera* spp. (Peters et al. 2000). Dissected seeds staining bright red throughout the embryo and endosperm were recorded as viable. Those not staining bright red throughout both seed parts were recorded as non-viable. Mean (\pm S. D.) viability was $70.7\pm 15.3\%$. This method produces a conservative estimate of seed viability, as viable seeds with low vigor may not stain evenly throughout (Peters et al. 2000).

Germination Assays

The experiment was initiated on February 18, 2012 and lasted until May 23, 2012 (a total of 95 days). To minimize risk of microbial contamination all seeds were surface sterilized with a 1% sodium hypochlorite solution. Mean viability of surface sterilized seeds was estimated as $65.1\pm 23.9\%$ using the TZ test method discussed previously. Additionally, all plasticware, tools and media were autoclaved.

Some seeds of *Lonicera maackii* exhibit morphophysiological dormancy, requiring seeds to be subjected to a period of stratification under cold, moist conditions before germination is possible (Hidayati et al. 2000). Seeds were cold stratified under one of three conditions (moist, saturated or inundated sand), then transitioned to a

different condition after stratification (also moist, saturated or inundated sand). A constantly moist and cool treatment was also included as a control and to serve as a reference simulating overwintering conditions in upland systems. Hereafter, these treatments are referred to as stratification treatments (i.e., the initial conditions in each treatment) and post-stratification treatments (e.g. treatment conditions after transition to different conditions), and are described in detail in the following sections. These transitions corresponded to either a flooding or drawdown event and were applied consecutively. The five treatments (indicating stratification to post-stratification transitions, respectively) were: moist control (no transition), moist-to-inundated transition, moist-to-saturated transition, saturated-to-moist transition and inundated-to-moist transition (Table 4-1).

Stratification Treatments

Sixty 250 mL polypropylene containers were filled with 100 g of sterilized white aquarium sand to 1 cm depth, and randomly assigned to one of five treatment groups. According to Hidayati et al. (2000), stratification under light enhanced germination rates, and therefore each of the three refrigerator shelves was equipped with two single-strip 24” fluorescent lighting fixtures, controlled by a timer to provide 14 hours of light each day. Bulbs were 17 watts and provided light in the 7800 K spectrum. To minimize the effects of any vertical variation in lighting (variation among shelves), trays holding the polypropylene containers were made of opaque foam board that limited the transmission of light from one shelf to another.

All containers were weighed before the addition of water. Replicates assigned moist stratification treatments received 15 mL of sterile distilled water, an amount sufficient to thoroughly wet the 100 g of substrate. Saturated treatments received 25 mL of water, raising the water level even with the sand surface. Inundated treatments received 80 mL of water, an amount sufficient to raise the water level 1 cm above the sand surface. These volumes of water were used as standards for moist, saturated and inundated conditions throughout the duration of the experiment. Thirty seeds were spaced evenly on the sand surface of each replicate container. Each container was sealed with a lid and weighed to the nearest 0.01 g.

Containers were immediately transferred to a commercial refrigerator for a cold stratification period. Based on results from Hidayati et al. (2000), high germination rates greater than 90% were achieved after cold stratification at 5 °C with a 14-hour photoperiod. Prior attempts to stabilize the refrigerator temperature at 5 °C revealed limitations in temperature control, and it was not possible to maintain an even, constant temperature throughout the unit. Data provided by temperature data loggers showed that temperature varied with both photoperiod (due to heat produced by the light fixtures) and vertically (due to the position of the condenser at the top of the unit). To minimize the differential effects of the vertical temperature gradient, trays holding the containers were rotated to a different shelf every 3 days (vertical rotation). Potential effects of horizontal variation in light levels (variation within a shelf) were minimized by rearranging replicates within a tray at each vertical shelf rotation. Rearrangement consisted of shifting replicates horizontally one position over, and rotating containers within each replicate one position front to back.

Despite scheduled rotations, it was anticipated that germination of seeds would be somewhat asynchronous, due to the vertical temperature gradient. For instance, if sufficient stratification had occurred (or if stratification was unnecessary) seeds on warmer shelves for 3 days between rotations would likely germinate before those on cooler shelves. In order to statistically account for any variance in germination rate due to this factor, each shelf contained a single seed tray holding 3-4 complete replicate sets, and each tray was treated as an experimental block.

Temperature of the refrigeration unit was recorded hourly for the majority of the experimental duration using 2-3 temperature data loggers (Hobo Pro Series, Onset). Temperature was monitored from 3/2/12 to 3/12/12 on the bottom and middle shelves, and from 3/13/12 to 3/25/12 on the top and bottom shelves. From 3/26/12 to 5/23/12, temperature was recorded on all 3 shelves.

Seeds were examined every 2-3 days for signs of germination, defined as protrusion of the radicle 1 mm or greater. It was not anticipated that seeds would show significant germination during the low temperature stratification period. However, germination was first observed on 3/23/12, 34 days after initiation of stratification treatments. Attempts to delay germination by lowering the refrigerator temperature were made. Despite these efforts, germination continued at low temperatures and the decision was made to continue the post-stratification flooding or drawdown manipulations in the low-temperature environment.

Post-stratification treatments

As in the stratification period, rotation of replicates within and between refrigerator shelves was carried out during post-stratification treatments. Post-stratification treatments were begun on 3/27/12 (day 38) after initial germination of seeds was observed on 3/23/12. Treatments simulating transitions to flooded conditions (e.g. moist to saturated or moist to inundated transitions) received additional sterile distilled water. Saturated treatments received 15 mL to achieve saturated conditions (~25 mL total of water). Similarly, moist to inundated transitions received an additional 65 mL of water to achieve a total water volume of 80 mL, the standard used here for inundated conditions. Because some evaporation occurred, the exact amount of water added was added by weight. The target weight of each treatment was determined by adding the amount of water by weight (1 mL = 1 g) needed to transition moist treatments to either saturated or inundated conditions, based on initial container weights. The target mass was calculated for each container receiving water, and sterile distilled water was added until the target weight was achieved within a tolerance of ± 1 g.

Simulating drawdown (e.g. saturated to moist or inundated to moist transition treatments) required the withdrawal of water from containers. Using an automatic pipette, all water that was possible to remove with a pipette was withdrawn. The accuracy of water removal in achieving intended water volumes was checked by comparing the target vs. actual container weights. The target mass of each container was calculated by adding 10 g (the amount of water corresponding to moist conditions) to the initial dry container weight. The average difference from target weight was 5.2 ± 0.31 g and 5.9 ± 1.4 g for saturated to moist and inundated to moist transitions, respectively.

Once germination was observed, total numbers of germinating seeds in each dish were recorded every 3 days until 5/3/11 (75 days after beginning of stratification), when all containers had achieved at least 70% germination (corresponding approximately to estimates of seed viability). During the incubation, seeds showing obvious signs of fungal colonization were removed to prevent further contamination. Seed germination for all samples between 5/14/11 (day 86) and 5/23/11 (day 95), revealed only a small number of new germinants gained between these two observation intervals (an average of less than 1 new germinant per dish), and the experiment was terminated.

Data Analysis

Mean germination time and germinability were calculated for each replicate container according to guidelines provided in Ranal and Garcia de Santana (2006). Mean germination time (\bar{t}) is a weighted mean of time to germination and was calculated as

$$\bar{t} = \frac{\sum_{i=1}^k n_i t_i}{\sum_{i=1}^k n_i} \quad (\text{Eq. 7})$$

where t_i is the time (in days) when the i^{th} observation was made, n_i is the number of seeds germinated in the interval between the i^{th} observation and the previous observation and k is the last day on which germination observations were made. Germinability was calculated as the total percentage of seeds germinated in each replicate by the end of the experiment.

A mixed linear model was used to test the effects of flooding treatment on mean germination time (MGT) and germinability using PROC MIXED in SAS 9.4. The

experimental “seed tray” (e.g. the group of replicates comprising a single seed tray) was treated as a random effect, and modeled using the variance components (VC) method. Flooding treatment was treated as a main, fixed effect. Modeling “seed tray” as a random effect allowed the effects of flooding treatment on MGT or germinability to vary with seed tray. The justification to treat seed tray as a random effect was made based on the observation of initial asynchronous timing of germination between replicates on different trays. One tray began germination earlier than the other two, although the differences between the trays dissipated through time. The model used the restricted maximum likelihood (REML) estimation method. Germinability was modeled by converting the percentage to a decimal fraction and using the arcsine transform (commonly used for percentage data) where:

$$Y(\text{Transformed}) = \arcsin(y^{-2})$$

Model residuals were visually examined for normality and homoscedasticity. Significant differences in fixed effects at the $p = 0.05$ level were followed up with pairwise comparisons among treatment groups using the Tukey-Kramer method.

Results

Mean Germination Time

The MGTs of all treatment groups ranged from 59.8 to 64.8 days and were longer than the moist control and the fixed effect of flooding treatment on MGT was significant ($p=0.012$). *Post-hoc* pairwise comparison of flooding treatment groups using the Tukey-Kramer method showed a significant difference in MGT between the moist control and moist-to-inundated transition group ($p=0.004$). No other groups significantly differed

from each other. The effect of “seed tray” modeled as a random effect, was not found to be significant ($p=0.175$).

Germinability

The mean germinability of all treatments was relatively high ($88.3\pm 8.50\%$ to $91.5\pm 6.35\%$). The fixed effect of flooding treatment on total germinability was not significant ($p=0.73$). The mean germinability of treatments inundated during either stratification or post-stratification was lower than all others, but the difference was not statistically detectable.

Environmental Variables: Temperature

As expected, a vertical temperature gradient was observed during the experimental period. The difference in mean daily average temperatures between each shelf was approximately $2\text{ }^{\circ}\text{C}$ (Table 4-1), ranging from $2.3\pm 0.5^{\circ}\text{C}$ in the top shelf to $6.3\pm 0.8\text{ }^{\circ}\text{C}$ the bottom (Fig. 4-1). The variation in mean daily temperature throughout the study period was close to the target temperature of $5\text{ }^{\circ}\text{C}$ —a stratification temperature that yielded high germination rates in Hidayati et al. (2000). A temperature adjustment to the refrigerator unit accounts for the temperature reduction seen on day 38 (see Methods). As seen in Fig. 4-1 temperature fluctuations became pronounced in the latter two-thirds of the experiment, possibly due to ambient temperature fluctuations in the surrounding laboratory,

Discussion

This study attempted to evaluate the potential effects of flooding stress on the germination of *Lonicera maackii* by mimicking natural hydrologic transitions in a

controlled experiment. These transitions corresponded to either a flooding or drawdown event from different initial moisture conditions during cold stratification. A constantly moist treatment was also included as a reference mimicking winter moisture conditions in upland forested systems where flooding does not occur. Temperatures during the experiment were within the range observed in soils in winter and spring in our region (NRCS 2015).

A statistically significant effect of flooding treatments on mean germination time was detected. This significant effect was explained by longer mean germination times of treatments undergoing transitions from moist to flooded conditions compared to treatments experiencing consistently moist conditions. However, there was no difference in total germinability between any treatments, which was high under all treatments, indicating that seeds have the physiological potential, under aseptic conditions, to germinate even when flooded at low temperatures.

Effects of Simulated Drawdown

These findings show that the mean germination time and germinability of *Lonicera maackii* seeds cold-stratified under inundated conditions for approximately 30 days and transferred to moist conditions did not differ significantly from that of seeds incubated under constant moist conditions. This furthers the possibility that seeds deposited into flooded areas may retain viability and thus be able to germinate when more suitable conditions for growth (drawdown at the beginning of the growing season) occur.

The ability of *L. maackii* seeds to remain viable under submersion also advances the possibility that hydrochory may be a secondary means of dispersal. Considering the origins of *L. maackii* from low-elevation and floodplain forests (Luken and Thieret 1996), it seems worth considering if its retention of viability under inundation and potential to germinate underwater is an adaptation to its native range and habitat. It should be noted that the ripe, fleshy fruits of *L. maackii* are not buoyant unless they have begun to dry (personal observation). Fruits ripening in the fall can be retained on the plant into January (Luken and Thieret 1996) and the high yield of fruit makes it likely that many seeds will fall to the forest floor (Luken and Goessling 1995). This timing of seed release would also match that of high flow conditions in floodplain systems, where *L. maackii* can be a dominant plant (White 2014). However, even if fruit characteristics do not encourage lateral dispersal via floodwaters, seeds could potentially be washed down from adjacent higher elevation areas and deposited in floodplains or microdepressions, where the ability to remain viable under prolonged submersion would be advantageous.

Effects of Simulated Flooding

Seeds subjected to a cold moist stratification followed by inundation germinated more slowly, but ultimately to similar percentages as all other treatments. Seeds used in this experiment did not germinate within 30 days, qualifying them as having either simple morphological dormancy (MD) or simple morphophysiological dormancy (MPD) (Hidayati et al. 2000, Baskin and Baskin 2001). Seeds of *L. maackii* have underdeveloped embryos, which must elongate to break simple MD (Hidayati et al. 2000). It is possible that water-logging slows, but does not halt, biochemical processes

that break MD requirements in *L. maackii* seeds. Although the water column was unlikely anaerobic in our experiment due to the initially sterile conditions, water still may limit the delivery of oxygen to developing plant embryos (Alani et al. 1985), thus retarding germination under field conditions.

The conditions for breaking dormancy in MPD seeds are more stringent. In addition to elongation of the embryo, seeds with MPD must also undergo physiological changes to break dormancy, and in *L. maackii* this is known to be accomplished by moist warm- or cold-stratification (Hidayati et al. 2000). It is unknown what percentage of seeds in this experiment had MD or MPD, thus it is not possible to know if seeds were able to break MPD requirements while inundated. Furthermore, since no treatments were consistently inundated, it is not possible to discern if consistently inundated conditions are sufficient to meet seed dormancy requirements and promote germination without a period of drawdown to moist conditions. However, since most woody plants do not establish in continuously flooded areas (Kozlowski 2002), it is unlikely that these would be areas of suitable habitat regardless. Finally, it is also possible that the somewhat underdeveloped dormancy mechanisms in *L. maackii* are insufficient to prevent germination in flooded conditions, even if these conditions are not optimal.

Lab-to-Field Implications

This study shows that *L. maackii* can germinate under saturated and inundated conditions, but only indicates the *potential* recruitment ability of *L. maackii* in flooded soils at low temperatures. The timing of germination in relation to seasonal hydrologic and climate changes is likely to restrict the establishment of new germinants. *L. maackii*

seeds vary in their dormancy breaking requirements, and have been characterized as either having no dormancy (Luken and Goessling 1995), simple MD or simple MPD (Hidayati et al. 2000). *L. maackii* seeds with MPD need moist warm- or cold-stratification, and are likely to germinate during this shrub's growing season, which in our region typically begins in the first week of March and ends in late November (Trammell et al. 2012 and personal observation). Freshly matured seeds with MD are capable of germinating in autumn after the embryo has elongated (Hidayati et al. 2000) and field observations from Luken and Thieret (1996)) indicate that *L. maackii* seeds germinate year-round. The findings of this study show the potential for additional germination outside the growing season, as seeds germinated under mean daily temperatures from 2.3-6.3 °C.

To my knowledge, it has not been determined whether this ability to germinate at varied temperature is advantageous, or increases the risk of seedling mortality. If germination of seedlings under flooded conditions is not matched closely with drawdown, this may ultimately contribute to mortality. This study demonstrated the potential of *L. maackii* to germinate soon after being transferred from cold/moist to cold/inundated conditions--environmental cues that signify the arrival of winter floods and may not be conducive to the survival of newly germinated seeds. Recently germinated seeds subjected to the pressure of winter flooding must contend with low-oxygen stress, water sheer stress, burial by sedimentation, as well as low/freezing temperatures. Additionally, small seedlings may not have developed the root systems sufficient for tolerating harsh winter conditions. Although soft tissues of adult plants have been shown to tolerate episodes of freezing temperatures (McEwan et al. 2009), the

resilience of young seedlings, to my knowledge, has not been studied. Therefore, it is unknown whether seedlings established in autumn or winter contribute significantly to *L. maackii* recruitment in either upland or wetland habitats. Because seeds began germinating after only a month, it was not possible to evaluate the potential of *L. maackii* seeds to remain viable and germinate after several months of flooding—as could occur with winter floods. It is possible that more consistent and/or lower temperatures would have stalled the germination of seeds, allowing evaluation of viability under longer flooding scenarios. However, the temperatures in this study were within the bounds of the normal monthly winter temperatures experienced over a significant portion of *L. maackii*'s invasion range in the United States, and thus may accurately reflect the winter and early spring germination potential of *L. maackii* in these areas (NRCS 2015).

Vulnerability to microbes under field conditions is another variable not evaluated by this study, and a factor that is likely to impact the germinability and mortality of seeds in the field. Relative susceptibility of seeds to infection under flooded as opposed to upland conditions would also need to be evaluated. Orrock et al. (2012) found that *L. maackii* was more susceptible to seed mortality due to fungal pathogens than two native shrub species. Blaney and Kotanen (2001) buried seeds of upland non-native and native species in wetland and upland soils, and then assessed the germination potential of these seeds in a greenhouse under moist conditions. The germination of seeds buried in wetland soils was lower than those in upland soils, and the number of seeds germinated increased when fungicide was applied, implicating greater seed loss due to fungal infection. Thus, fungal activity was implicated in explaining high seed mortality in wetland soils, and it was suggested that this might be one mechanism by which upland

species are excluded from wetland areas. Studies in tropical forests also provide evidence for greater activity of soil plant pathogens with increasing soil moisture (Augspurger 1983, Augspurger and Kelly 1984). Certainly, the longer germination time under flooded conditions would increase the probability of seeds being lost to microbial infection. Based on these findings, it is reasonable to suspect that the high germinability of seeds under sterile, inundated conditions in this experiment may overestimate germinability in the field.

Conclusions

Previous studies have shown that the presence of *Lonicera maackii* is restricted to higher elevation areas in bottomland hardwood forests. This study examined the potential of flooding—during or after cold stratification—to serve as an ecological filter limiting the passage of *L. maackii* past the seed stage in these environments. Mean germination time, but not germinability, differed significantly between moist controls and treatments simulating moist to inundated transitions. Seeds subjected to inundated or saturated conditions during the stratification period and followed by simulated drawdown had mean germination times and germinability similar to moist controls. This finding advances the possibility that seeds of *L. maackii* seeds can remain viable in flooded areas, and germinate successfully after drawdown. These results also suggest that temporary, winter flooding of wetland microsites may not impose a major limitation on *L. maackii* germination.

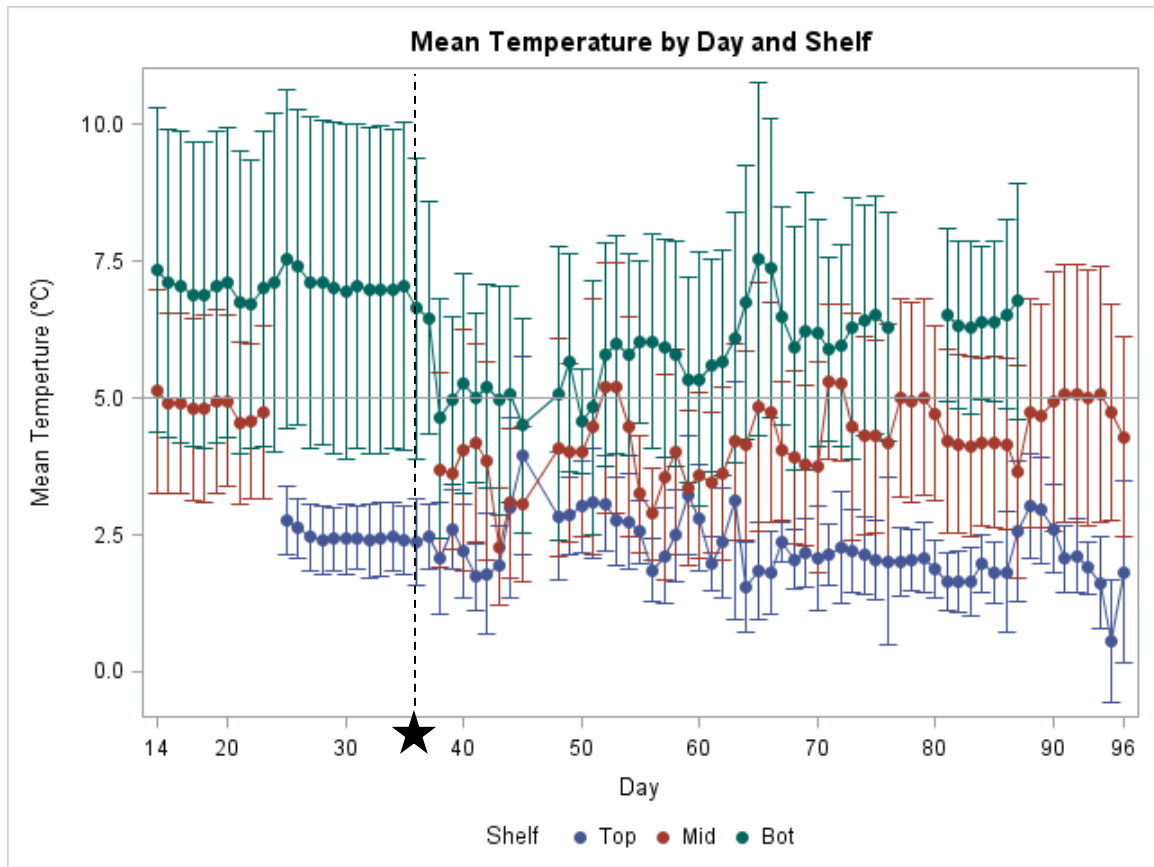


Figure 4-1. Mean daily temperature in experimental chamber (refrigerator) from days 14-96. Error bars indicate ± 1 S.D. The horizontal line indicates 5 °C. Breaks in graph lines indicate missing data. The black star indicates when germination was first noted at day 34. On Day 38 the temperature in the unit was reduced purposely so that bottom shelf could be closer to the target temperature of 5 °C. Trays containing seed plates were rotated between shelves as described in *Methods*.

Table 4-1. Summary of stratification and post-stratification treatments for all five treatment groups in germination assay.

Stratification Treatment	Post-Stratification Treatment	Transition simulates flooding/drawdown?
Moist	Moist	No flooding (control)
Moist	Inundated	Flooding
Moist	Saturated	Flooding
Inundated	Moist	Drawdown
Saturated	Moist	Drawdown

Table 4-2. Means of mean germination time (MGT) for all flooding treatments and moist controls. Means with different letters indicate a significant difference $p \leq 0.05$ between treatments according to the Tukey-Kramer test.

Flooding Treatment	n	Mean Germination Time (days)	Std. Dev	Minimum	Maximum
Control (Moist)	20	59.8 ^{ac}	4.04	51.8	67.3
Inundated → Moist	10	62.1 ^b	3.57	55.1	67.5
Moist → Inundated	10	64.8 ^{ab}	5.87	56.4	73.8
Moist → Saturated	10	61.5 ^{ab}	4.10	55.6	68.6
Saturated → Moist	10	61.3 ^{ab}	3.90	53.5	66.4

Table 4-3. Means of total seed germinability of flooding treatments (as a percentage). Global tests of fixed effects show no significant difference between groups. Values for n indicate the number of containers per treatment. Minimum and maximum values correspond to the minimum and maximum values of germinability observed among n containers in each flooding treatment group.

Flooding Treatment	n	Germinability	Std. Dev	Minimum	Maximum
Control (Moist)	20	91.5	6.4	80.0	100.0
Inundated → Moist	10	88.3	8.5	76.7	100.0
Moist → Inundated	10	88.7	7.6	70.0	96.7
Moist → Saturated	10	90.7	3.8	83.3	96.7
Saturated → Moist	10	90.0	7.5	76.7	100.0

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Appendix Table 1. Summary of all environmental variables measured for all sites.

Site	Per. Transect	Parallel Transect	% Herb Cover ±SE		% Bare Soil ±SE		% Leaf Litter ±SE		% CWD ±SE		% Canopy Closure ±SE		LA
1	N1	1	14	8	32	6	68	6	3	3	90	1	5.23
1	N1	5	11	9	6	3	74	24	2	1	84	2	4.32
1	N1	10	18	15	3	0	98	0	9	8	87	3	4.4
1	N1	30	3	0	3	0	98	0	0	0	90	3	4.59
1	N1	60	6	3	49	12	39	14	0	0	89	2	4.44
1	N2	1	9	4	6	3	79	6	28	3	87	1	4.92
1	N2	5	6	3	74	6	26	6	7	3	86	2	4.62
1	N2	10	14	8	79	6	21	6	3	2	87	2	4.85
1	N2	30	23	9	14	8	83	7	2	1	76	6	4.23
1	N2	60	26	6	3	0	94	3	4	2	88	2	4.49
1	S1	1	32	6	9	4	91	4	3	2	92	2	3.83
1	S1	5	18	7	3	0	91	4	1	1	90	2	3.75
1	S1	10	56	18	6	3	94	3	1	1	93	1	4.08
1	S1	30	3	0	3	0	94	3	1	1	92	2	4.58
1	S1	60	3	0	85	0	15	0	0	0	93	2	4.23
1	S2	1	3	0	3	0	91	4	1	0	92	1	4.76
1	S2	5	6	3	23	9	74	6	2	2	91	3	4.31
1	S2	10	3	0	18	7	71	13	0	0	93	3	4.43
1	S2	30	6	3	9	4	88	3	4	2	97	1	4.17
1	S2	60	12	3	15	0	85	0	1	1	95	2	4.21
2	N1	1	62	17	3	0	94	3	0	0	97	1	1.96
2	N1	5	32	6	6	3	74	6	1	1	97	1	2.35
2	N1	10	71	13	3	0	94	3	4	2	94	1	2.51
2	N1	30	36	16	14	8	65	18	7	4	95	1	2.97

Site	Per. Transect	Parallel Transect	% Herb Cover ±SE		% Bare Soil ±SE		% Leaf Litter ±SE		% CWD ±SE		% Canopy Closure ±SE		LA
2	N1	60	3	0	3	0	98	0	1	1	93	1	2.78
2	N2	1	74	6	18	7	83	7	1	1	94	1	2.33
2	N2	5	68	6	3	0	98	0	3	2	91	3	2.32
2	N2	10	94	3	9	4	88	3	0	0	83	3	2.69
2	N2	30	56	15	15	0	74	6	27	6	83	5	3.23
2	N2	60	68	22	3	0	94	3	1	1	90	1	2.57
2	S1	1	59	14	3	0	98	0	0	0	91	4	4.17
2	S1	5	14	8	6	3	88	3	13	6	91	2	3.45
2	S1	10	59	19	3	0	88	3	5	2	89	3	2.85
2	S1	30	73	12	3	0	91	4	8	3	85	3	2.31
2	S1	60	94	3	3	0	98	0	3	3	90	4	2.33
2	S2	1	77	9	12	3	88	3	0	0	95	3	2.62
2	S2	5	14	8	9	4	83	7	2	1	95	0	3.57
2	S2	10	77	9	3	0	98	0	0	0	91	2	3.17
2	S2	30	89	9	3	0	98	0	0	0	88	3	2.35
2	S2	60	88	3	26	24	71	23	0	0	93	1	2.67
3	N1	1	94	3	3	0	98	0	0	0	83	3	2.72
3	N1	5	76	13	3	0	98	0	0	0	95	1	4.78
3	N1	10	38	17	6	3	94	3	4	2	93	2	4.84
3	N1	30	11	9	18	15	83	15	0	0	89	2	4.11
3	N1	60	33	11	3	0	94	3	1	0	93	1	4.18
3	N2	1	94	3	3	0	98	0	0	0	78	8	3.53
3	N2	5	68	6	3	0	98	0	0	0	96	1	4
3	N2	10	68	6	3	0	98	0	0	0	89	1	3.75
3	N2	30	29	19	3	0	98	0	0	0	94	2	4.05

Site	Per. Transect	Parallel Transect	% Herb Cover ±SE		% Bare Soil ±SE		% Leaf Litter ±SE		% CWD ±SE		% Canopy Closure ±SE		LAI
3	N2	60	44	11	3	0	98	0	0	0	87	6	4.12
3	S1	1	80	10	3	0	94	3	0	0	90	4	2.19
3	S1	5	68	11	44	24	56	24	4	3	95	1	2.52
3	S1	10	77	9	64	21	33	22	3	2	91	2	2.66
3	S1	30	32	20	3	0	98	0	0	0	91	2	2.76
3	S1	60	44	11	6	3	94	3	1	0	93	3	4.52
3	S2	1	94	3	91	4	9	4	2	1	81	1	3.45
3	S2	5	77	9	91	4	9	4	2	1	81	5	4.36

Appendix Table 2. Legend of species codes used in NMS ordination graphs.

Species	Code
TREES	
<i>Acer</i> sp.	ACER
<i>Acer rubrum</i>	AcRu
<i>Asimina triloba</i>	AsTr
<i>Celtis laevigata</i>	CeLa
<i>Diospyros virginiana</i>	DiVi
<i>Fraxinus pennsylvanica</i>	FrPe
<i>Liriodendron styraciflua</i>	LiSt
<i>Nyssa sylvatica</i>	NySy
<i>Quercus bicolor</i>	QuBi
<i>Quercus michauxii</i>	QuMi
<i>Quercus palustris</i>	QuPa
<i>Ulmus rubra</i>	UIRu
SHRUBS	
<i>Cephalanthus occidentalis</i>	CeOc
<i>Cornus foemina</i>	CoFo
<i>Lindera benzoin</i>	LiBe
<i>Lonicera maackii</i>	LoMa
Rosaceae	ROSA
<i>Rubus</i> sp.	RUBU
<i>Sambucus canadensis</i>	SaCa
VINES	
<i>Campsis radicans</i>	CaRa
<i>Euonymus fortunei</i>	EuFo
<i>Lonicera japonica</i>	LoJa
<i>Menispermum canadense</i>	MeCa
<i>Parthenocissus quinquefolia</i>	PaQu
<i>Smilax</i> sp.	SMIL
<i>Toxicodendron radicans</i>	ToRa
Vitaceae	VITA

Appendix Table 3. Mean density, basal area and importance values for adult trees (>2.5 cm dbh) in forest edges in interiors. Values are averaged over four edge and interior 12x12m plots per site (8 plots per site).

Site	Species	Edge						Interior					
		Mean Density	Std. Error	Mean IV	Std. Error	Mean BA	Std. Error	Mean Density	Std. Error	Mean IV	Std. Error	Mean BA	Std. Error
1	<i>Acer negundo</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Acer rubrum</i>	712	265	33	4	14.7	2.5	469	182	49	7	27.0	5.8
1	<i>Acer saccharinum</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Carya</i>	17	17	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Celtis laevigata</i>	35	20	1	0	0.0	0.0	35	35	6	6	2.6	2.6
1	<i>Cornus florida</i>	17	17	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Diospyros virginiana</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Fagus grandifolia</i>	17	17	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Fraxinus pennsylvanica</i>	365	173	22	7	9.7	3.3	260	171	24	11	11.1	5.4
1	<i>Juniperus virginiana</i>	35	35	1	1	0.5	0.5	0	0	0	0	0.0	0.0
1	<i>Liquidambar styraciflua</i>	174	104	13	9	11.3	10.2	87	66	4	2	0.3	0.2
1	<i>Liriodendron tulipifera</i>	104	60	5	3	3.2	2.0	0	0	0	0	0.0	0.0
1	<i>Nyssa sylvatica</i>	35	35	2	2	1.2	1.2	0	0	0	0	0.0	0.0
1	<i>Platanus occidentalis</i>	104	45	5	2	2.8	1.1	104	66	14	10	5.5	3.8
1	<i>Populus deltoides</i>	35	20	2	2	1.1	1.0	0	0	0	0	0.0	0.0
1	<i>Quercus bicolor</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Quercus lyrata</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Quercus palustris</i>	17	17	1	1	0.3	0.3	17	17	2	2	0.0	0.0
1	<i>Salix nigra</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
1	<i>Ulmus americana</i>	17	17	1	1	0.8	0.8	17	17	2	2	0.9	0.9
1	<i>Ulmus rubra</i>	226	72	12	6	1.1	0.4	17	17	1	1	0.0	0.0
	TOTAL	1910		100		46.8		1007		100		47.4	
2	<i>Acer negundo</i>	17	17	1	1	0.2	0.2	17	17	1	1	0.1	0.1
2	<i>Acer rubrum</i>	399	87	29	5	16.9	4.6	313	128	34	7	19.9	8.4
2	<i>Acer saccharinum</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Carya</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0

Site	Species	Edge						Interior					
		Mean Density	Std. Error	Mean IV	Std. Error	Mean BA	Std. Error	Mean Density	Std. Error	Mean IV	Std. Error	Mean BA	Std. Error
2	<i>Celtis laevigata</i>	677	187	25	5	6.1	2.0	382	174	23	9	2.7	0.9
2	<i>Cornus florida</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Diospyros virginiana</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Fagus grandifolia</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Fraxinus pennsylvanica</i>	174	104	6	4	1.7	1.4	243	115	23	6	12.7	3.9
2	<i>Juniperus virginiana</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Liquidambar styraciflua</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Liriodendron tulipifera</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Nyssa sylvatica</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Platanus occidentalis</i>	17	17	5	5	2.9	2.9	0	0	0	0	0.0	0.0
2	<i>Populus deltoides</i>	52	33	5	5	2.2	2.2	69	69	10	10	9.2	9.2
2	<i>Quercus bicolor</i>	17	17	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Quercus lyrata</i>	0	0	0	0	0.0	0.0	17	17	4	4	1.8	1.8
2	<i>Quercus palustris</i>	87	33	10	7	10.4	9.9	0	0	0	0	0.0	0.0
2	<i>Salix nigra</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Ulmus americana</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
2	<i>Ulmus rubra</i>	382	146	18	7	5.2	2.2	69	49	5	4	0.4	0.2
	TOTAL	1823		100		45.5		1111		100		46.8	
3	<i>Acer negundo</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Acer rubrum</i>	729	454	29	8	11.3	3.8	938	500	41	11	11.5	4.2
3	<i>Acer saccharinum</i>	52	33	2	1	0.3	0.3	0	0	0	0	0.0	0.0
3	<i>Carya</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Celtis laevigata</i>	365	365	11	11	3.5	3.5	208	208	14	14	2.1	2.1
3	<i>Cornus florida</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Diospyros virginiana</i>	52	33	1	1	0.1	0.1	0	0	0	0	0.0	0.0
3	<i>Fagus grandifolia</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0

Site	Species	Edge						Interior					
		Mean Density	Std. Error	Mean IV	Std. Error	Mean BA	Std. Error	Mean Density	Std. Error	Mean IV	Std. Error	Mean BA	Std. Error
3	<i>Fraxinus pennsylvanica</i>	694	235	24	6	7.0	2.7	313	205	17	6	7.1	2.6
3	<i>Juniperus virginiana</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Liquidambar styraciflua</i>	69	40	3	3	0.7	0.7	17	17	7	7	5.4	5.4
3	<i>Liriodendron tulipifera</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Nyssa sylvatica</i>	139	139	7	7	0.9	0.9	0	0	0	0	0.0	0.0
3	<i>Platanus occidentalis</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Populus deltoides</i>	35	35	1	1	0.1	0.1	17	17	1	1	0.5	0.5
3	<i>Quercus bicolor</i>	35	35	1	1	0.0	0.0	17	17	4	4	1.8	1.8
3	<i>Quercus lyrata</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Quercus palustris</i>	330	284	9	8	1.3	0.9	69	49	11	6	6.0	3.7
3	<i>Salix nigra</i>	52	52	4	4	1.1	1.1	0	0	0	0	0.0	0.0
3	<i>Ulmus americana</i>	0	0	0	0	0.0	0.0	0	0	0	0	0.0	0.0
3	<i>Ulmus rubra</i>	139	49	8	3	3.7	2.0	104	45	5	2	0.7	0.3
	TOTAL	2691		100		30.1		1684		100		35.0	

Appendix Table 4. Results of mixed model regression testing for effects of site, side (north vs. south edge orientation) and position (edge vs. interior position) on adult tree species richness (PROC MIXED, SAS 9.4). Shannon diversity was based on basal area of adults and was modeled with fixed effects only because of overfitting when random effects were included (see Statistical Analysis). Bolded p-values are significant at the 0.05 level.

Fixed Effects				
Response	Effect	DF	Chi-Square	p
Species Richness	Site	2	0.39	0.8232
	Side	1	0.23	0.6313
	Position (Edge vs. Interior)	1	7.83	0.0051
	Site*Side	2	0.19	0.9099
	Side*Position	1	0.03	0.8555
	Site*Position	2	0.79	0.6746
	Site*Side*Position	2	0.7	0.7036

Appendix Table 5. Shannon-Weiner diversity index values (H) and species richness of all woody vegetation layers, across all sites and with distance from edge. Values of H are based on basal area and percent cover for adult trees and vines, respectively, and stem density for all other vegetation layers. For adult trees, 12 x 12 m edge plots began at the forest edge and extended 12 m in, and interior plots were centered at 60 m from the edge. All other data was collected by subsampling in parallel 12 x 2 m transects centered at 1, 5, 10, 30 and 60 m from the forest edge, in four locations per site. Values in bold represent the highest values of H and species richness within each vegetation layer and site, and across sites.

Layer	Distance from Edge	n	Site 3: Wet Site		Site 2: Intermediate Site		Site 1: Dry Site		Across Sites	
			Mean H ±SE		Mean H ±SE		Mean H ±SE		Mean H ±SE	
Adults	EDGE	4	1.37	0.17	1.22	0.12	1.38	0.20	1.32	0.05
Adults	INT	4	1.17	0.15	0.95	0.13	0.87	0.07	1.00	0.09
Sapling	1 m	4	0.79	0.15	0.98	0.22	1.35	0.21	1.04	0.16
Sapling	5 m	4	1.13	0.23	0.63	0.26	1.15	0.19	0.97	0.17
Sapling	10 m	4	1.01	0.16	0.98	0.21	0.92	0.31	0.97	0.03
Sapling	30 m	4	0.53	0.31	0.73	0.10	0.94	0.10	0.73	0.12
Sapling	60 m	4	0.65	0.28	0.34	0.23	1.07	0.18	0.68	0.21
Seedling	1 m	4	0.65	0.26	0.50	0.23	0.61	0.35	0.59	0.04
Seedling	5 m	4	0.45	0.26	0.39	0.23	0.35	0.20	0.39	0.03
Seedling	10 m	4	0.31	0.13	0.59	0.29	0.77	0.32	0.56	0.13
Seedling	30 m	4	0.40	0.27	0.34	0.26	0.80	0.17	0.51	0.14
Seedling	60 m	4	0.36	0.20	0.37	0.17	0.49	0.31	0.41	0.04
Shrubs	1 m	4	0.54	0.24	0.00	0.00	0.77	0.28	0.44	0.23
Shrubs	5 m	4	0.26	0.15	0.37	0.21	0.73	0.25	0.45	0.14
Shrubs	10 m	4	0.17	0.17	0.16	0.16	0.72	0.15	0.35	0.18
Shrubs	30 m	4	0.53	0.19	0.40	0.15	0.82	0.12	0.58	0.12
Shrubs	60 m	4	0.06	0.06	0.10	0.10	0.89	0.03	0.35	0.27
Vines	1 m	4	0.48	0.22	0.68	0.16	1.14	0.13	0.77	0.20
Vines	5 m	4	0.57	0.20	0.60	0.10	0.96	0.29	0.71	0.12
Vines	10 m	4	0.61	0.25	0.44	0.24	0.64	0.22	0.56	0.06
Vines	30 m	4	0.30	0.18	0.44	0.27	1.12	0.27	0.62	0.25
Vines	60 m	4	0.13	0.09	0.45	0.12	1.11	0.17	0.56	0.29

Appendix Table 6. Results of mixed model regression testing for significance of fixed and random effects on sapling (dbh <2.5 cm, >0.5 dbh) species richness. Modeled fixed effects were *site*, *side* (north vs. south edge), *position* (edge or interior location), 2 and 3 way interactions between these variables. Edge-to-interior transect (in table as EITransect) was included as a random blocking effect, nested within each site and side.

	Fixed Effects					Random Effects				
	Effect	Num DF	Den DF	F Value	p	Covariance Parameter	Estimate	Standard Error	Z Value	p
Species Richness	Site	2	6	0.16	0.8542	EITransect(Site*side)	0.009923	0.04221	0.24	0.4071
	Side	1	6	2.62	0.1569					
	Distance from Edge	1	42	6.81	0.0125					
	Site*Side	2	6	1.57	0.2824					
	Side*Distance from Edge	1	42	0.08	0.7789					
	Site*Distance from Edge	2	42	0.41	0.6636					
	Site*Side*Distance from Edge	2	42	0.8	0.458					

Appendix Table 7. Mean frequencies, densities and IV values for saplings at varying distance from the forest edge, at each site, and across sites. The highest density and IV values at each distance and site (and across sites) are in bold.

Dist.	Species	Site 3: Wet Site						Site 2: Intermediate						Site 1: Dry Site						Overall Means (Across Sites)			
		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean IV \pm SE	Mean Density \pm SE		
1	<i>Acer rubrum</i>	0.19	0.12	625	442	5	3	0.19	0.12	1563	1362	7	4	0.25	0.18	1094	898	7	5	7	0	1094	271
1	<i>Acer saccharinum</i>	0.06	0.06	156	156	1	1	0.06	0.06	156	156	1	1	0.06	0.06	156	156	1	1	1	0	156	0
1	<i>Celtis laevigata</i>	0.00	0.00	0	0	0	0	0.44	0.19	3438	1813	15	5	0.38	0.22	1094	693	18	14	11	2	1510	1014
1	<i>Diospyros virginiana</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	1	1	0	0	52	52
1	<i>Fraxinus pennsylvanica</i>	0.63	0.22	13750	7548	43	17	0.81	0.19	18750	6832	46	12	0.50	0.23	2656	1452	23	8	37	7	11719	4756
1	<i>Liquidambar styraciflua</i>	0.25	0.25	3438	3438	8	8	0.00	0.00	0	0	0	0	0.44	0.21	1563	972	15	7	8	4	1667	994
1	<i>Liriodendron tulipifera</i>	0.06	0.06	156	156	1	1	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0	0	52	52
1	<i>Nyssa sylvatica</i>	0.19	0.19	469	469	3	3	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	1	0	156	156
1	<i>Platanus occidentalis</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	8	8	3	2	52	52
1	<i>Quercus bicolor</i>	0.06	0.06	156	156	1	1	0.06	0.06	156	156	2	2	0.00	0.00	0	0	0	0	1	1	104	52
1	<i>Quercus michauxii</i>	0.06	0.06	156	156	1	1	0.00	0.00	0	0	0	0	0.06	0.06	156	156	3	3	2	1	104	52
1	<i>Quercus palustris</i>	0.63	0.16	2344	822	24	10	0.31	0.19	2188	1362	10	6	0.13	0.07	313	180	10	8	15	2	1615	653
1	<i>Salix nigra</i>	0.00	0.00	0	0	0	0	0.06	0.06	625	625	8	8	0.00	0.00	0	0	0	0	3	2	208	208
1	<i>Sassafras albidum</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	1	1	0	0	52	52
1	<i>Ulmus rubra</i>	0.25	0.18	781	592	10	9	0.31	0.12	938	403	11	6	0.31	0.19	1250	722	9	5	10	1	990	138
1	Unidentified	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.07	313	180	3	2	1	1	104	104

		Site 3: Wet Site						Site 2: Intermediate						Site 1: Dry Site						Overall Means (Across Sites)			
Dist.	Species	Mean Freq. ± SE		Mean Density ± SE		Mean IV ± SE		Mean Freq. ± SE		Mean Density ± SE		Mean IV ± SE		Mean Freq. ± SE		Mean Density ± SE		Mean IV ± SE		Mean IV ± SE	Mean Density ± SE		
5	<i>Acer rubrum</i>	0.38	0.13	2656	1123	28	11	0.06	0.06	156	156	6	6	0.06	0.06	156	156	8	8	14	2	990	833
5	<i>Celtis laevigata</i>	0.25	0.25	781	781	7	7	0.38	0.24	1094	738	27	16	0.19	0.12	625	442	20	15	18	3	833	138
5	<i>Crataegus spp.</i>	0.06	0.06	156	156	2	2	0.06	0.06	156	156	3	3	0.00	0.00	0	0	0	0	2	1	104	52
5	<i>Fraxinus pennsylvanica</i>	0.50	0.23	5938	3998	31	12	0.13	0.07	313	180	10	6	0.19	0.12	781	469	16	10	19	3	2344	1802
5	<i>Liquidambar styraciflua</i>	0.19	0.19	2500	2500	5	5	0.00	0.00	0	0	0	0	0.13	0.07	313	180	13	8	6	4	938	786
5	<i>Liriodedron tulipifera</i>	0.06	0.06	156	156	1	1	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0	0	52	52
5	<i>Nyssa sylvatica</i>	0.25	0.25	2656	2656	6	6	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	2	1	885	885
5	<i>Quercus bicolor</i>	0.06	0.06	156	156	2	2	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	1	0	52	52
5	<i>Quercus michauxii</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	2	1	52	52
5	<i>Quercus palustris</i>	0.25	0.10	1094	534	7	2	0.13	0.07	313	180	8	4	0.19	0.06	469	156	17	7	11	3	625	239
5	<i>Ulmus rubra</i>	0.25	0.18	938	744	11	9	0.25	0.25	938	938	21	21	0.19	0.12	625	361	17	10	16	1	833	104
5	Unidentified	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	2	1	52	52
10	<i>Acer rubrum</i>	0.50	0.29	1875	1112	24	15	0.06	0.06	156	156	6	6	0.00	0.00	0	0	0	0	10	3	677	601
10	<i>Celtis laevigata</i>	0.19	0.12	938	541	6	4	0.38	0.13	1719	738	46	11	0.06	0.06	156	156	4	4	19	12	938	451
10	<i>Fraxinus pennsylvanica</i>	0.50	0.23	6563	5355	32	11	0.06	0.06	313	313	7	7	0.25	0.10	938	403	22	9	20	5	2604	1987
10	<i>Liquidambar styraciflua</i>	0.19	0.19	1406	1406	5	5	0.00	0.00	0	0	0	0	0.06	0.06	156	156	8	8	4	2	521	445
10	<i>Nyssa sylvatica</i>	0.19	0.19	2344	2344	6	6	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	2	1	781	781
10	<i>Prunus spp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	4	4	1	1	52	52
10	<i>Quercus bicolor</i>	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	0.00	0.00	0	0	0	0	2	1	52	52

Dist.	Species	Site 3: Wet Site						Site 2: Intermediate						Site 1: Dry Site						Overall Means (Across Sites)			
		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean IV \pm SE	Mean Density \pm SE		
10	<i>Quercus michauxii</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.13	313	313	6	6	2	2	104	104
10	<i>Quercus palustris</i>	0.19	0.06	469	156	18	11	0.19	0.06	625	255	17	6	0.19	0.19	781	781	11	11	15	2	625	90
10	<i>Ulmus rubra</i>	0.13	0.13	469	469	7	7	0.13	0.07	313	180	19	12	0.25	0.10	781	299	20	8	15	1	521	138
10	Unidentified	0.06	0.06	156	156	2	2	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	1	0	52	52
30	<i>Acer rubrum</i>	0.25	0.10	938	313	36	22	0.00	0.00	0	0	0	0	0.06	0.06	156	156	8	8	15	4	365	290
30	<i>Asimina triloba</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.19	0.12	1250	884	24	14	8	7	417	417
30	<i>Celtis laevigata</i>	0.00	0.00	0	0	0	0	0.63	0.24	4375	1943	43	16	0.19	0.06	469	156	25	9	23	6	1615	1387
30	<i>Fraxinus pennsylvanica</i>	0.38	0.16	1875	1112	50	20	0.19	0.06	469	156	14	6	0.19	0.06	469	156	19	7	28	4	938	469
30	<i>Quercus palustris</i>	0.13	0.07	313	180	8	5	0.38	0.16	1250	571	20	10	0.06	0.06	156	156	5	5	11	4	573	342
30	<i>Ulmus rubra</i>	0.13	0.13	469	469	6	6	0.31	0.19	938	541	24	17	0.13	0.07	469	299	19	14	16	2	625	156
60	<i>Acer rubrum</i>	0.31	0.24	938	744	20	17	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	7	2	313	313
60	<i>Asimina triloba</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.19	0.19	1094	1094	13	13	4	4	365	365
60	<i>Carya spp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.07	313	180	7	4	2	2	104	104
60	<i>Celtis laevigata</i>	0.13	0.07	469	299	17	14	0.25	0.10	1875	807	54	21	0.13	0.13	469	469	9	9	27	13	938	469
60	<i>Diospyros virginiana</i>	0.00	0.00	0	0	0	0	0.06	0.06	156	156	4	4	0.00	0.00	0	0	0	0	1	1	52	52
60	<i>Fraxinus pennsylvanica</i>	0.19	0.12	1094	898	20	11	0.19	0.12	469	299	17	10	0.31	0.06	1406	393	32	7	23	4	990	276
60	<i>Liquidambar styraciflua</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.13	313	313	17	17	6	5	104	104
60	<i>Quercus bicolor</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	6	6	2	2	52	52
60	<i>Quercus michauxii</i>	0.06	0.06	156	156	25	25	0.00	0.00	0	0	0	0	0.06	0.06	156	156	4	4	10	3	104	52

Dist.	Species	Site 3: Wet Site						Site 2: Intermediate						Site 1: Dry Site						Overall Means (Across Sites)			
		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean Freq. \pm SE		Mean Density \pm SE		Mean IV \pm SE		Mean IV \pm SE		Mean Density \pm SE	
60	<i>Quercus palustris</i>	0.25	0.14	625	361	13	8	0.00	0.00	0	0	0	0	0.06	0.06	156	156	4	4	6	2	260	188
60	<i>Ulmus rubra</i>	0.13	0.13	313	313	5	5	0.00	0.00	0	0	0	0	0.13	0.07	313	180	9	6	5	3	208	104

Appendix Table 8. Results of mixed model regression testing for significance of fixed and random effects on species richness in the tree seedling stratum (dbh<0.3m). Modeled fixed effects were *site*, *side* (north vs. south edge), *position* (edge or interior location), 2 and 3 way interactions between these variables. Edge-to-interior transect (in table as EITransect) was included as a random effect, nested within each site and side.

Fixed Effects						Random Effects				
Response	Effect	Num DF	Den DF	F Value	p	Covariance Parameter	Estimate	Standard Error	Z Value	p
Total Stems	Site	2	6	0.51	0.6227	EITransect(Site*Side)	0.5513	0.4121	1.34	0.0905
	Side	1	6	4.37	0.0815	Scale	0.5775	0.1697	3.4	0.0003
	Distance from Edge	1	41	3.75	0.0598					
	Site*Side	2	6	1.49	0.2985					
	Side*Distance from Edge	1	41	6.26	0.0164					
	Site*Distance from Edge	2	41	1.41	0.2558					
	Site*Side*Distance from Edge	2	41	0.39	0.6793					
Richness	Site	2	6	0.41	0.6812	EITransect(Site*Side)	0.1098	0.1143	0.96	0.1685
	Side	1	6	4.14	0.0881					
	Distance from Edge	1	42	0.15	0.7019					
	Site*Side	2	6	0.88	0.4617					
	Side*Distance from Edge	1	42	2.23	0.1431					
	Site*Distance from Edge	2	42	0.08	0.9227					
	Site*Side*Distance from Edge	2	42	0.15	0.8618					

Appendix Table 9. Mean frequencies, densities and IV values for all tree seedlings at varying distances from the forest edge (in meters), at each site, and across sites. The highest density and IV values at each distance and site (and across sites) are in bold.

Dist.	Species	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site						Across Sites			
		Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE								
1	<i>Acer spp.</i>	0.06	0.06	156	156	13	13	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	52	52	4	4
1	<i>Celtis laevigata</i>	0.06	0.06	156	156	10	10	0.13	0.07	469	299	15	8	0.13	0.07	313	180	33	24	313	90	19	7
1	<i>Fraxinus pennsylvanica</i>	0.19	0.06	1406	822	44	22	0.19	0.06	4063	3447	41	15	0.06	0.06	313	313	7	7	1927	1113	31	12
1	<i>Liquidambar styraciflua</i>	0.06	0.06	469	469	8	8	0.00	0.00	0	0	0	0	0.06	0.06	313	313	7	7	260	138	5	3
1	<i>Quercus palustris</i>	0.06	0.06	313	313	7	7	0.13	0.07	313	180	20	12	0.06	0.06	156	156	8	8	260	52	12	4
1	<i>Rosaceae</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	52	52	2	2
1	<i>Ulmus rubra</i>	0.13	0.07	313	180	17	12	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	156	90	8	5
1	Unidentified	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	8	8	52	52	3	3
5	<i>Acer spp.</i>	0.06	0.06	156	156	6	6	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	52	52	2	2
5	<i>Carya sp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	13	13	52	52	4	4
5	<i>Celtis laevigata</i>	0.00	0.00	0	0	0	0	0.13	0.07	938	598	24	14	0.06	0.06	625	625	7	7	521	276	10	7
5	<i>Diospyros virginiana</i>	0.00	0.00	0	0	0	0	0.06	0.06	156	156	6	6	0.00	0.00	0	0	0	0	52	52	2	2
5	<i>Fraxinus pennsylvanica</i>	0.13	0.07	2813	2065	24	14	0.13	0.07	625	442	39	24	0.19	0.06	2656	2047	63	24	2031	705	42	11
5	<i>Liquidambar styraciflua</i>	0.06	0.06	469	469	5	5	0.00	0.00	0	0	0	0	0.06	0.06	156	156	13	13	208	138	6	4
5	<i>Nyssa sylvatica</i>	0.13	0.07	313	180	29	24	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	104	104	10	10

Dist.	Species	Site 3: Wet Site				Site 2: Intermediate Site				Site 1: Dry Site				Across Sites									
		Mean Freq.	±SE	Mean Density (stems/ha)	Mean IV ±SE	Mean Freq.	±SE	Mean Density (stems/ha)	Mean IV ±SE	Mean Freq.	±SE	Mean Density (stems/ha)	Mean IV ±SE	Mean Density (stems/ha)	Mean IV ±SE								
5	<i>Quercus michauxii</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	52	52	2	2
5	<i>Quercus palustris</i>	0.13	0.07	469	299	11	6	0.06	0.06	156	156	6	6	0.00	0.00	0	0	0	0	208	138	6	3
10	<i>Celtis laevigata</i>	0.00	0.00	0	0	0	0	0.19	0.06	1094	693	42	21	0.19	0.06	938	403	46	22	677	342	29	15
10	<i>Diospyros virginiana</i>	0.00	0.00	0	0	0	0	0.06	0.06	156	156	3	3	0.00	0.00	0	0	0	0	52	52	1	1
10	<i>Fraxinus pennsylvanica</i>	0.25	0.00	8125	3545	74	9	0.13	0.07	2031	1180	25	16	0.06	0.06	313	313	5	5	3490	2370	34	20
10	<i>Liquidambar styraciflua</i>	0.06	0.06	469	469	5	5	0.00	0.00	0	0	0	0	0.13	0.07	938	598	18	11	469	271	8	5
10	<i>Liriodendron tulipifera</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	4	4	52	52	1	1
10	<i>Quercus palustris</i>	0.19	0.06	469	156	21	8	0.13	0.07	625	361	19	14	0.13	0.07	313	180	11	7	469	90	17	3
10	<i>Ulmus rubra</i>	0.00	0.00	0	0	0	0	0.13	0.07	313	180	11	7	0.06	0.06	156	156	9	9	156	90	7	3
10	Unidentified	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	7	7	52	52	2	2
30	<i>Carya sp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	9	9	52	52	3	3
30	<i>Celtis laevigata</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.07	1094	644	18	10	365	365	6	6
30	<i>Diospyros virginiana</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	52	52	2	2
30	<i>Fraxinus pennsylvanica</i>	0.13	0.07	2656	1775	25	16	0.13	0.07	11094	10886	26	17	0.19	0.06	1875	988	33	14	5208	2951	28	2
30	<i>Nyssa sylvatica</i>	0.13	0.07	313	180	29	24	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	104	104	10	10

Dist.	Species	Site 3: Wet Site				Site 2: Intermediate Site				Site 1: Dry Site				Across Sites									
		Mean Freq.	±SE	Mean Density (stems/ha)	Mean IV ±SE	Mean Freq.	±SE	Mean Density (stems/ha)	Mean IV ±SE	Mean Freq.	±SE	Mean Density (stems/ha)	Mean IV ±SE	Mean Density (stems/ha)	Mean IV ±SE								
30	<i>Prunus spp.</i>	0.00	0.00	0	0	0	0	0.06	0.06	156	156	8	8	0.00	0.00	0	0	0	0	52	52	3	3
30	<i>Quercus michauxii</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.07	313	180	14	9	104	104	5	5
30	<i>Quercus palustris</i>	0.19	0.06	2188	1409	41	21	0.13	0.07	469	299	33	24	0.06	0.06	469	469	16	16	1042	573	30	8
30	<i>Ulmus rubra</i>	0.06	0.06	625	625	5	5	0.06	0.06	938	938	7	7	0.06	0.06	156	156	5	5	573	227	6	1
60	<i>Asimina triloba</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	5	5	52	52	2	2
60	<i>Celtis laevigata</i>	0.00	0.00	0	0	0	0	0.19	0.06	625	255	43	22	0.13	0.07	625	361	19	12	417	208	21	13
60	<i>Fraxinus pennsylvanica</i>	0.25	0.00	10938	5440	71	12	0.13	0.07	5625	3489	33	19	0.13	0.07	781	469	21	13	5781	2933	41	15
60	<i>Liquidambar styraciflua</i>	0.06	0.06	156	156	3	3	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	52	52	1	1
60	<i>Prunus spp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	25	25	52	52	8	8
60	<i>Quercus palustris</i>	0.19	0.06	2500	2089	22	7	0.13	0.07	313	180	19	12	0.00	0.00	0	0	0	0	938	786	14	7
60	<i>Ulmus rubra</i>	0.06	0.06	313	313	4	4	0.06	0.06	156	156	5	5	0.13	0.07	313	180	30	24	260	52	13	9

Appendix Table 10. Results of mixed model regression testing for significance of fixed and random effects on shrub species richness. Modeled fixed effects were *site*, *side* (north vs. south edge), *position* (edge or interior location), 2 and 3 way interactions between these variables. Edge-to-interior transect (in table as EITransect) was included as a random effect, nested within site. Post-hoc pairwise comparisons of *L. japonica* cover between research sites are shown at the bottom. Adjusted P values were calculated using the Tukey-Kramer method.

Fixed Effects						Random Effects			
Response Variable	Effect	Num DF	Den DF	F Value	p	Covariance Parameter	Estimate	Standard Error	Z Value
Species Richness	Site	2	9	10.26	0.0048	EITransect(Site)	0.008172	0.07565	0.11 0.457
						Scale	0.3821	0.1436	2.66 0.0039
Between Site Comparisons: Differences of Least Squares Means									
Effect	Site	Site	Estimate	SE	DF	t Value	p	Adj P	
Site	2	1	-1.151	0.2666	9	-4.32	0.0019	0.005	
Site	2	3	-0.379	0.2813	9	-1.35	0.2105	0.4059	
Site	1	3	0.7715	0.2533	9	3.05	0.0139	0.0337	

Appendix Table 11. Mean frequencies, percent cover and IV values for all vine species at varying distance from the forest edge, at each site, and across sites. Bold values indicate the highest mean stem density or IV at each combination of distance and site. In the “Across Sites” column, the highest mean IV and stem density for species occurring at all sites is in bold.

Dist.	Species	Site 3				Site 2				Site 1				Across Sites									
		Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean IV ±SE	Mean Density (stems/ha) ±SE	Mean IV ±SE	Mean IV ±SE	Mean IV ±SE						
1	<i>Aralia spinosa</i>	0.06	0.06	469	469	2	2	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	156	156	1	1
1	<i>Cephalanthus occidentalis</i>	0.13	0.07	469	299	12	10	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	156	100	4	3
1	<i>Cornus foemina</i>	0.31	0.16	2031	1621	30	19	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	677	540	10	6
1	<i>Euonymus alatus</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	469	469	3	3	156	156	1	1
1	<i>Lindera benzoin</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.63	0.24	5313	2558	23	10	1771	853	8	3
1	<i>Lonicera maackii</i>	0.19	0.12	781	592	11	7	0.00	0.00	0	0	0	0	0.38	0.22	4219	2466	17	11	1667	743	9	3
1	<i>Rosa spp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	781	781	2	2	260	260	1	1
1	<i>Rubus spp.</i>	0.19	0.19	5469	5469	14	14	0.25	0.14	3594	2259	50	29	0.75	0.14	12031	3639	55	16	7031	930	39	5
1	<i>Sambucus canadensis</i>	0.06	0.06	156	156	2	2	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	52	52	1	1
1	<i>Symphoricarpos orbiculatus</i>	0.06	0.06	156	156	4	4	0.00	0.00	0	0	0	0	0.06	0.06	156	156	1	1	104	52	2	1
5	<i>Cephalanthus occidentalis</i>	0.13	0.07	469	299	7	5	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	156	100	2	2
5	<i>Cornus foemina</i>	0.50	0.14	13438	10994	85	9	0.06	0.06	469	469	3	3	0.13	0.13	2031	2031	7	7	5313	3279	32	2
5	<i>Lindera benzoin</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.56	0.21	7969	4659	28	12	2656	1553	9	4
5	<i>Lonicera maackii</i>	0.00	0.00	0	0	0	0	0.63	0.16	10000	3197	75	15	0.31	0.19	2500	1926	11	7	4167	929	29	4
5	<i>Rosa spp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.13	4375	4375	12	12	1458	1458	4	4
5	<i>Rubus spp.</i>	0.19	0.19	2969	2969	8	8	0.25	0.14	1719	1180	21	14	0.19	0.12	2188	1985	9	7	2292	517	13	2
5	<i>Sambucus canadensis</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.13	781	781	4	4	260	260	1	1
5	<i>Unidentified</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	938	938	3	3	313	313	1	1

Appendix Table 11 (cont'd)		Site 3: Wet Site				Site 2: Intermediate Site				Site 1: Dry Site				Across Sites									
Dist.	Species	Mean Freq. ±SE		Mean Density (stems/ha) ±SE		Mean IV ±SE		Mean Freq. ±SE		Mean Density (stems/ha) ±SE		Mean IV ±SE		Mean Freq. ±SE		Mean Density (stems/ha) ±SE		Mean IV ±SE					
10	<i>Cephalanthus occidentalis</i>	0.13	0.13	469	469	12	12	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	156	156	4	4
10	<i>Cornus foemina</i>	0.13	0.13	625	625	13	13	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	208	208	4	4
10	<i>Euonymus americanus</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	469	469	2	2	156	156	1	1
10	<i>Lindera benzoin</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.75	0.18	13125	5846	58	9	4375	1949	19	3
10	<i>Lonicera maackii</i>	0.00	0.00	0	0	0	0	0.56	0.12	6875	3217	92	8	0.38	0.16	3438	1624	24	11	3438	929	38	3
10	<i>Rubus spp.</i>	0.00	0.00	0	0	0	0	0.06	0.06	469	469	8	8	0.19	0.19	4219	4219	10	10	1563	1335	6	3
10	<i>Sambucus canadensis</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	2	2	52	52	1	1
10	<i>Unidentified</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	469	469	5	5	156	156	2	2
30	<i>Cornus foemina</i>	0.19	0.06	4688	3172	32	11	0.31	0.16	3906	2316	31	15	0.00	0.12	2969	2215	7	5	3854	303	24	3
30	<i>Lindera benzoin</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.75	0.18	16094	7673	46	15	5365	2558	15	5
30	<i>Lonicera maackii</i>	0.19	0.12	1094	644	29	17	0.31	0.12	5469	2171	44	18	0.38	0.16	8125	5007	20	10	4896	1278	31	2
30	<i>Prunus sp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	2	2	52	52	1	1
30	<i>Rosa spp.</i>	0.06	0.06	781	781	5	5	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	260	260	2	2
30	<i>Rubus spp.</i>	0.13	0.13	1250	1250	9	9	0.00	0.00	0	0	0	0	0.56	0.16	3438	1263	23	7	1563	419	11	3
30	<i>Sambucus canadensis</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	156	156	1	1	52	52	0	0
60	<i>Cornus foemina</i>	0.31	0.24	9375	9168	30	24	0.38	0.22	12500	10861	71	24	0.06	0.06	156	156	2	2	7344	3322	34	7
60	<i>Euonymus alatus</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	1094	1094	3	3	365	365	1	1
60	<i>Lindera benzoin</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.88	0.07	16719	2880	55	2	5573	960	18	1
60	<i>Lonicera maackii</i>	0.13	0.13	2188	2188	20	20	0.06	0.06	1875	1875	4	4	0.50	0.00	3750	884	22	3	2604	393	15	5
60	<i>Rubus spp.</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.25	0.14	2969	1829	12	7	990	610	4	2
60	<i>Sambucus canadensis</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.13	0.07	313	180	4	2	104	60	1	1
60	<i>Unidentified</i>	0.00	0.00	0	0	0	0	0.00	0.00	0	0	0	0	0.06	0.06	313	313	2	2	104	104	1	1

Appendix Table 12. Results of mixed model regression testing for significance of fixed effects on the density of *Lonicera maackii* (modeled as stem counts in each parallel transect). Modeled fixed effects were *site*, *side* (north vs. south edge), *position* (edge or interior location), 2 and 3 way interactions between these variables. P values are based on Type 3 tests of significance. Random effects (the block variable edge-to-interior transect) were omitted from this model due to concerns about over-fitting (see Methods, Statistical Analysis). Post-hoc pairwise comparisons of stem counts between research sites are shown at the bottom. Adjusted p values were calculated using the Tukey-Kramer method.

Fixed Effects								
Response	Effect		Num DF	Den DF	F Value	p		
<i>L. maackii</i> stems	Site		2	48	7.28	0.0017		
	Side		1	48	0.62	0.4338		
	Distance from Edge		1	48	0.02	0.8997		
	Site*Side		2	48	0.14	0.8696		
	Side*Distance from Edge		1	48	0.11	0.7419		
	Site*Distance from Edge		2	48	1.68	0.1976		
	Site*Side*Distance from Edge		2	48	1.04	0.3613		
	Between Site Comparisons: Differences of Least Squares Means							
Effect	Site	Site	Estimate	Standard Error	DF	t Value	p	Adj P
Site	2	1	-0.062	0.4908	48	-0.13	0.9001	0.9913
Site	2	3	2.0785	0.5644	48	3.68	0.0006	0.0017
Site	1	3	2.1404	0.5587	48	3.83	0.0004	0.0011

Appendix Table 13. Results of mixed model regression testing for significance of fixed and random effects on total cover of *Lonicera japonica*. Modeled fixed effects were *site*, *side* (north vs. south edge), *position* (edge or interior location), 2 and 3 way interactions between these variables. Edge-to-interior transect (in table as EITransect) was included as a random effect, nested within each site and side. Post-hoc pairwise comparisons of *L. japonica* cover between research sites are shown at the bottom. Adjusted p values were calculated using the Tukey-Kramer method.

Response	Effect	Fixed Effects				Random Effects				
		Num DF	Den DF	F Value	p	Covariance Parameter	Estimate	Standard Error	Z Value	p value
Total <i>L. japonica</i> Cover	Site	2	12.5	7.1	0.0087	EITransect(Site*side)	0.006757	0.007803	0.87	0.1933
	Side	1	12.5	0	0.9586	Scale	0.03266	0.007126	4.58	<.0001
	Distance from Edge	1	42	6.97	0.0116					
	Site*Side	2	12.5	3.64	0.0567					
	Side*Distance from Edge	1	42	0	0.9988					
	Site*Distance from Edge	2	42	0.25	0.7763					
	Site*Side*Distance from Edge	2	42	0.79	0.4616					
Between Site Comparisons: Differences of Least Squares Means										
Effect	Site	Site	Estimate	Standard Error	DF	t Value	p value	Adjustment	Adj P	
Site	2	1	-0.2695	0.08151	6	-3.31	0.0163	Tukey	0.0153	
Site	2	3	0.0441	0.08151	6	0.54	0.6081	Tukey	0.8529	
Site	1	3	0.3136	0.08151	6	3.85	0.0085	Tukey	0.0057	

Appendix Table 14. Mean frequencies, percent cover and IV values for all vine species at varying distance from the forest edge, at each site, and across sites. Bold values indicate the highest mean stem density or IV at each combination of distance and site. In the “Across Sites” column, the highest mean IV and stem density for species occurring at all sites is in bold.

Distance	Species	Site 3: Wet Site				Site 2: Intermediate Site				Site 1: Dry Site				Across Sites									
		Mean Freq. ±SE	Mean Percent Cover ±SE	Mean IV ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Percent Cover ±SE	Mean IV ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Percent Cover ±SE	Mean IV ±SE	Mean IV ±SE	Mean Percent Cover ±SE	Mean IV ±SE								
1	<i>Campsis radicans</i>	0.25	0.25	4.69	4.69	20	20	0.50	0.23	3.59	2.05	22	15	0.19	0.19	2.81	2.81	5	5	3.7	0.5	16	6
1	<i>Euonymus fortunei</i>	0.06	0.06	0.16	0.16	2	2	0.00	0.00	0.00	0.00	0	0	0.25	0.14	1.41	1.03	5	3	0.5	0.4	2	1
1	<i>Lonicera japonica</i>	0.44	0.26	11.41	9.81	20	12	0.50	0.20	8.91	6.91	15	6	0.88	0.07	22.50	4.63	33	5	14.3	4.2	23	5
1	<i>Parthenocissus quinifolia</i>	0.13	0.13	0.31	0.31	2	2	0.19	0.19	0.47	0.47	3	3	0.44	0.19	1.09	0.47	6	3	0.6	0.2	4	1
1	<i>Smilax spp.</i>	0.06	0.06	0.16	0.16	1	1	0.00	0.00	0.00	0.00	0	0	0.31	0.12	0.78	0.30	5	2	0.3	0.2	2	1
1	<i>Toxicodendron radicans</i>	0.75	0.14	15.00	10.29	53	17	0.75	0.18	39.22	21.17	43	15	0.88	0.07	28.13	10.52	35	3	27.4	7.0	44	5
1	<i>Vitaceae</i>	0.06	0.06	0.16	0.16	1	1	0.38	0.22	4.84	4.24	16	9	0.50	0.18	5.00	1.71	11	2	3.3	1.6	9	4
5	<i>Campsis radicans</i>	0.44	0.26	4.84	3.39	24	14	0.25	0.18	2.19	1.98	7	5	0.31	0.19	1.56	1.18	7	5	2.9	1.0	13	6
5	<i>Euonymus fortunei</i>	0.00	0.00	0.00	0.00	0	0	0.13	0.13	2.50	2.50	4	4	0.00	0.00	0.00	0.00	0	0	0.8	0.8	1	1
5	<i>Lonicera japonica</i>	0.13	0.13	1.25	1.25	10	10	0.50	0.18	5.16	2.39	12	4	0.88	0.07	25.00	12.01	50	10	10.5	7.4	24	13
5	<i>Menispermum canadensis</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.06	0.06	0.94	0.94	3	3	0.3	0.3	1	1
5	<i>Parthenocissus quinifolia</i>	0.13	0.13	1.09	1.09	9	9	0.44	0.21	2.34	1.74	9	4	0.50	0.18	1.41	0.53	9	3	1.6	0.4	9	0
5	<i>Smilax spp.</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.19	0.12	2.19	1.98	5	4	0.7	0.7	2	2
5	<i>Toxicodendron radicans</i>	0.56	0.21	7.97	6.54	31	13	1.00	0.00	61.25	8.69	61	4	0.81	0.12	6.09	1.88	23	2	25.1	18.1	38	11
5	<i>Vitaceae</i>	0.06	0.06	0.16	0.16	25	25	0.31	0.06	0.78	0.16	7	2	0.19	0.12	0.47	0.30	3	2	0.5	0.2	12	7

Distance	Species	Site 3: Wet Site						Site 2: Intermediate Site						Site 1: Dry Site						Across Sites			
		Mean Freq. ±SE		Mean Percent Cover ±SE		Mean IV ±SE		Mean Freq. ±SE		Mean Percent Cover ±SE		Mean IV ±SE		Mean Freq. ±SE		Mean Percent Cover ±SE		Mean IV ±SE		Mean Percent Cover ±SE	Mean IV ±SE		
10	<i>Campsis radicans</i>	0.25	0.18	1.41	1.21	13	8	0.31	0.16	0.78	0.39	9	4	0.00	0.00	0.00	0.00	0	0	0.7	0.4	7	4
10	<i>Euonymus fortunei</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.06	0.06	0.16	0.16	1	1	0.1	0.1	0	0
10	<i>Lonicera japonica</i>	0.19	0.12	1.41	1.03	7	4	0.31	0.16	1.56	1.16	7	3	0.75	0.25	26.56	10.84	37	12	9.8	8.4	17	10
10	<i>Menispermum canadensis</i>	0.00	0.00	0.00	0.00	0	0	0.13	0.13	1.09	1.09	2	2	0.13	0.07	0.47	0.30	2	1	0.5	0.3	2	1
10	<i>Parthenocissus quinquefolia</i>	0.25	0.14	0.78	0.47	7	4	0.31	0.24	8.28	8.07	11	8	0.50	0.23	2.03	1.26	10	5	3.7	2.3	9	1
10	<i>Smilax spp.</i>	0.00	0.00	0.00	0.00	0	0	0.06	0.06	0.16	0.16	2	2	0.25	0.18	0.63	0.44	4	3	0.3	0.2	2	1
10	<i>Toxicodendron radicans</i>	0.63	0.16	8.75	4.60	69	12	0.94	0.06	39.69	11.14	67	11	0.69	0.19	8.59	4.66	42	20	19.0	10.3	59	9
10	<i>Vitaceae</i>	0.13	0.07	0.47	0.30	4	2	0.13	0.07	0.31	0.18	2	1	0.19	0.12	0.47	0.30	3	2	0.4	0.1	3	0
30	<i>Campsis radicans</i>	0.31	0.19	3.91	3.13	30	24	0.00	0.00	0.00	0.00	0	0	0.06	0.06	0.16	0.16	2	2	1.4	1.3	11	10
30	<i>Euonymus fortunei</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.25	0.25	16.25	16.25	12	12	5.4	5.4	4	4
30	<i>Lonicera japonica</i>	0.19	0.12	2.66	2.45	11	9	0.25	0.25	11.72	11.72	8	8	0.81	0.19	12.03	7.16	34	11	8.8	3.1	18	8
30	<i>Menispermum canadensis</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.19	0.19	0.47	0.47	6	6	0.2	0.2	2	2
30	<i>Parthenocissus quinquefolia</i>	0.06	0.06	0.16	0.16	3	3	0.44	0.26	10.16	6.45	13	7	0.19	0.12	0.47	0.30	5	4	3.6	3.3	7	3
30	<i>Smilax spp.</i>	0.00	0.00	0.00	0.00	0	0	0.06	0.06	0.16	0.16	2	2	0.31	0.06	1.56	0.74	12	4	0.6	0.5	5	4
30	<i>Toxicodendron radicans</i>	0.50	0.20	25.63	18.93	55	21	0.75	0.25	47.97	16.23	46	18	0.44	0.21	1.41	0.82	14	6	25.0	13.4	38	13
30	<i>Vitaceae</i>	0.06	0.06	0.16	0.16	2	2	0.31	0.16	1.56	1.16	7	3	0.31	0.12	4.53	3.91	16	9	2.1	1.3	8	4

Distance	Species	Site 3: Wet Site				Site 2: Intermediate Site				Site 1: Dry Site				Across Sites									
		Mean Freq. ±SE	Mean Percent Cover ±SE	Mean IV ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Percent Cover ±SE	Mean IV ±SE	Mean IV ±SE	Mean Freq. ±SE	Mean Percent Cover ±SE	Mean IV ±SE	Mean IV ±SE	Mean Percent Cover ±SE	Mean IV ±SE								
60	<i>Campsis radicans</i>	0.13	0.13	1.88	1.88	25	25	0.00	0.00	0.00	0.00	0	0	0.19	0.12	0.47	0.30	6	4	0.8	0.6	10	8
60	<i>Lonicera japonica</i>	0.19	0.19	0.47	0.47	4	4	0.00	0.00	0.00	0.00	0	0	0.63	0.22	11.88	6.14	35	10	4.1	3.9	13	11
60	<i>Menispermum canadensis</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.06	0.06	0.16	0.16	1	1	0.1	0.1	0	0
60	<i>Parthenocissus quinquefolia</i>	0.25	0.18	0.63	0.44	7	4	0.19	0.12	1.25	0.88	11	6	0.69	0.24	1.72	0.59	19	9	1.2	0.3	12	4
60	<i>Smilax spp.</i>	0.00	0.00	0.00	0.00	0	0	0.00	0.00	0.00	0.00	0	0	0.31	0.12	4.69	4.07	16	6	1.6	1.6	5	5
60	<i>Toxicodendron radicans</i>	0.50	0.29	22.34	13.74	37	22	0.69	0.06	16.25	10.02	71	7	0.44	0.12	2.81	1.78	16	4	13.8	5.8	41	16
60	<i>Vitaceae</i>	0.06	0.06	0.16	0.16	2	2	0.19	0.12	0.47	0.30	18	12	0.19	0.06	0.47	0.16	6	3	0.4	0.1	9	5

Appendix Table 15. Plant-level data for all individuals of *Lonicera maackii* surveyed. Days flooded refers to the transect, not the individual plant. Rank elevation refer to the relative elevation of each plant at the transect level. Individuals ranked as having rank elevations of 100 had absolute elevations equal to or greater than the highest elevation recorded in the ground survey of transect elevations. Individuals ranked as having rank elevation of 0 had absolute elevations less than or equal to the lowest elevation recorded in the ground survey of transect elevations. Transect ID is in the format: (site)-(edge-to-interior transect ID)-(distance from edge).

Transect ID	Number of Stems	Stem Height	Rank Elevation	Days Flooded (Transect Average)
3-N1-30m	3	2	100	42.5
3-N2-1m	1	0.25	99.3	40.9
1-N2-30m	9	2.5	49.7	28.1
1-N2-30m	3	2	72.4	28.1
1-N2-30m	5	2.5	76.9	28.1
2-S2-10m	3	0.5	100	21.4
2-S1-30m	8	2	95.6	17.3
2-S1-30m	1	0.25	58.9	17.3
2-S1-10m	3	2	98.8	15.3
2-S1-10m	3	2.5	91.4	15.3
2-N2-5m	3	3	56.4	10.85
2-N2-5m	3	3	61.5	10.85
2-N2-5m	2	2	44.8	10.85
2-N2-5m	4	4	87.1	10.85
2-N2-5m	2	2	89.7	10.85
2-N2-5m	3	1	91.4	10.85
2-N2-5m	2	1	89.7	10.85
2-N2-5m	2	0.5	83.8	10.85
2-N2-5m	2	1	48.7	10.85
2-N2-5m	5	2	92.6	10.85
2-N1-10m	1	0.25	96.3	10.65
2-N1-10m	3	2	100	10.65
2-N1-10m	2	2	95.9	10.65
2-N1-10m	2	2	96.3	10.65
2-N1-10m	3	2	100	10.65
2-N1-10m	4	2	97.2	10.65
2-N1-10m	5	2	100	10.65
2-N1-10m	3	0.25	96.9	10.65
2-N1-10m	1	0.5	96.6	10.65
2-N1-10m	3	1	95.3	10.65
1-N2-60m	2	0.5	69	10.25
3-S1-30m	3	0.5	89.7	8.7

Transect ID	Number of Stems	Stem Height	Rank Elevation	Days Flooded (Transect Average)
3-S1-30m	1	0.25	92.1	8.7
2-S1-5m	2	0.5	33.3	8.2
2-S1-5m	5	1	84.9	8.2
2-S1-5m	2	1	79.4	8.2
2-S1-5m	3	1	96.2	8.2
2-S2-5m	6	2	100	5.4
2-S2-5m	5	1	73.6	5.4
2-S2-5m	4	1	100	5.4
2-S2-5m	7	2	98.3	5.4
2-5m	9	2	0	4.05
1-S2-5m	2	2	33.3	4.05
3-S1-1m	2	2	100	2.6
3-S1-1m	2	2	100	2.6
3-S1-1m	1	0.25	100	2.6
3-S1-60m	11	2	90.1	2.2
3-S1-60m	3	2.5	89.4	2.2
1-S2-60m	1	0.25	94.8	1.2
1-S2-60m	2	1	88.2	1.2
1-S2-60m	2	1	33.3	1.2
1-S1-60m	3	1	32.3	0.925
1-S1-60m	7	2	4.1	0.925
1-N2-10m	3	0.5	100	0.8
1-S2-30m	7	2.5	89.1	0.575
1-S2-30m	1	1	76	0.575
1-S2-30m	2	2.5	7.6	0.575
1-S2-30m	7	2	38.4	0.575
1-S2-30m	3	2	61.5	0.575
1-S2-30m	4	2	61.5	0.575
1-S2-30m	1	0.25	85.8	0.575
1-S2-30m	.	.	85.8	0.575
1-S2-30m	.	.	85.8	0.575
1-S2-30m	3	2	87.1	0.575
2-N1-5m	3	2	98.9	0.4
1-S1-1m	2	1	41	0
1-S1-1m	3	1	72.6	0
1-S1-1m	3	1	85.4	0
1-S1-1m	5	1	25.6	0
1-S1-1m	2	0.5	13.6	0
1-S1-10m	1	1	33.3	0
1-S1-10m	5	1	56.4	0
1-S1-10m	1	0.25	97.4	0
1-S1-30m	1	0.25	69.2	0

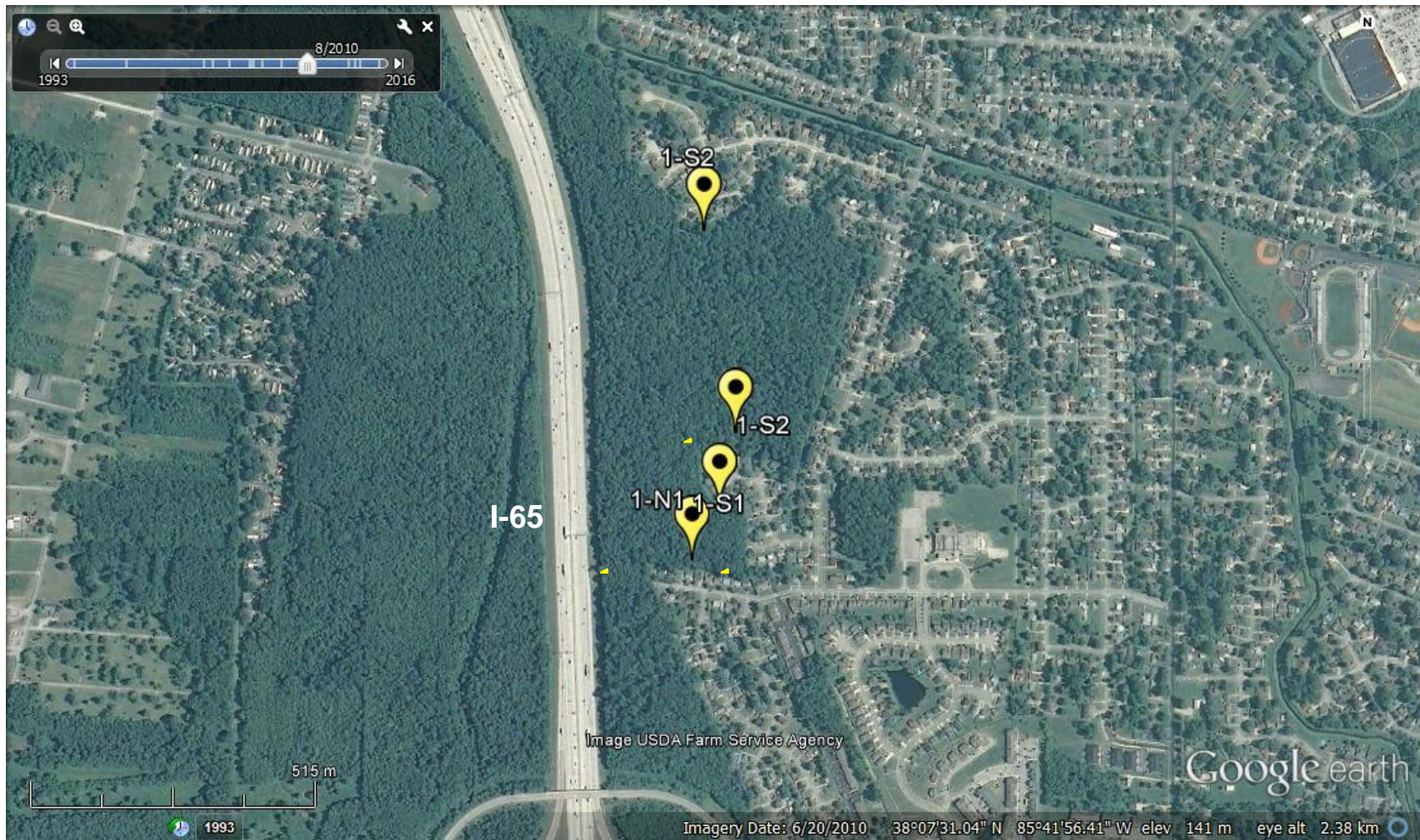
Transect ID	Number of Stems	Stem Height	Rank Elevation	Days Flooded (Transect Average)
1-N1-1m	1	0.25	18.6	.
1-N1-1m	1	0.25	31.4	.
1-N1-1m	1	0.25	48.7	.
1-N1-1m	1	0.25	14.1	.
1-N1-1m	1	0.25	14.1	.
1-N1-1m	1	0.25	40.3	.
1-N1-1m	1	0.25	40.3	.
1-N1-1m	1	2	47	.
1-N1-5m	1	0.5	97.9	.
1-N1-5m	2	2.5	100	.
1-N1-60m	2	0.5	100	.
1-N1-60m	2	2	97.4	.

Appendix Table 16. Wetland indicator status code, and species designations for species encountered in this study.

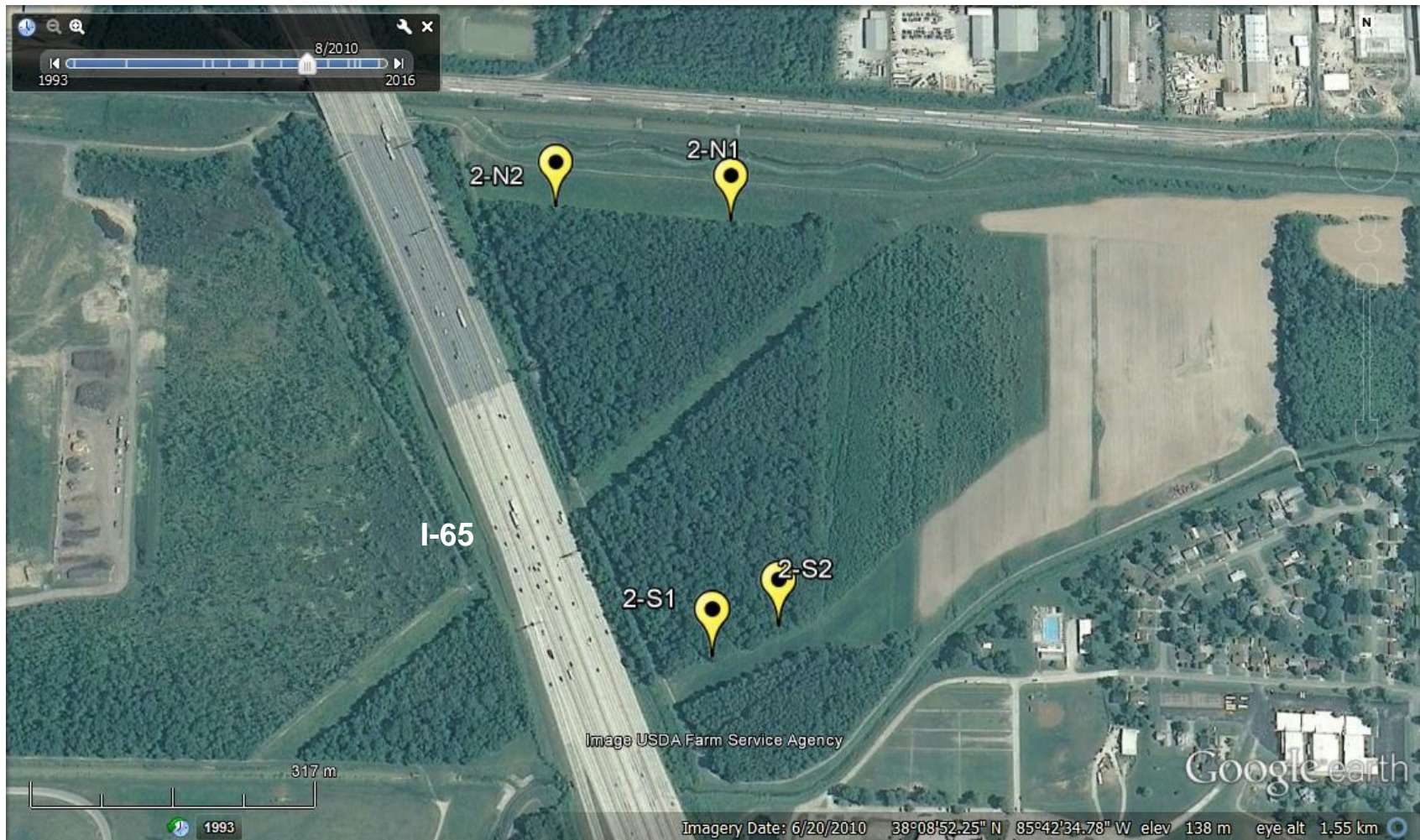
Indicator Code	Indicator Status	Designation	Comment
OBL	Obligate Wetland	Hydrophyte	Almost always occur in wetlands
FACW	Facultative Wetland	Hydrophyte	Usually occur in wetlands, but may occur in non-wetlands
FAC	Facultative	Hydrophyte	Occur in wetlands and non-wetlands
FACU	Facultative Upland	Non-hydrophyte	Usually occur in non-wetlands, but may occur in wetlands
UPL	Obligate Upland	Non-hydrophyte	Almost never occur in wetlands
NE	Not Evaluated		

Species	Form	WIS
<i>Aralia spinosa</i>	SHRUB	FAC
<i>Cephalanthus occidentalis</i>	SHRUB	OBL
<i>Cornus foemina</i>	SHRUB	FACW
<i>Euonymus americanus</i>	SHRUB	FAC
<i>Lindera benzoin</i>	SHRUB	FAC
<i>Lonicera maackii</i>	SHRUB	NE
<i>Symphoricarpos orbiculatus</i>	SHRUB	FACU
<i>Sambucus canadensis</i>	SHRUB	FAC
<i>Acer negundo</i>	TREE	FAC
<i>Acer rubrum</i>	TREE	FAC
<i>Acer saccharinum</i>	TREE	FACW
<i>Asimina triloba</i>	TREE	FAC
<i>Celtis laevigata</i>	TREE	FACW
<i>Cornus florida</i>	TREE	FACU
<i>Diospyros virginiana</i>	TREE	FAC
<i>Fagus grandifolia</i>	TREE	TREE
<i>Fraxinus pennsylvanica</i>	TREE	FACW
<i>Juniperus virginiana</i>	TREE	FACU

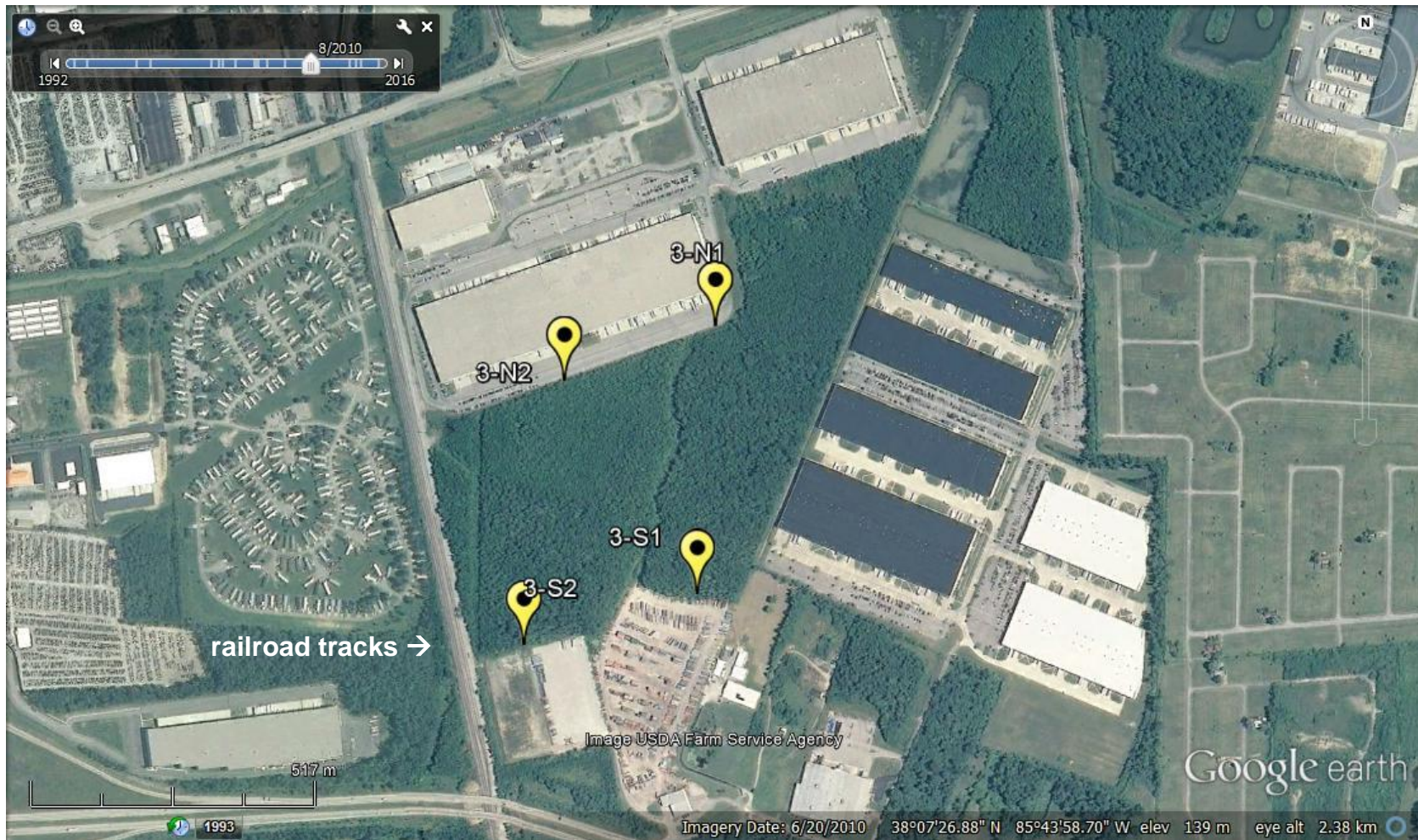
Liquidambar styraciflua	TREE	FAC
Liriodendron tulipifera	TREE	FACU
Nyssa sylvatica	TREE	FAC
Platanus occidentalis	TREE	FACW
Populus deltoides	TREE	FAC
Quercus bicolor	TREE	FACW
Quercus lyrata	TREE	OBL
Quercus michauxii	TREE	FACW
Quercus palustris	TREE	FACW
Salix nigra	TREE	OBL
Ulmus americana	TREE	FACW
Ulmus rubra	TREE	FAC
Campsis radicans	VINE	FAC
Euonymus fortunei	VINE	NE
Lonicera japonica	VINE	FAC
Menispermum canadense	VINE	FACU
Parthenocissus quinquefolia	VINE	FACU
Toxicodendron radicans	VINE	FAC



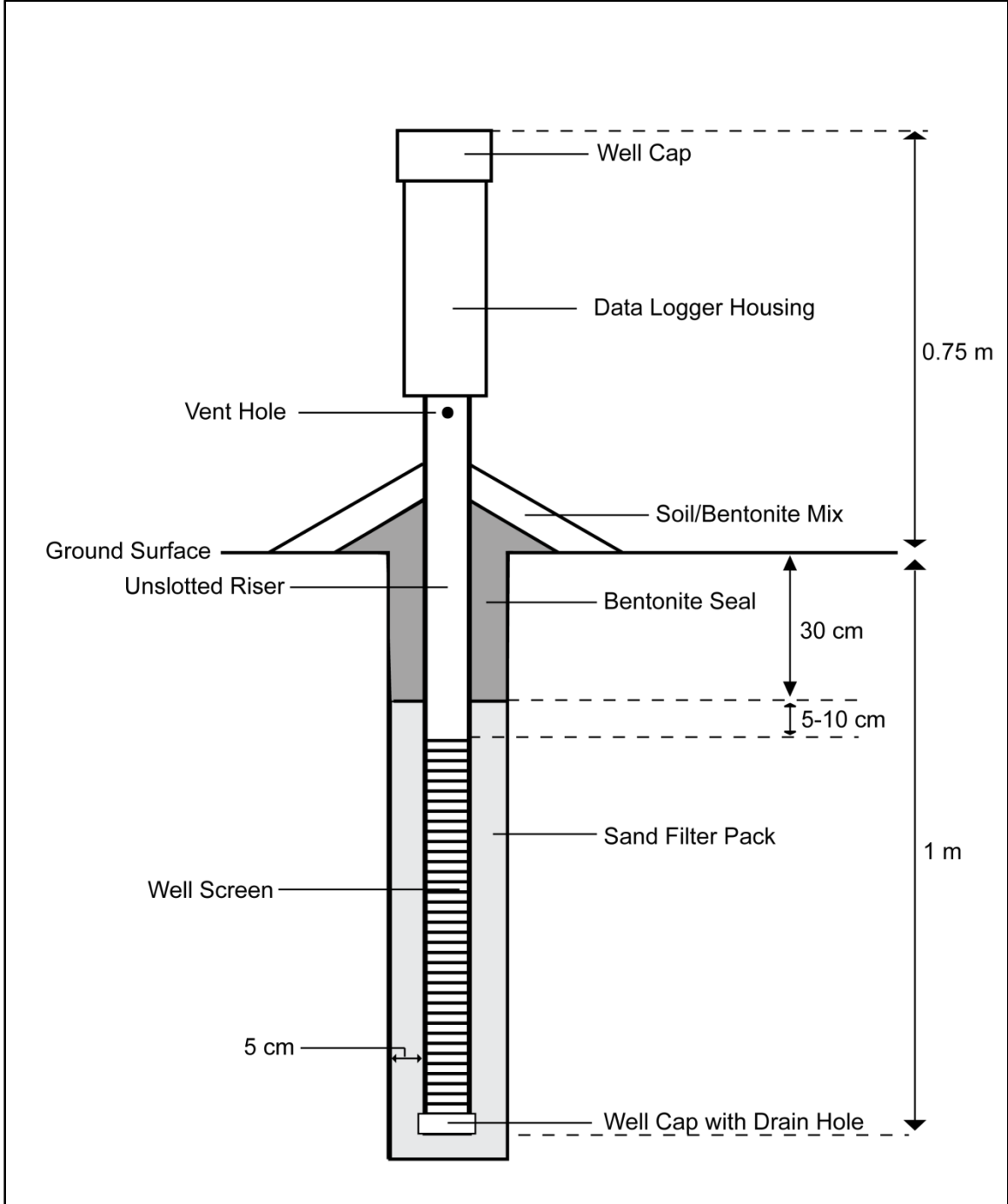
Appendix Figure 1. Aerial imagery showing Site 1 (dry site) in Jefferson County, Kentucky (Louisville Metro Area). Each tagged marker represents the location of an edge-to-interior transect.



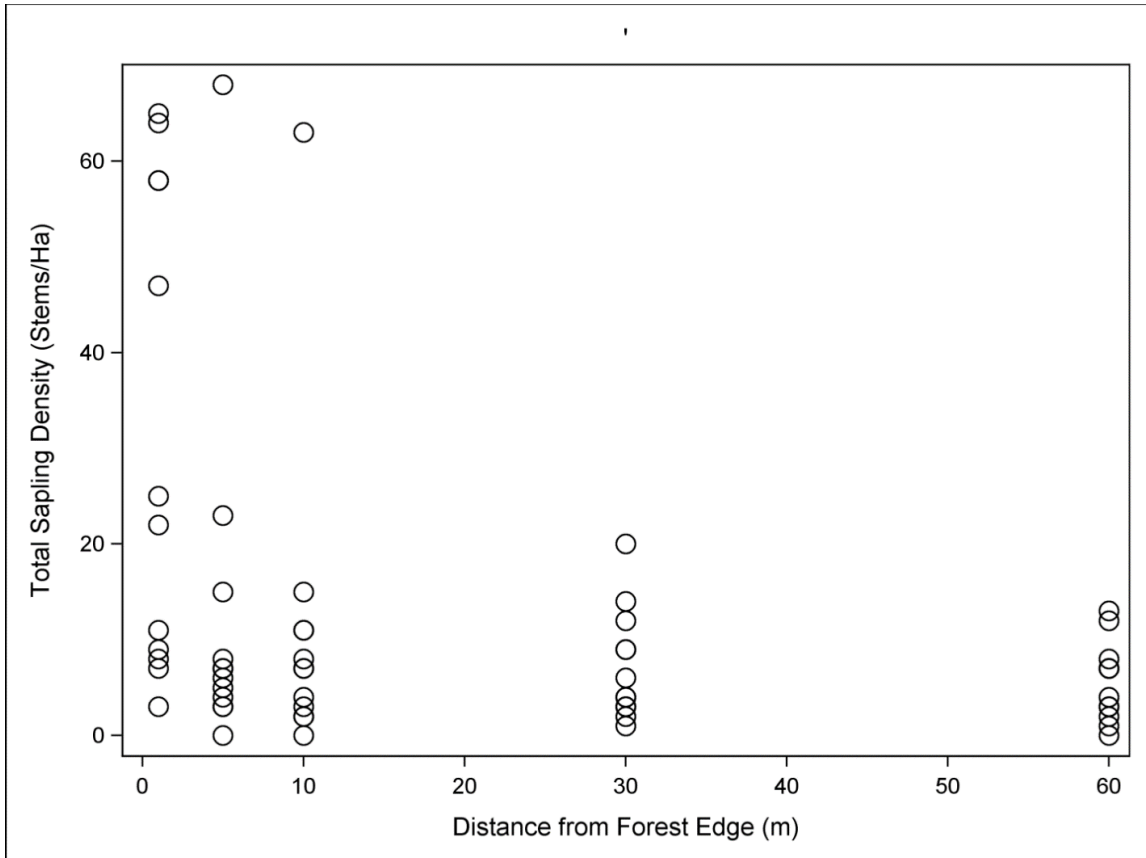
Appendix Figure 2. Aerial imagery showing Site 2 (intermediate site) in Jefferson County, Kentucky (Louisville Metro Area). Each tagged marker represents the location of an edge-to-interior transect.



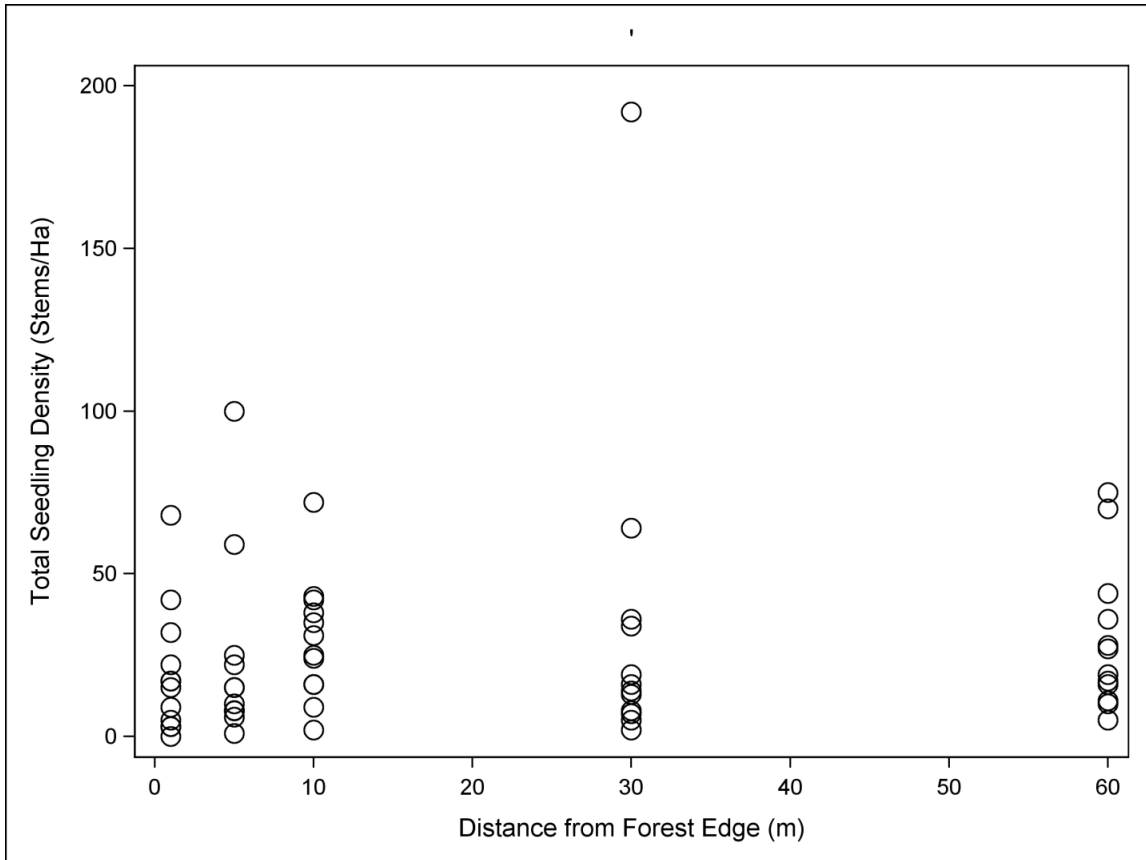
Appendix Figure 3. Aerial imagery showing Site 3 (wet site) in Jefferson County, Kentucky (Louisville Metro Area). Each tagged marker represents the location of an edge-to-interior transect.



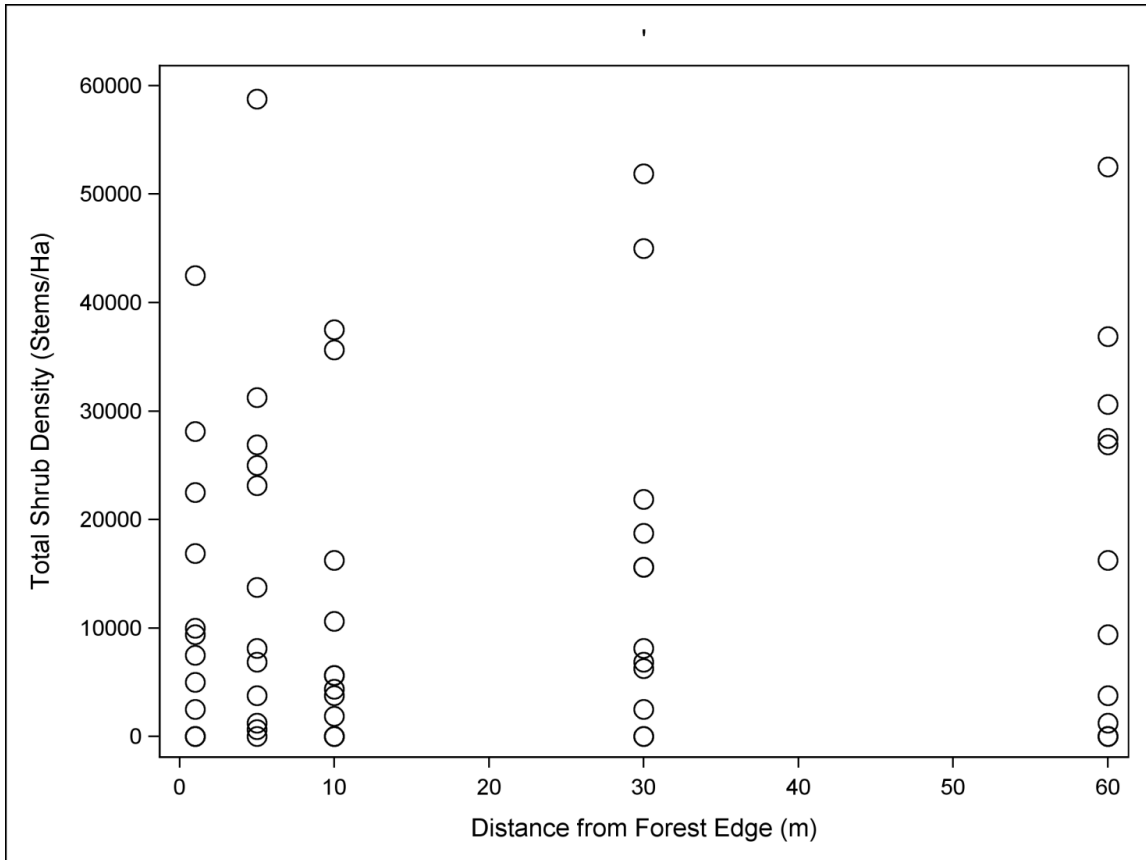
Appendix Figure 4. Diagram depicting general construction of the groundwater monitoring wells used in this study. In this study, wells extended 1 m below the ground surface, with the riser and PVC housing for a data logger extending 0.75 m above the ground surface. Image adapted from Sprecher (2008). Image is not to scale.



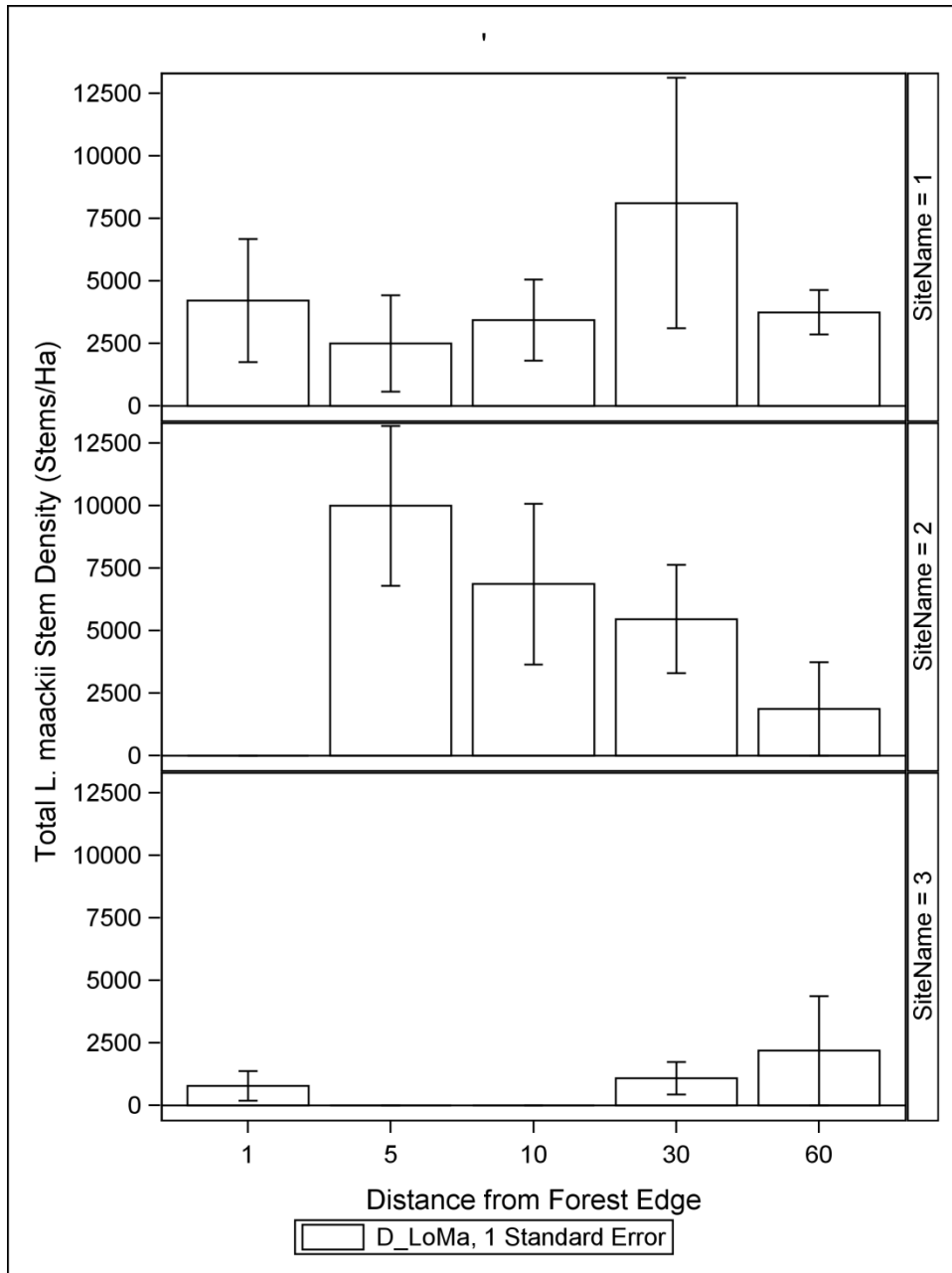
Appendix Figure 5. Total sapling stem density (stems/Ha) vs. distance from forest edge. Each data point represents the mean vine cover in a transect at 1, 5, 10, 30 or 60 meters from the forest edge. Data from all 60 transects (20 per site) is included.



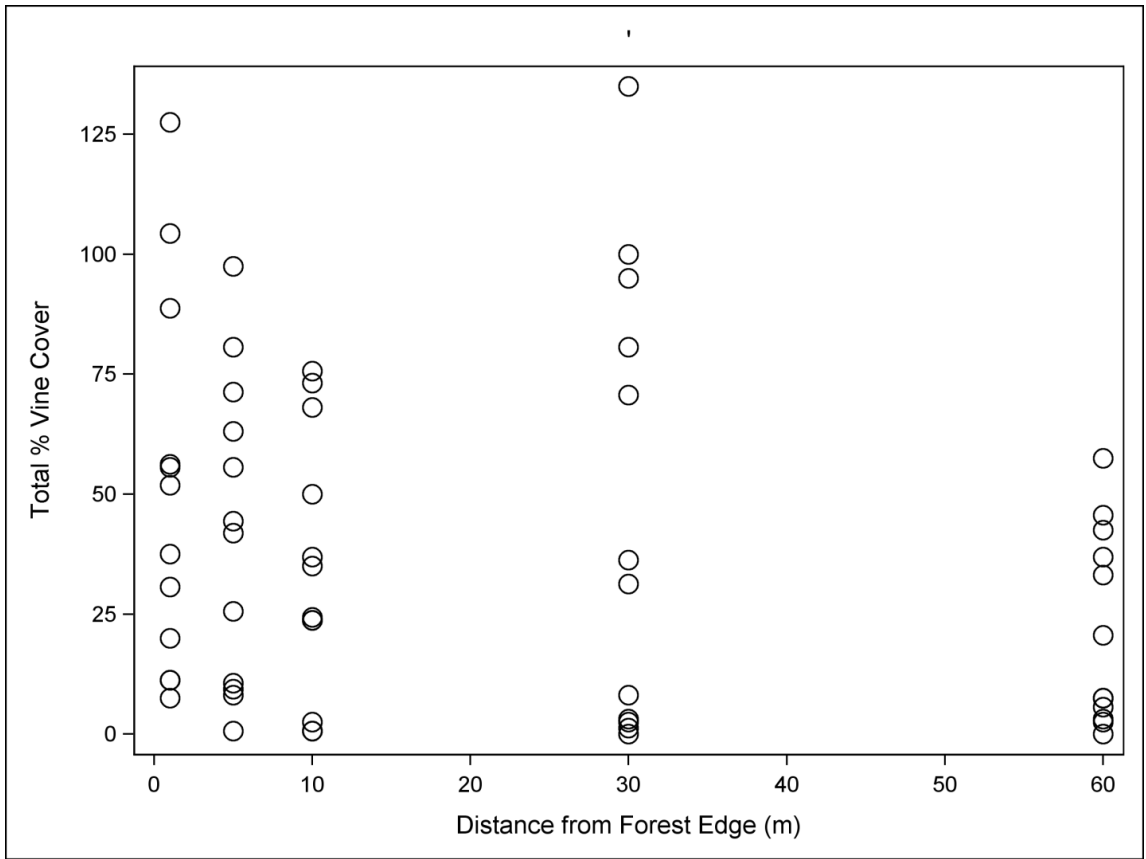
Appendix Figure 6. Total seedling stem density (stems/Ha) vs. distance from forest edge. Each data point represents the seedling density in a transect at 1, 5, 10, 30 or 60 meters from the forest edge. Data from all 60 transects (20 per site) is included.



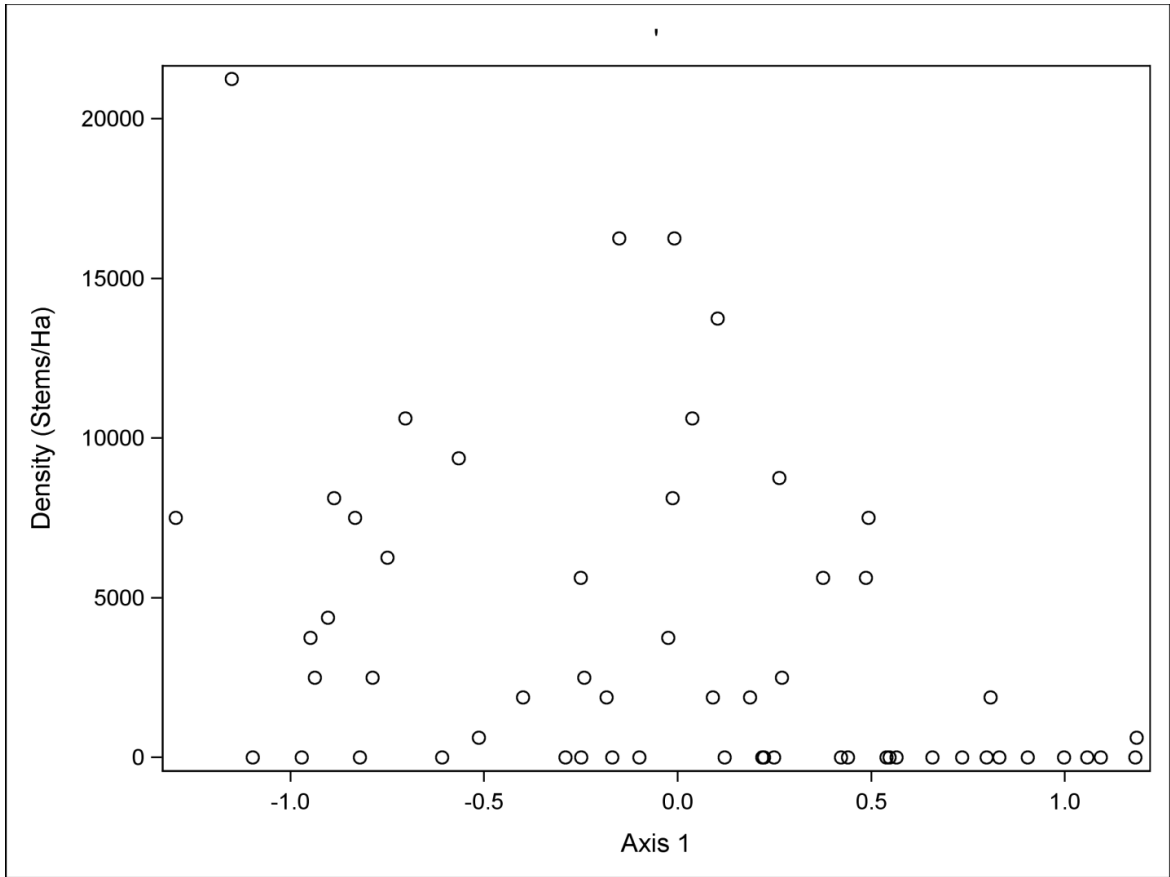
Appendix Figure 7. Total shrub stem density (stems/Ha) vs. distance from forest edge. Each data point represents the mean shrub density in a transect at 1, 5, 10, 30 or 60 meters from the forest edge. Data from all 60 transects (20 per site) is included.



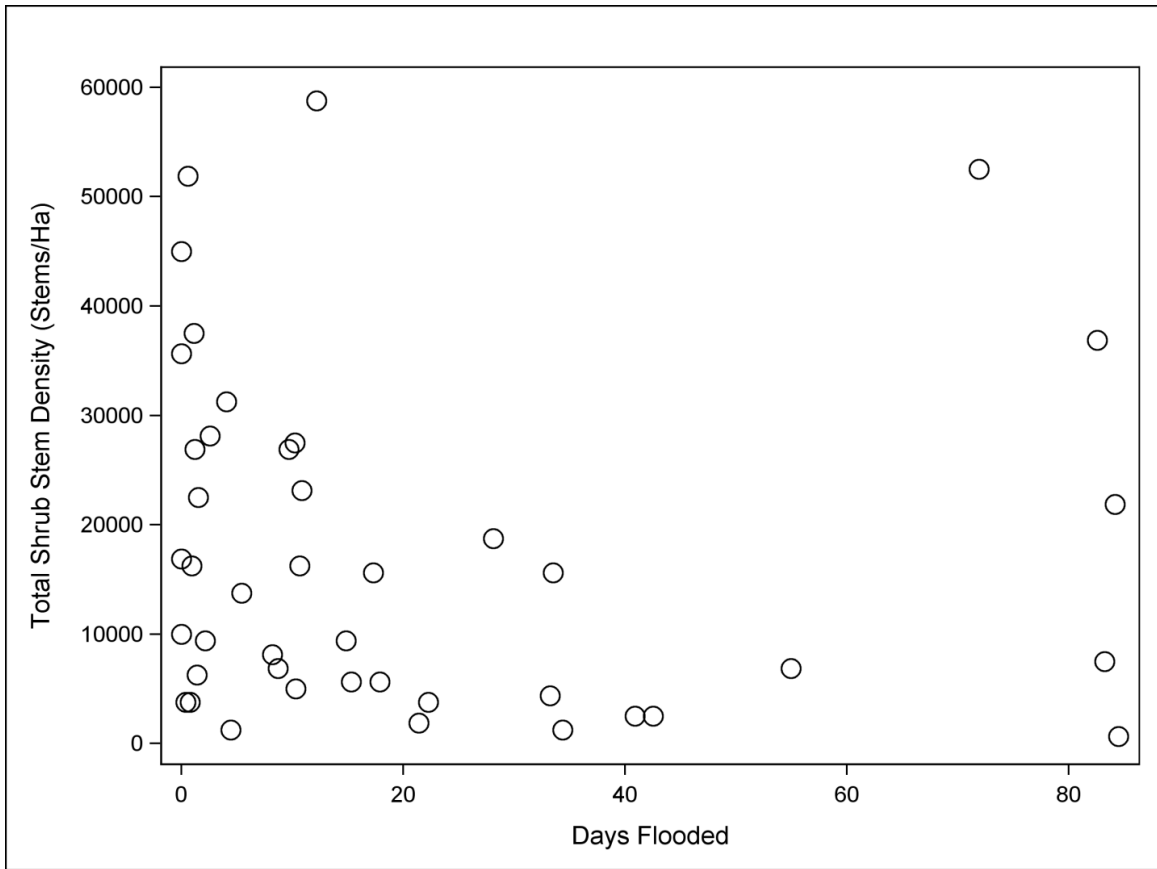
Appendix Figure 8. Total stem density of *Lonicera maackii* shrubs with distance from the forest edge at all three research sites. Each bar represents the mean shrub density of *L. maackii* stems at four transects per site, corresponding to 1, 5, 10, 30 or 60 meters from the forest edge. Sites 1, 2 and 3 refer to the dry, intermediate, and wet sites, respectively. Error bars are ± 1 SE.



Appendix Figure 9. Total percent vine cover vs. distance from forest edge. Each data point represents the mean vine cover in a transect at 1, 5, 10, 30 or 60 meters from the forest edge. Data from all 60 transects (20 per site) is included.



Appendix Figure 10. Density of *Lonicera maackii* plotted against values of Axis 1 for all transects that were included in the NMS ordination of woody plants species data at all sites. Note that the value zero for Axis 1 is in the center of the x-axis. Axis 1 was positively related to days flooded.



Appendix Figure 11. Total shrub stem density as it relates to the number of days flooded in the 55 transects where flooding was estimated. Only data points where values of total stem density were greater than zero are shown.

CURRICULUM VITAE

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EDUCATION

B.S Biology, Centre College, 2004. Graduated *cum laude*.

PROFESSIONAL POSITIONS

Supplementary Instruction (SI) Leader and Peer Mentor. REACH Center, University of Louisville, Louisville, Kentucky. 8/2012-12/2012.

Graduate Teaching Assistant. REACH Center, University of Louisville, Louisville, Kentucky. 8/2011-5/2012.

Graduate Teaching Assistant. University of Louisville, Department of Biology, Louisville, KY. 8/2006-8/2011.

Student Conservation Association (SCA) Conservation Intern. U.S. Fish and Wildlife Service, Ecological Services and Fisheries Field Office, Panama City, Florida. 4/2005-4/2006.

SCHOLASTIC AND PROFESSIONAL HONORS

Student Research Grant, 2010. Awarded by the International Society of Wetland Scientists.

Bernadine Meyer Memorial Scholarship, 2009. Awarded by Kentucky Natural History Society.

Type 1 Travel Grant, 2008. Awarded by The Wetland Foundation.

Beechmont Garden Club Award, 2008. Awarded by University of Louisville, Biology Department.

Woody Boebinger Memorial Scholarship, 2007. Awarded by Kentucky Natural History Society.

John C. Young Research Scholar, 2010. Centre College, Danville, Kentucky.

Omicron Delta Kappa, 2004. Inducted for exceptional leadership skills.

Research Experience for Undergraduates Funding Recipient, 2002. Awarded by the National Science Foundation.

LEADERSHIP POSITIONS

President, Biology Graduate Student Association. University of Louisville, Louisville, Kentucky. 8/10-8/11.

Vice-President/Treasurer, Biology Graduate Student Association. University of Louisville, Louisville, Kentucky. 8/9-8/10.

PRESENTATIONS

Effects of flooding duration, depth, and simulated canopy closure on the growth and survival of the invasive shrub *Lonicera maackii* (Rupr.) Herder. Ecological Society of America, Annual Meeting, 2011, Austin, TX. (Oral Presentation).

Effects of flooding duration, depth, and simulated canopy closure on the growth and survival of *Lonicera maackii* (Rupr.) Herder. Meghan R. Langley, Kaycee E. Stone and Margaret M. Carreiro. Kentucky Academy of Sciences Annual Meeting, 2010, Bowling Green, KY. (Poster Presentation).