ABSTRACT

ECOLOGICAL AND EVOLUTIONARY INVASION DYNAMICS OF *LONICERA MAACKII* (AMUR HONEYSUCKLE) IN RELATION TO WHITE OAK SAVANNA RESTORATION MANAGEMENT AT NACHUSA GRASSLANDS, ILLINOIS, USA

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This interdisciplinary research explores the ecological impacts and underlying evolutionary mechanisms associated with the spread of *Lonicera maackii* (Amur honeysuckle), one of the most aggressive and abundant invasive species throughout the Midwest United States. The main goal of this research is to better understand how the encroachment of Amur honeysuckle impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration project (Nachusa Grasslands) located in Lee County, Illinois, USA, with particular focus on mechanisms required for successful oak regeneration and recruitment (i.e. carbon assimilation, soil quality, soil moisture/ temperature, and plant available nutrients). This study also aims to explore the spatial-temporal long distance dispersal patterns of Amur honeysuckle, as inferred by population genetics, in order to better understand the mechanisms and pathways by which Amur honeysuckle is spreading throughout Illinois.

Ultimately, the low light levels measured in the understory of the oak savanna restoration study site at Nachusa Grasslands yielded marginal seasonal carbon assimilation totals for white oak seedlings, especially when compared to the high

seasonal carbon assimilation totals modeled for white oak seedlings had they been growing in full sun light conditions. In relation to belowground properties, this study found no significant differences between any of the soil characteristics (i.e. wet macro-aggregate soil stability, moisture, temperature, carbon nitrogen ratios, and nutrient levels) measured in adjacent soil samples collected under and away from Amur honeysuckle within the oak savanna restoration study site at Nachusa Grasslands. Findings from the population genetics analyses in this research supports previous research that Amur honeysuckle displays characteristics associated with stratified dispersal. Specifically, a lack of correlation between genetic distance and geographic distance for the Illinois Amur honeysuckle subpopulations suggest that active gene flow between these subpopulations occurs via regional long distance dispersal events. The New York Botanical Garden subpopulation was identified as genetically isolated from all other subpopulations. The Arnold Arboretum at Harvard University and The Morton Arboretum also displayed patterns of genetic isolation from the other subpopulations, more so than from each other. Management recommendations, based off findings from this research, are provided.

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BY

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CHAPTER 1: RESEARCH OBJECTIVES

1.1 INTRODUCTION

Throughout Eastern and Central North America, aggressive and abundant invasive plant species, such as the shrub *Lonicera maackii* (Rupr.) Maxim (Amur honeysuckle), have encroached upon the understory canopies of many oak forests and open oak savannas at high environmental and economic costs (Pimentel et al. 2000; Collier et al. 2002; Pimentel et al. 2005; Lodge et al. 2006). Furthermore, *Quercus alba* (white oak), the keystone species of the geographically restricted and rare Midwestern tall-grass savanna ecosystem, has experienced a decline in regeneration and recruitment, defined as the ability to transition into subsequent life stages (i.e. seedling to sapling) (Henderson 1995; Peterson and Reich 2001; Abrams 2005; Brudvig and Evans 2006; Wang and Bauerle 2006; Brudvig et al. 2011; McEwan et al. 2011). As plant invasions increase within Midwest oak savannas, competition for limited understory resources (e.g. space, soil moisture, nutrients, light, etc.) intensifies, which may constrain the regeneration, growth, recruitment, and survival of white oak seedlings (Bowles and McBride 1998; Albrecht and McCarthy 2006; Meiners 2007; Brudvig and Asbjornsen 2008; Kuebbing et al. 2014). Dominance of white oaks throughout Midwest oak savanna is vital to maintaining composition and species habitat (Rogers 1990; Abrams 2005; Brudvig and Evans 2006; Wang and Bauerle 2006). Without a

competitive advantage over encroaching species, Schulte et al. (2011) predicts that oaks will lose their historical dominance within the next few decades.

The interdisciplinary research presented in this dissertation integrates methods from physical geography, conservation biogeography, soil science, and population genetics in order to explore the ecological impacts and underlying evolutionary mechanisms associated with the spread of one of the most aggressive and abundant invasive species throughout the Midwest United States: Amur honeysuckle. More specifically, the main goals of this research are to better understand how the encroachment of Amur honeysuckle impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration project located in Lee County, Illinois, USA, with particular focus on mechanisms required for successful oak regeneration and recruitment (i.e. adequate carbon assimilation, soil quality, soil moisture, soil temperature, and plant available nutrients). This study also aims to explore the spatial-temporal long distance dispersal patterns of Amur honeysuckle, as inferred by population genetics, in order to better understand the mechanisms and pathways by which Amur honeysuckle is spreading throughout Illinois.

Past studies have explored the role of Amur honeysuckle in altering vegetation community dynamics of native tree seedlings (e.g. regeneration, recruitment, growth, composition, mortality, etc.) (Hutchinson and Vankat 1997; Gould and Gorchov 2000; Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2004; Bartuszevige et al. 2006; McEwan et al. 2009). Previous work has also found no significant difference between soil property characteristics and the abundance or

presence of Amur honeysuckle, but at the same time request that more research is needed to support this finding before the role of soil characteristics can be fully teased out (McEwan et al 2012; Wilson et al. 2013). Furthermore, populations of Amur honeysuckle in Ohio have been successfully analyzed using genetic population structure analyses (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015) that identify geographic and genetic differentiation and variation between populations, which can be used to estimate dispersal distances, colonization patterns, and infer potential sources of both founding and newly established individuals (Cain et al. 2000; DeWoody et al. 2004; Hu et al. 2010). Few studies, however, have explicitly addressed how Amur honeysuckle impacts white oak regeneration and recruitment, in relation to carbon assimilation, soil quality, soil moisture, soil temperature, and plant available nutrients; nor have they utilizes the known invasion history of Amur honeysuckle in order to assess whether anthropogenic influences need to be considered when defining long-distance dispersal events of invasive species. Therefore, any research on these topics are necessary, in order to effectively guide restoration efforts for white oak and other important native species trying to survive in invasive-dominated systems.

1.2 RESEARCH OBJECTIVES

Overall, this study was designed to explore a subset of underlying mechanisms and ecological impacts of Amur honeysuckle as they relate to the regeneration and recruitment of native white oak. Understanding the role of invasive species encroachment in the regeneration and recruitment gap of white oak, is important to the

long-term sustainable management, restoration, and conservation of white oak. The broader research objectives of this study were threefold. First, the study aimed to assess the impact of the extended leaf phenology and invasive encroachment of Amur honeysuckle on understory light environments and seasonal carbon assimilation rates. Second, the study aimed to analyze soil quality, moisture, temperature, and nutrient characteristics in areas with and without Amur honeysuckle encroachment. Last, this study aimed to describe the general geographic and evolutionary patterns associated with Amur honeysuckle's historic range expansion throughout the eastern and central United States, with implications for identifying past and future invasion pathways and potentially redefining our understanding of long distance dispersal with regards to invasive species. More specifically, the following research questions were proposed within each broad objective:

A. What role does the extended leaf phenology of Amur honeysuckle play in its leaf-level seasonal carbon gain? What are the existing *in situ* light levels above and below Amur honeysuckle canopies and do those light levels inhibit the ability of *in situ* white oak seedlings to maintain a positive net leaf-level seasonal carbon balance? Answers to these questions will assess the impact of extended leaf phenology and invasive encroachment of Amur honeysuckle on understory light environments and seasonal carbon assimilation rates, with regards to the physiological health and recruitment of white oak seedlings.

B. Do aggregate stability, soil moisture/temperature, carbon/nitrogen ratios, and levels of other soil nutrients significantly differ in soil found under and away from Amur

honeysuckle? Answers to this question will assess soil quality, moisture/temperature, and nutrient characteristics in areas with and without Amur honeysuckle encroachment, with implications for impact on white oak regeneration and recruitment.

C. Did Amur honeysuckle spread into Illinois via natural and/or anthropogenically facilitated long-distance dispersal followed by outward expansion through local and/or regional diffusion and do the results from a genetic structure analysis support any of the following three proposed invasion pathways, identified based on historical records, specifically: 1) west via anthropogenically facilitated long-distance dispersal from the first recorded U.S. locations of entry for Amur honeysuckle: *The New York Botanical Garden, NY and The Arnold Arboretum of Harvard University, MA* (Luken and Thieret 1996); 2) west from the site that first recorded the invasive and escapable nature of Amur honeysuckle near Chicago: *The Morton Arboretum, Lisle, IL* (Luken and Thieret 1996); and/or 3) north and south from regional sites in IL: *Hidden Springs State Forest, Strasburg, IL and Trail of Tears State Forest, Jonesboro, IL* (EDDMapS 2015). Answers to this question will assess the general geographic and evolutionary patterns associated with Amur honeysuckle's historic range expansion throughout the eastern and central United States, with implications for identifying past and future invasion pathways and potentially redefining our understanding of long distance dispersal with regards to invasive species.

In the end, this study integrates stand dynamics, light and physiological efficiency measurements, soil moisture and soil quality characteristics, and the exploration of Amur honeysuckle invasion patterns throughout central and eastern United States. The

findings from this research will ultimately inform management and conservation efforts designed to target Amur honeysuckle for *in situ* eradication and stimulate white oak regeneration and recruitment in Illinois.

1.3 DISSERTATION ORGANIZATION

A comprehensive literature review chapter follows, in which key terminology and concepts associated with invasion ecology (as a discipline in general and with particular focus on Amur honeysuckle), the history and ecological status of Midwestern oak savannas, the role of understory light environments and dynamic soil properties in white oak regeneration and recruitment, and the dispersal mechanisms of Amur honeysuckle are discussed and defined. Chapter three describes the study area Lee County, Illinois (i.e. topography, geology, soils, climate, and land use), as well as the study species *Quercus alba* and *Lonicera maackii*. Chapter three also provides a detailed description of the white oak savanna restoration study site at Nachusa Grasslands (i.e. geology, soils, climate, and vegetation). The methods used in this study are then outlined in chapter four. Chapters five through seven report results found in this research, each concluding with explanations and discussions. The closing chapter, chapter eight, synthesizes all findings with regards to the research objectives outlined in this first chapter, and draw conclusions in relation to the management of Amur honeysuckle and the conservation of white oak in the white oak savanna restoration site at Nachusa Grasslands, Illinois, USA.

CHAPTER 2: BACKGROUND

2.1 INTRODUCTION

Interdisciplinary research that blends the study of physical geography, climate, ecology, and evolution provides a comprehensive method by which to explore and better understand the underlying mechanisms controlling complex and dynamic natural systems (Sax et al. 2005). Movement, between and within populations, is an inherent mechanism by which species interact (Sax et al. 2005). Modern globalization has expanded the mobility of many species, including humans, and in turn has also enabled the widespread transportation and introduction (defined by Richardson et al. (2000) as the anthropogenically facilitated movement of non-native plant propagules or whole plants across an otherwise insurmountable geographic barrier) of non-native species to new geographic regions (Lockwood et al. 2007). Most non-native species do not survive to become naturalized or damage the ecosystems to which they were introduced (Mack et al. 2000; Parker et al. 2013). The process of naturalization is defined by Richardson et al. (2000) as initiating when both abiotic and biotic barriers to natural reproduction and to survival are overcome by a non-native species. There are however, some non-native species (labeled invasive) that successfully establish themselves in their newly introduced geographic range, become dominant, and ultimately cause damage to the new community or pose a major threat to the health and well-beings of humans, animals, and/or the economy (Elton 1958; Pimentel et al. 2000; Rossman 2001; Colautti

and MacIsaac 2004; Miller and Gorchov 2004; Hartman and McCarthy 2007; Lockwood et al. 2007; Devine and Fei 2011).

A successful biological invasion occurs as a process in stages that include transportation, introduction, establishment, range expansion, impact, and response (Colautti and MacIsaac 2004; Lockwood et al. 2007). Once established, invasive species often alter the structure, function, and available resources of their invaded ecosystems in various ways (Bazzaz 1986; Collier et al. 2002), including the disruption of ecosystem stability and ecosystem services (i.e. the processes and natural cycles by which ecosystems fulfill and sustain humanity) (Ehrenfeld 2003; Devine and Fei 2011). Overall, scientists have estimated that invasive species cost hundreds of billions of dollars annually in destroyed agriculture, environmental degradation and damages to industries, as well as in expensive eradication and prevention programs (Pimentel et al. 2000, 2005; Lodge et al. 2006) and have contributed, in part, to the risk of about 42% of all threatened or endangered species (Pimentel et al. 2005). The biodiversity loss and damage that has resulted from the increased spread of non-native invasive species are topics of global, regional, and local concern, especially to invasion ecologists, conservation biogeographers, and restoration land managers (Ehrenfeld 2003; Levine et al. 2003; McEwan et al. 2012; Wilson et al. 2013; Prins and Gordon 2014).

Invasion ecology is the study of non-native and invasive encroachment by plants, animals, fungus, and bacteria, their ecological impacts on ecosystems, and the theories gained about the natural world from their study (Sax et al. 2005; Lockwood et al. 2007; Simberloff and Rejmánek 2010; Prins and Gordon 2014). As a discipline, Invasion

Ecology is relatively modern and has prospered from a rapid ascent in scholarly interest subsequent to Charles Elton's foundational publication, *The Ecology of Invasions by Animals and Plant*, in 1958 (Sax et al. 2005; Lockwood et al. 2007; Simberloff and Rejmánek 2010; Prins and Gordon 2014). Studies documenting problems on invasive species published in the Scientific Committee on Problems of the Environment (SCOPE) by the International Council for Science between 1982 and 1989 also initiated increased interest for the new discipline (Lockwood et al. 2007).

Over the years, invasion ecologists have proposed and tested a number of hypotheses (e.g. natural enemies, disturbance, empty niche, species richness, propagule pressure, evolution of invasiveness, novel weapons, etc.) in an attempt to explain the success of non-native invasive plant species (Simberloff and Rejmánek 2010). The natural enemies' hypothesis, also known as the "enemy release hypothesis" or "biological control," has roots in the work of Darwin (1859), Williams (1954), and Elton (1958). The hypothesis states that the success of an invasive species is due to its release from natural enemies that would have controlled population growth in its native range (e.g. diseases, herbivores, etc.) (Hierro et al. 2005; Blossey 2010). The biological control aspect of the hypothesis is primarily used as a pest control against an invasive species by introducing exotic natural enemies to reduce the population of invasive species (Pitcairn 2010).

The disturbance hypothesis proposes that some invasive species have adapted to different intensities and types of disturbances (defined by Hobbs (2010) as an event that alters an ecosystems resource availability and structure in a way that drives

ecosystem dynamics, including those related to regeneration) as compared to native vegetation and are therefore more likely to succeed in those conditions (Gray 1879; Baker 1974). Additional studies exploring the disturbance hypothesis found that while disturbance can facilitate invasions, invasions are not inherent to all disturbances, even though invasions themselves can constitute a disturbance event (Hobbs 2010).

Furthermore, the empty niche hypothesis states that invasive species become dominant by using unused local resources, known as empty niches (Elton 1958; MacArthur 1970). The species richness hypothesis states that areas with higher species richness are often more resistant and less vulnerable to invasions (Elton 1958; MacArthur 1970, 1972). The propagule pressure hypothesis states that the more propagules of a non-native species that arrive in an area, the more likely the non-native species will successfully establish and become invasive (di Castri 1989; Williamson 1996; Lonsdale 1999; Duncan 2010). The evolution of invasiveness hypothesis states that rapid evolutionary (i.e. genetic) responses of non-native species triggered by new selection pressures encountered in the introduced geographic region drive their invasion success (Blossey and Nötzold 1995; Lee 2002; Stockwell et al. 2003; Lee 2010).

Finally, the novel weapons hypothesis (Callaway and Ridenour 2004; Callaway 2010) states that the biochemical advantages possessed by some invasive species result from regional differences in the expression of evolutionary trajectories, not simply for the purpose of poisoning or interfering with competitive species (Callaway and Ridenour 2004; Callaway 2010). Many plants possess ambiguous metabolic byproducts

and harmless biochemical traits that were probably initially introduced through selection pressures associated with necessary biological functions, such as root communication, defense against herbivory, antimicrobial protection, and soil nutrient acquisition (Callaway and Ridenour 2004). The key element that seems to shift the possession of biochemical traits from harmless to poisonous, is the lack of overlapping evolutionary histories between native and invasive species (Grove et al. 2012). Without overlap, selective pressures have not been placed on native species to develop mechanisms to counter the natural biochemical toxicity of an invasive species, therefore making it novel and potentially allelopathic to the native species upon its successful colonization and establishment (Grove et al. 2012). In the end, many of these hypotheses suggest that most invasive plant species tend to possess unique mechanisms and advantageous physiological characteristics that frequently outcompete native species in propagule pressure, growth and fecundity, survivorship to reproductive maturity, and dispersal efficiency (Luken 1997a; Lieurance 2004).

Research conducted in restoration ecology and conservation biogeography (a modern sub-discipline of conservation biology, proposed by Whittaker et al. (2005) as encompassing the theory, analysis, and application of biogeographical principles to the distributional dynamics and problems specifically associated with biodiversity conservation) have also begun to acknowledge and account for the dynamic nature of ecosystems and the need for invasive species management in their restoration and conservation recommendations for protected areas (Franklin 2009; Richardson and Whittaker 2010; Keenleyside et al. 2012). Ultimately, restoration, conservation, and

invasion ecologists strive to develop, test, and apply various ecological theories using scientific procedures, in order to repair highly destroyed or damaged ecosystems, inform regulatory agencies and land managers, and learn from the outcomes of various restoration and management practices in order to combat invasions and their ecological impacts (Palmer et al. 1997; Dettman and Mabry 2008; Prach 2011).

2.2 ECOLOGICAL STATUS OF WHITE OAK SAVANNAS IN THE MIDWEST

Between 10,000 to 500 years before present (ybp), oak forests dominated the eastern United States (Abrams 1992, 2005). Within that timeframe, from between 6,500 to 3,500 ybp, fire frequencies in the Midwest increased, causing many oak forests to shift to oak savannas (Abrams 1992, 2005). The geographic extent of historic Midwest oak savannas has been estimated to have once covered 10 to 13 million hectares throughout central North America and were primarily found in dry, warm, low-lying, and flat landscapes (Figure 1) (Nuzzo 1986; Vellend et al. 2008; Brudvig and Asbjornsen 2009; Brudvig et al. 2011).

A savanna is characterized as an important transitional community found either isolated within or dividing prairies, grasslands or forests (Madany 1981; Nuzzo 1986; Leach and Givnish 1999; Vellend et al. 2008). The term “barren” is frequently used to describe areas with oak savanna-like characteristics, specifically plant communities occurring on sandy soils dominated by scattered large trees, small trees, low shrubs, and grasses (Nuzzo 1986; Eckstein & Moss 1995). Tall-grass oak savannas, a subset of the broader savanna community, were historically found throughout temperate regions and were composed of open-grown, fire-tolerant trees and a dense herbaceous

understory (e.g. prairie grasses and forbs, forest forbs, etc.) that often lacked a shrub layer (Nuzzo 1986; Anderson 1998; Asbjornsen et al. 2005).

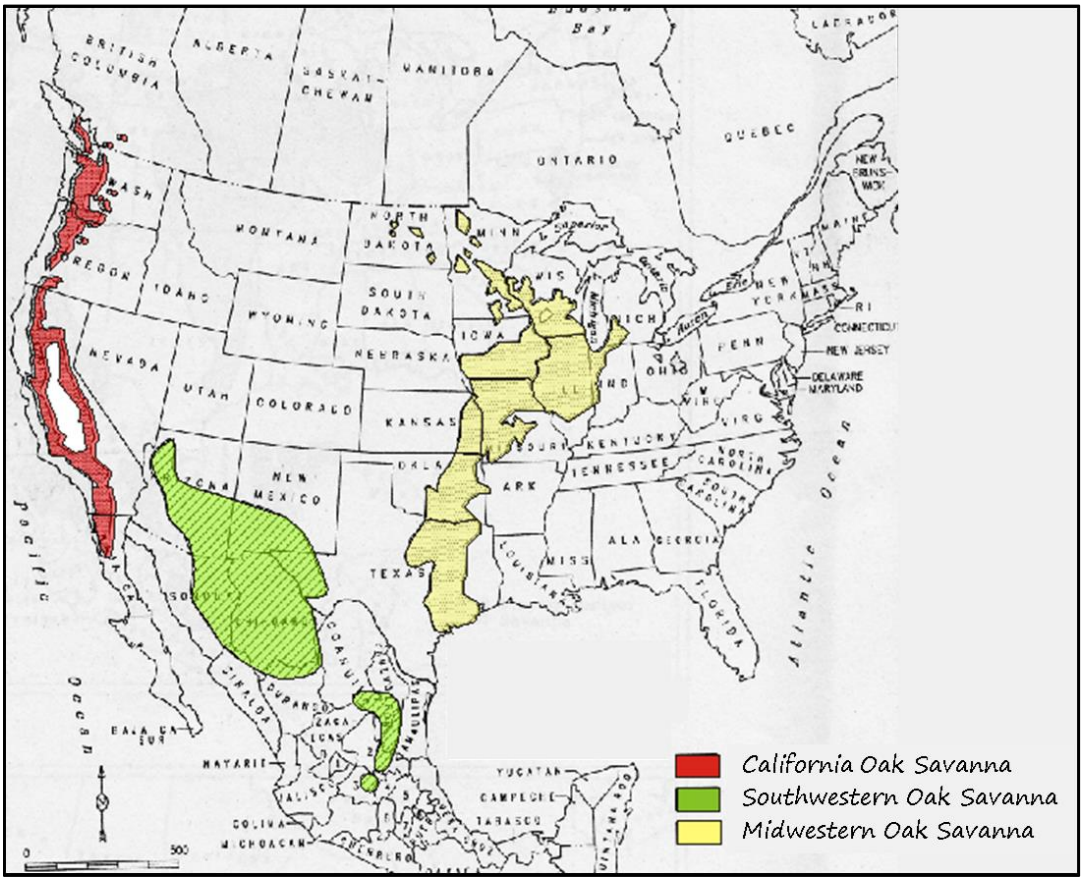

Figure 1. Geographic distribution of historic oak savannas throughout the United States. Midwestern Oak Savannas are delineated in yellow across central United States. (After McPherson (1997); modified from McPherson, G. R. Ecology and Management of North American Savannas. University of Arizona Press, Tucson).

Specifically in Illinois, three historic subclasses of savanna once occurred: 1) Dry and dry mesic sand savanna established on very sandy soils containing very little humus; 2) Dry, dry-mesic, and mesic barren; and 3) Dry-mesic and mesic savanna established in lowlands and till plains on fine-textured soils (Nuzzo 1986; Madany 1981). What constitutes an oak savanna in relation to tree density varies geographically, ranging from extremes as low as 2.5 trees per hectare to as high as 100 percent cover in locations undergoing restoration (Nuzzo 1986). In general however, an average oak

savanna canopy tends to have between 10 percent and 50 percent cover retained by regular light fires interspersed with sporadic catastrophic disturbance events (usually related to climate patterns or intense fire events) that encourage regeneration and recruitment of oak once every 35 to 100 years (Nuzzo 1986; Apfelbaum and Haney 1991; Peterson and Reich 2001). When compared to mesophytic species, oak seedlings are less sensitive to fire in any frequency (Peterson and Reich 2001).

The presence and geographic distribution of oak savanna communities in presettlement Illinois were primarily influenced by wildfire frequency and topography, and with the exception of the bottomlands of the Wabash and Ohio Rivers in southern Illinois, occurred throughout the state mainly on hilly terrain (Madany 1981; Nuzzo 1986; Peterson and Reich 2001). Frequent, low intensity fires maintained the open understory of oak savannas, which were uniquely composed of herbaceous species adapted to frequent large-scale disturbances (Nuzzo 1986; Tenney 2007). While high intensity, irregular fires promoted dense sprouting that ultimately formed thickets rather than open savanna (Nuzzo 1986). Areas with frequent fire regimes are often more open and have canopy gaps that tend to provide high light in localized bursts, while areas that have more contemporary, infrequent fire regimes have fewer and smaller canopy gaps that are often inadequate for supporting shade-intolerant species (Cowell et al. 2010).

White oak was the dominant species of oak before European settlement throughout the eastern and central United States, having the largest range when compared to other eastern oaks (Abrams 2003). The composition, structure, and function of Midwest oak savanna ecosystems are reliant on maintaining white oak as a

dominant species (Rogers 1990; Abrams 1992; Brudvig and Evans 2006; Wang and Bauerle 2006). According to Abrams (2003), presettlement oak-hickory vegetation communities had the highest distribution of white oak in the Midwest and central United States. White oak also has economic importance, especially to the wine industry, since wine barrels are only produced using three species of oak, white oak being one of them (Thomas 2014). Maintaining a healthy, viable regeneration layer of white oak seedlings in the understory is crucial for sustaining its presence among the scattered canopy trees, since the fittest seedlings will eventually grow to be saplings and survive to replace the aging canopy trees that can live for hundreds of years (Apfelbaum and Haney 1991; Gazol and Ibanez 2010; Rebbeck et al. 2012).

During the last 3,500 years, the precise range of Midwest oak savanna has varied in structure, position, and size (Abrams 1992; Clark et al. 2001; Brudvig and Asbjornsen 2009). Post-settlement fire suppression regulations, fragmentation due to changing land uses, deer herbivory, as well as increased native and invasive woody encroachment in North America have amplified the geographic restriction and diminishment of Midwest oak savanna communities, isolating them primarily to steep, wet, and cool rocky hill-tops with shallow soils (Bowles & McBride 1998; Madany 1981; Peterson & Reich 2001; Vellend et al. 2008; Cowell et al. 2010; Brudvig et al. 2011). Many Midwest oak savanna remnants, defined as having an active fire history for at least 10 years that maintains a scattered canopy of open-grown oaks and a ground layer dominated by native plants (Leach and Givnish 1999), have undergone structural, successional, and ecosystem-level transformations.

Common transformations, supported by historical stand structure dynamics reconstructed from dendroecological data, include: an increase in tree density, basal area and cover of mesophytic, shade-tolerant, fire-sensitive species and an increased decline in white oak regeneration and recruitment during the 20th century (Abrams 1992; Henderson 1995; Bowles and McBride 1998; Peterson and Reich 2001; Albrecht and McCarthy 2006; Wang and Bauerle 2006; Cowell et al. 2010; Brudvig et al. 2011; McEwan et al. 2011). To date, invasive species have been estimated to have impacted as much as 39% of forested systems (including those that have transitioned from open canopy savannas to closed canopy woodlands), especially in the eastern United States (Oswalt et al. 2015). This increased density of shade-tolerant and invasive species within previously open oak savanna communities suppresses the oaks and prevents them from ultimately recruiting to the canopy layer (Albrecht and McCarthy 2006). The under-representation of oak seedlings and sapling in present-day understories of Midwest oak savanna communities has led to significant declines in white oak frequency, even when mature white oaks remain dominant in the canopy layer (Apfelbaum and Haney 1991; Abrams 2005; Albrecht and McCarthy 2006; Cowell et al. 2010; Schulte et al. 2011). Furthermore, without competitive advantage over both native and invasive encroaching species, Schulte et al. (2011) predicts that oaks will lose their historical dominance within the next few decades.

White oak regeneration and recruitment gaps, combined with the degradation and loss of high quality Midwest oak savanna in part due to invasive species encroachment, threatens the sustainable management of white oak, as well as the

species richness of breeding bird populations and native plant communities found within savannas (Apfelbaum and Haney 1991; Wang and Bauerle 2006). Although there are no known species considered endemic to oak savannas (Nuzzo 1986), there are savanna specialists whose geographic distributions are now limited to savanna remnants and fringes of lightly grazed pastures, oak woods, and brushy areas (Henderson 1995).

Henderson (1995) identifies yellow pimpernel, woodland thistle, pale Indian plantain, horse gentian, downy wild rye, sessile-leaved eupatorium, New Jersey tea, and elm-leaved goldenrod as uncommon savanna specialists; kitten tails, Virginia lespedeza, and cream gentian as threatened savanna specialists; and wild hyacinth and purple milkweed as endangered savanna specialists. Edge habitats have maintained enough savanna structure to sustain most of the amphibians, birds, reptiles, and mammals found within historical oak savannas (Henderson 1995). Many large savanna species, such as elk, timber wolf, bison, black bear, and bobcat were either extirpated from their former savanna regions or reduced to very small populations due primarily to their incompatibility with the increasing human populations rather than simply due to their habitat loss (Henderson 1995). Two mammals species (the Franklin's ground squirrel and the least shrew) and two reptiles species (the eastern massasauga rattlesnake and the western slender glass lizard), however, are currently threatened or endangered due to their close association with the most open savannas, most of which have become overgrown or converted to other land uses (Henderson 1995). As a result of the change in land use, from savanna to agriculture, nesting grounds of the

threatened Blanding's turtle have also decreased, which puts the turtles future at more risk (Henderson 1995).

The dynamic nature of the Midwest oak savannas are ideal for exploring regeneration and recruitment mechanisms, as they naturally exhibit range contraction in unfavorable years and range expansion in favorable years (Brudvig and Asbjornsen 2009). In an experiment conducted by Brudvig and Asbjornsen (2008, 2009), restoration (defined as the removal of large shrubs and mesophytic trees) had no impact on white oak seed densities, however overall survival rates for the four year study revealed that seedlings found in the sites undergoing restoration treatments were more likely to survive than those found in areas undergoing no restoration. Furthermore, attributes such as, basal diameter, number of leaves, and seedlings growth, competitiveness, and survival were found to be greater in restoration sites and areas with inter-canopy gaps upon implementation of midstory removal (Brudvig and Asbjornsen 2008, 2009; Craig 2012). Ultimately, this indicates that restoration of oak savannas may in fact be a viable way to promote white oak regeneration and recruitment. More specific information on white oak responses to individual site characteristics and invasive species would benefit restoration activities, given that they would provide guidance for site specific goals and management practices. More information on white oak dynamics in oak savannas is therefore necessary, especially given that far more is known about North American oak forests than Midwest oak savannas (Brudvig and Asbjornsen 2008).

2.3 INVASIVE SPECIES: AMUR HONEYSUCKLE

The top three most common invasive species in Lee County are *Lonicera* spp. (honeysuckle), *Ribes missouriense* (Missouri Gooseberry), and *Rhamnus* spp. (Buckthorn), respectively (Illinois Department of Natural Resources 2003). Specifically, Amur honeysuckle has become one of the most aggressive, abundant, and problematic non-native invasive species in the Midwest and eastern United States (Luken and Thieret 1996; Hutchinson and Vankat 1997; Collier et al. 2002; McNutt 2010; Barriball 2012; Castellano and Gorchov 2013; Wilson et al. 2013; Barriball et al. 2015). The Southern Region of the U.S. Forest Service identifies Amur honeysuckle as a category one weed, meaning it is known to be invasive and extensive throughout all or most of its range, can spread into and survive in native plant communities, can displace native plant species, and therefore poses a significant threat to the quality and integrity of the natural plant communities it invades (Munger 2005).

Of the invasive species hypotheses discussed earlier, the novel weapons hypothesis (Callaway and Ridenour 2004; Callaway 2010) is particularly relevant to Amur honeysuckle, as it is an example of a species that possess biochemical advantages (Hutchinson and Vankat 1997; Collier et al. 2002; McNutt 2010; Barriball 2012). More specifically, Amur honeysuckle has been identified as producing phenolic metabolites that provide chemical resistance against insect herbivores (Collier et al. 2002; Cipollini et al. 2008; McEwan et al. 2009; McEwan et al. 2012). Results from laboratory bioassays, have also confirmed that the aqueous leachate from Amur honeysuckle leaves, roots, and fruits negatively impact both native and non-native

understory species throughout its invaded habitat (i.e. germination inhibition or reduction with increased leachate concentrations) (Leopoldini et al. 2004; Dorning and Cipollini 2006; Cipollini and Dorning 2008; Cipollini et al. 2008; McEwan et al. 2010; Bauer et al. 2012; McEwan et al. 2012). Following the logic of the Novel Weapons Hypothesis, the phenolic metabolites produced by Amur honeysuckle may have originally been produced for one purpose (possibly chemical resistance against insect herbivores), but their negative impacts on native species in newly invaded habitats suggest that the allelochemicals produced by Amur honeysuckle play a role in its invasive success.

Beyond producing allelochemicals, Amur honeysuckle also exhibits other invasive characteristics. More specifically, the leaves of Amur honeysuckle in some geographic locations, such as Kentucky, have shown immunity to early freeze thaw cycles, unlike their native counterparts that experience high leaf mortality after frost events (McEwan et al. 2009). Amur honeysuckle leaves also exhibit an extended leaf phenology, meaning they possess the ability to open before and fall after the leaves of native shrub; a mechanism known to be advantageous for non-native invasive species (Luken and Thieret 1996; Trisel 1997; Collier et al. 2002; Bartuszevige et al. 2006; Xu et al. 2007; McEwan 2009).

Robert Fortune collected the first recorded herbarium specimen of Amur honeysuckle in 1843, however the species was officially described based on specimen collected in 1855 near the Amur River by Richard Maack (Luken and Thieret 1996). Figure 2 displays the known introduction patterns of Amur honeysuckle around the

world. The St. Petersburg Botanical Garden was the location of the first successful cultivation of Manchurian Amur honeysuckle propagules in 1883 (Luken and Thieret 1996). Records indicate that St. Petersburg was distributing seeds to other locations by around 1887, which is also the hypothesized source of plants in Western Europe (Luken and Thieret 1996). By 1896, Amur honeysuckle was successfully cultivated at the Royal Botanic Gardens at Kew, as well as in North America for the first time at Dominion Arboretum in Ottawa, Canada from German propagates (Luken and Thieret 1996). The New York Botanical Garden was the first U.S. location to record successful cultivation of Amur honeysuckle obtained from Washington D.C. in 1898, followed by Arnold Arboretum at Harvard University in 1903 (Luken and Thieret 1996). At minimum, Amur honeysuckle was distributed seven different times between 1898 and 1927, and was available from about eight commercial nurseries by 1931 (Luken and Thieret 1996). The ability of Amur honeysuckle to reproduce and spread beyond the point of its introduction in the U.S. was first recorded by Morton Arboretum in Lisle, IL in the mid-1920s, and reports of naturalized populations within the United States began by the late 1950s (Luken and Thieret 1996; Cipollini and Dorning 2008). Between 1960 and 1984, the Natural Resources Conservation Services (NRCS; then the USDA Soil Conservation Service (SCS)) was responsible for manipulating Amur honeysuckle cultivars (i.e. selecting genotypes from naturalized populations that enhance fruit production) and distributing them throughout the United States (i.e. Maryland in 1970, Mississippi in 1979, Texas in 1980, North Dakota in 1983, and Michigan in 1984), so that they could

be used to achieve soil stabilization and reclamation, in addition to improving ornamental landscapes and bird habitats (Luken and Thieret 1996).

The aesthetically pleasing foliage, floral, and fruit displays of Amur honeysuckle contributed to its popularity, successful distribution, and common incorporation into multiple landscape types (Luken and Thieret 1996). The extended leaf phenology of Amur honeysuckle combined with its capacity to vegetatively resprout, produce an abundant amount of seed, and exude allelopathic compounds, lends to its aggressive nature, ability to regenerate after disturbances and compete with native vegetation (Luken and Mattimiro 1991; Callaway and Ridenour 2004; Cipollini et al. 2008). Ultimately, the spread of Amur honeysuckle populations were probably only limited by competitive pressures (e.g. light availability, etc.) and distribution efficiency, although anthropogenic distribution via the Section of Foreign Seed and Plant Introduction within the USDA and commercial nurseries made it so distribution efficiency was less of an issue (Luken and Thieret 1996; Bauer et al. 2012).

Since its introduction, dense thickets of Amur honeysuckle have grown to replace the relatively open understories of many oak dominated landscapes throughout the Midwest (Hutchinson and Vankat 1997; Collier et al. 2002). Optimal habitats for Amur honeysuckle range from urban areas or urban fringe and floodplains to interior forest patches, open woodlands, and forest edges (Luken and Thieret 1996; Collier et al. 2002). Ultimately, Amur honeysuckle has been associated with altering vegetation community dynamics by: 1) decreasing native herbaceous plant reproduction, seed recruitment, growth, and species richness, abundance, and diversity; and 2) reducing

native tree seedling richness and survival, as well as overall forest density and diversity (Hutchinson and Vankat 1997; Gould and Gorchov 2000; Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2004; Bartuszevige et al. 2006; McEwan et al. 2009). Few studies, however, have specifically addressed how Amur honeysuckle impacts white oak regeneration and recruitment. Therefore, any research that specifically identifies how the underlying mechanisms of Amur honeysuckle affect white oak seedlings is necessary, in order to effectively guide restoration efforts for this and other important native species trying to survive in invasive-dominated systems.

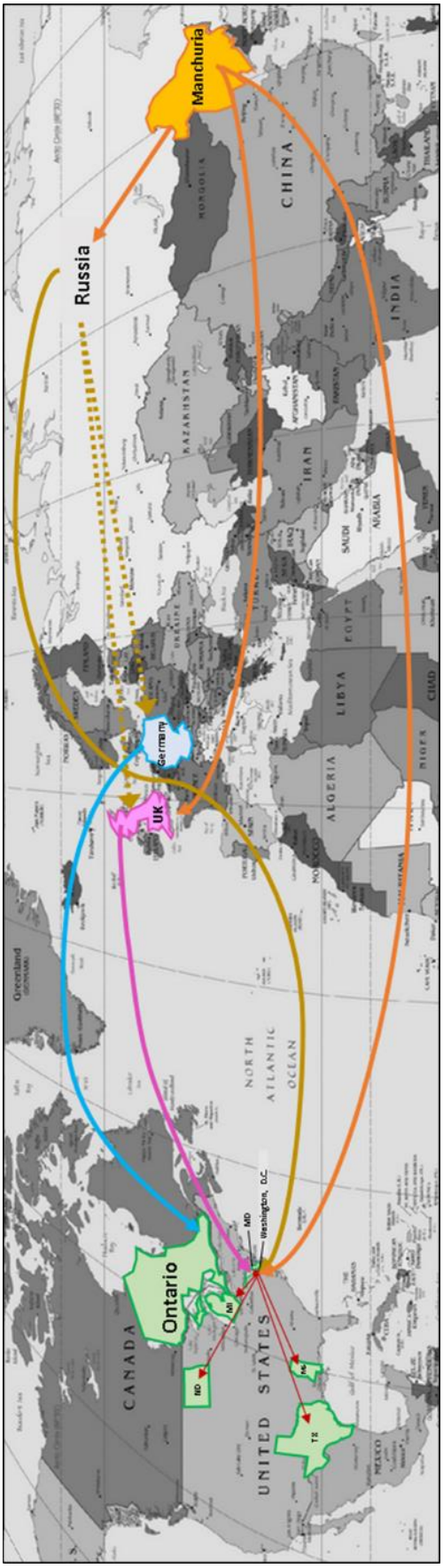

Figure 2. Map of known historical introduction pathways of Amur honeysuckle throughout Europe and North America from Northeastern China. Dotted lines represent probable route; Solid lines represent confirmed routes (After Luken and Thieret 1996).

2.4 IMPORTANCE OF UNDERSTORY LIGHT ENVIRONMENTS TO THE REGENERATION AND RECRUITMENT OF WHITE OAK

White oak, has been classified as having intermediate shade tolerance, but is generally not well adapted to low light levels (Abrams 1992; Dey 2002). Survival of white oak seedlings may be possible at low light levels for short periods of time, but low light levels are often insufficient for long-term survival, particularly in the early life stages (Minckler 1965; Rogers 1990; Abrams 1992; Dey 2002; Wang and Bauerle 2006; Gazol and Ibanez 2010; Parrott et al. 2012). According to Albrecht and McCarthy (2009), higher light levels (i.e. 35 percent full sunlight) are required by white oak in order to reproduce adequately from seed, maintain positive carbon assimilation rates once the initial seed reserves are exhausted, and produce a sufficient amount of carbohydrates for recruitment into their next stage of development (Rogers 1990; Dey 2002). More specifically, the survival and growth of oak seedlings relies on their ability to maintain net photosynthesis rates above zero once the seed reserves are exhausted, meaning the photosynthetic CO_2 fixation rates must exceed the respiration requirements of the seedlings (Dey 2002). This is especially important within shaded microsites (Dey 2002).

Aubuchon et al. (1978) calculated the average photosynthetic rate for mature white oak and found that photosynthetic activity was statistically uniform at leaf-level. Sullivan et al. (1996), estimated a mean, light-saturated net assimilation rate for mature white oak trees in the southern Appalachian Mountains as being 7.6 μmol/m^2/s. While, Rebbeck et al. (2012) found that white oak light compensation point was representative of deep shade (7.2 μmol/m^2/s), and may therefore be more shade tolerant than

previously thought, while chestnut oak and northern red oak had on average a higher light compensation point (17.8 μmol/m^2/s). This finding seems to indicate that white oak is also a more efficient user of light as compared to other oaks (Rebbeck et al. 2012), and may therefore have the potential to maintain positive season carbon balances in shaded environments.

Rebbeck et al. (2012), also observed that more carbon was allocated to root systems when compared to the other oaks, so not only is it more efficient, but it is also displays different growth and physiological attributes (e.g. slow growth, low light compensation point and dark respiration rates, higher root to shoot ratios, lower ratio of leaf biomass) as possible adaptations to shade tolerance. Ultimately, Rebbeck et al. (2012) concluded that there would be no added benefit to opening or increasing light environments any higher than 18% of full sun (equivalent to about 360 μmol PAR/m^2/s), while at the same time suggesting that light levels need not be increased to more than 25% of full sun (equivalent to about 500 μmol PAR/m^2/s) for less shade tolerant oak species like chestnut and northern red oak. To achieve these light levels, Rebbeck et al. (2012) suggests that the stand basal area be reduced by 35%-40% in a shelterwood harvest.

Amur honeysuckle, on the other hand, has been classified as being moderately shade tolerant, with plastic physiological and morphological responses to changing light environments (e.g. branch architecture, germination viability, etc.) (Luken et al. 1995, Luken and Thieret 1996; Luken et al. 1997b; Bartuszevige et al. 2006). Even with its moderate shade tolerance, light is still an important variable in the success of Amur

honeysuckle. For example, light was identified as the most important factor influencing Amur honeysuckle cover in a particular site, along with distance from seed source (Hutchinson and Vankat 1997). Light availability was also found to be a limitation to the growth of Amur honeysuckle at the seedlings stage, with increased growth rates occurring under higher light conditions (Luken and Thieret 1996).

Amur honeysuckle encroachment creates shaded microsites within habitats they invade, since research has found that they decrease light availability, mainly as a result of their dense growth patterns and extended phenology (Luken et al. 1997a; Collier et al. 2002; Cipollini and Dorning 2008; McEwan et al. 2009, 2012). Therefore, decline in light availability may be a major limiting factor to white oak regeneration and recruitment, as open savanna communities continue to transition to denser canopy forests (Lorimer 1993; Dey 2002). As encroachment increases in former Midwest tall-grass oak savannas and their canopies continue to become denser, the survival and growth of white oak seedlings are becoming constrained, due in part to competition for limited understory light resources (Lorimer 1993; Bowles and McBride 1998; Dey 2002; Albrecht and McCarthy 2006; Meiners 2007; Brudvig and Asbjornsen 2008).

Previous studies have explored many topics regarding the impact of Amur honeysuckle on its invaded surroundings, including its ability to alter understory light levels (Luken et al. 1997a; Collier et al. 2002; Cipollini and Dorning 2008), the subsequent reductions in tree seedling survival, in part due to light competition (Trisel 1997), and the response of Amur honeysuckle to varying light environments (Luken et al. 1995, 1997b; Lieurance 2004). Ultimately, multiple studies that have linked Amur

honeysuckle cover to decreases in native seed recruitment, tree seedling richness and density in forests, as well as increased native tree seedling mortality (Hutchinson and Vankat 1997; Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2004). While other studies have concluded that the net primary productivity of dense open grown thickets of honeysuckle (1350 g/m-2/yr-1) are nearly as productive as an entire woodland community (Whittaker 1975; Luken and Thieret 1996), potentially due to its extended leaf phenology, which allows a greater access to carbon (McEwan et al. 2006).

To date, however, the amount of leaf-level seasonal carbon gained by Amur honeysuckle as a result of their extended leaf phenology has not been quantified (McEwan 2009), nor has the ecological impacts of the altered light environments under Amur honeysuckle on white oak seedling physiological health, as inferred from photosynthetic response and leaf-level seasonal carbon balance. Understanding the physiologic response of white oak to light manipulations is crucial to determining a critical light level at which regeneration and recruitment are feasible, in order to inform future management treatments (Rebbeck et al. 2012).

More research is necessary to understand what role invasive shrubs have on the light environment and carbon gain of white oak, and to broaden the physiological understanding of white oak. This research will help explain the role Amur honeysuckle plays in altering resource competition dynamics and its impacts on native species, which will ultimately strengthen the interpretations concerning its invasive mechanisms and ecology. It will also provide a case study in which carbon gain is calculated based

on physiological variables measured *in situ*, which will allow for the differentiation between potential ability to maintain a positive carbon gain and actual ability. White oak variables may also vary from location to location, so this study will add to the pool of knowledge from which we may eventually be able to extract maximum and minimum physiological attributes, in order to make broader conclusions and suggestions for oak conservation.

2.5 IMPORTANCE OF SOIL DYNAMIC PROPERTIES TO THE REGENERATION AND RECRUITMENT OF WHITE OAK

Soil is an important component of terrestrial ecosystems, including oak savannas, as it is the major substrate within which white oaks establish and regenerate, and the interactions between aboveground and belowground ecosystem properties are strongly linked (Kardol and Wardle 2010). Ultimately, white oak seedlings establish best on loose, deep, well-drained loamy soils with light to moderate litter cover and an adequate amount of soil moisture (Minckler 1965; Rogers 1990; Dey 2002). The Midwest tall-grass oak savannas often developed on deep silty clay loam soils (Apfelbaum and Haney 1991).

Soil moisture and temperature is especially important to white oak seed germination and early seedling establishment, since these younger life stages may be particularly sensitive to environmental gradients and the level of moisture in the soil signifies how much water is available for plant utilization (Collins and Carson 2004; Legates et al. 2010). Soil moisture has also been reported as being essential for maintaining oak seed viability, supporting seedling survival until root maturity, regulating

leaf-level plant carbon dynamics, and influencing soil respiration rates; which itself is an environmental indicator of root respiration and microbial decomposition of soil organic matter (Hanson et al. 1993; Raich and Tufekciogul 2000; Dey 2002; Smith and Johnson 2004; Tang and Baldocchi 2005; Tang et al. 2005; Curiel Yuste et al. 2007; Kuzyakov and Gavrichkova 2010; Lewis 2011).

Alternatively, Collins and Carson (2004) found that the abundance of white oak seedlings was only correlated (R^2=0.53) with seed-producing adult white oak trees rather than to site characteristics (i.e. aspect, slope position, site index, stand age, and elevation), while site characteristics played a strong role in the abundance of white oak saplings (R^2=0.75). Furthermore, previous research has also found that white oak seedlings and saplings in Wisconsin had a higher density on transitional dry mesic sites (Nowacki et al. 1990), while xeric slopes promoted the highest abundance for both white oak seedlings and saplings in Missouri (Pallardy et al. 1988; Rochow 1972).

Ultimately, white oak seedlings are usually categorized as having a drought tolerance, Larson and Whitmore (1970), on the other hand, found that low soil moisture can slow the development of roots. These findings, suggest that more research associated with how varying site characteristics impact regeneration and recruitment dynamics is necessary in order to tease out the role of site characteristics in the varying life stages of white oak, as different biotic and abiotic conditions may impact each life stage differently (Collins and Carson 2004). Ultimately, soil moisture and temperature are indispensable variables for understanding and evaluating vegetation patterns and dynamics, especially in relation to vegetation with dense canopy cover (e.g. invasive

species encroachment, etc.) that might compete for water resources by altering transpiration rates, intercepting precipitation, creating shaded microsites, and lowering soil temperature (Breshears et al. 1998; Legates et al. 2010).

In addition to soil moisture and temperature, plant-available mineral macronutrients (e.g. nitrogen, phosphorus, potassium, calcium, magnesium, etc.) are also important to the initial establishment and growth of seedlings, as well as to the long-term survival of many plants, including white oak (Dey 2002). Late successional, shade tolerant, gap-opportunistic species compete heavily for understory resources with oak seedlings in all but the most dry (i.e. xeric) and nutrient-poor sites (Abrams 2003). The availability of nutrients and water for plant growth, as well as the activity of soil microbes are ultimately determined by soil biogeochemical processes and soil chemical properties which vary over space and through time (Bhandari and Ficklin 2009). Understanding these properties and processes are key to environmental monitoring, developing management strategies, and conducting soil quality assessments (Bhandari and Ficklin 2009).

Beyond soil moisture, temperature, and nutrients, the quality of a soil characterizes its ability to function within an ecosystem, in relation to supporting biological productivity (e.g. plant regeneration, growth, recruitment, etc.), improving plant and animal health, and preserving overall environmental quality; goals that are often also important for restoration projects (Doran and Parkin 1994; Doran et al. 1996; Karlen et al. 1997; Page-Dumroese et al. 2000, 2010). Hence, monitoring soil quality is important when making land management decisions, as it identifies how those

management and restoration strategies have maintained, diminished, or improved soil quality through time (Wander and Drinkwater 2000; Herrick 2000). Among the dynamic soil properties that convey soil quality, soil aggregate stability has been identified as one of the most functionally important properties, since it can be used to assess the status of other critical ecosystem processes (i.e. soil permeability and infiltration rates, vulnerability to erosion, soil organic matter functions, crop production, and overall soil sustainability) that are central components to developing and appropriately applying successful conservation land management strategies (Amezketa 1999; Bird et al. 2002, 2007; Carter 2002; Bronick and Lal 2005; Yoo et al. 2011; Breetzke et al 2013; Nciizah and Wakindiki 2015). Furthermore, aggregates stability can also be used to infer healthy microbial activity and leaf litter abundance under plants, since these variables have also been identified as promoting soil aggregation (i.e. the binding of soil particles to one another) and therefore increasing aggregate stability, which in turn conserves and stores the soil organic matter contained within the aggregate and serves as a reservoir of plant energy and nutrients (Jastrow et al. 1998; Carter 2002). The landmark work by Tisdall and Oades (1982) explored the relationship between aggregate stability and soil organic matter and found that spatial and temporal distributions of soil organic matter and other binding agents play key roles in the mechanisms of aggregation and the stabilization of the aggregates (Jarvis et al. 2012). More specifically, Tisdall and Oades (1982) developed a hierarchical aggregate model, or the notion that particles (<20 µm) bind together via persistent binding agents to form stable micro-aggregates (20-250 µm) that are less impacted by management regimes and those stable micro-aggregates then

are bound together by temporary binding agents to form macro-aggregates (>250 µm) that are potentially more vulnerable to management practices.

Soil aggregate stability is also an essential component to investigate how dynamic soil properties and site characteristics (both abiotic and biotic) respond to changes within an ecosystem (e.g. invasive species encroachment, etc.) (Corbin and D'Antonio 2004; Bird et al. 2007). This is especially important for forested ecosystems, as site characteristics may cause a site to be more or less vulnerable depending on whether they are acting as drivers or regulators of invasion by non-native species, respectively (Wilson et. al 2013). For example, Wilson et al. (2013) emphasized that it is experimentally difficult to determine whether a non-native invasive species was successful in a particular site as a result of: 1) historical land uses altering the site's soil nutrient characteristics in a way that would later facilitate the invasion; 2) pre-existing, unaltered soil nutrient characteristics that make the site more vulnerable to the invasion; or 3) a post-invasion modification to the site's ecosystem processes affecting its soil nutrient characteristics by the non-native invasive species, as a result of the invasion. The use of adjacent sites with similar land-use histories, in future research exploring variation in soil dynamic properties related to the invasion of non-native species, may be able to isolate a causal relationship and therefore differentiate between these scenarios (Kourtev et al. 1998; Ehrenfeld 2003; Wilson et al. 2013; Iannone et al. 2015).

According to Corbin and D'Antonio (2004), restoration efforts can be significantly hindered by non-native invasive species, especially if they have the capacity to impact soil nitrogen dynamics. Soils within forested sites containing non-native invasive

species were found to have higher nutrient and pH levels, with thinner litter and organic horizons when compared to uninvaded sites (Kourtev et al. 1998; Ehrenfeld et al. 2001). The unique characteristics displayed by non-native invasive species that are currently hypothesized as being influential to a site's nutrient cycling process, include: 1) a larger amount of fast growing standing biomass with a higher net primary productivity; 2) rapidly decaying organic litter; 3) higher amount of extractable inorganic nitrogen in underlying soil; 4) higher nitrification rates; 5) potential symbiotic relationships with nitrogen-fixing organisms; 6) ability to disrupt or alter nitrogen-fixing relationships possessed by native species; 7) ability to alter the spatial distribution and timing of nutrient fluxes within soil pools; and 8) altering soil moisture and pools of nitrogen and carbon (Ehrenfeld 2003; Corbin and D'Antonio 2004). Soil cation distribution and organic matter content were also found to be impacted by non-native invasive species (Levine et al. 2003; Corbin and D'Antonio 2004). What remains to be determined, however, is the exact mechanisms through which non-native invasive plants could alter nutrient dynamics (Ehrenfeld 2003). Differences related to leaf phenology (in relation to throughfall nutrient cycling), tissue chemistry, leaf litter quality, net primary productivity, total biomass, and plant morphology were hypothesized as being important components to a non-native invasive species ability to alter a site's soil nutrient dynamics (Ehrenfeld 2003; Corbin and D'Antonio 2004; McEwan et al. 2012).

Research on Amur honeysuckle found altered soil moisture levels in invaded sites, in part as a result of its dense (almost monoculture) growth patterns, higher total foliar biomass, widespread shallow root systems, and extended phenology that allows

less water to reach the forest floor (Trisel 1997; Collier et al. 2002; Cipollini and Dorning 2008; McEwan et al. 2012). The shallow root system of Amur honeysuckle may also reduce availability of nutrients in the upper soil and therefore decrease tree seedling survival as a result of root competition (Trisel 1997; Collier et al. 2002). Besides altering moisture and light levels, the extended leaf phenology of Amur honeysuckle has also been linked to altering rainwater chemistry, which results in a decreased depositions of ammonium nitrogen (NH4+-N) and higher cation concentrations (particularly magnesium (Mg2+) and potassium (K+)) (McEwan et al. 2012). Additionally, Amur honeysuckle frequently occurs in sites that have little to no native leaf litter on the forest floor, which may be related to its ability to further modify soil nutrient pools, cycles, and moisture characteristics, since the bare soil is more likely to be exposed to the rapid release of nitrogen from the rapidly decaying Amur honeysuckle organic matter (Bartuszevige et al. 2006; Blair and Stowasser 2009; McEwan et al. 2012; Poulette and Arthur 2012; Trammell et al. 2012; Wilson et al. 2013). Corbin and D'Antonio (2004) found that increased nitrogen availability often favors fast-growing, non-native invasive species.

Site characteristics that have been found to be insignificant to the establishment and proliferation of Amur honeysuckle, include: 1) the physical presence or absence of native shrubs within an invaded site; and 2) the species composition and basal area of a forest's vegetation (Wilson et al. 2013). Furthermore, both McEwan et al (2012) and Wilson et al. (2013), found no significant difference between soil property characteristics and the abundance or presence of Amur honeysuckle. At face value, this new finding

suggests that soil characteristics may not be a useful attribute for the prediction of invasion success in forested ecosystems; however, more research is needed to support this finding before the role of soil characteristics can be fully teased out (Wilson et al. 2013).

Expanding our understanding of how dynamic soil and forest floor properties (e.g. soil moisture, carbon, nitrogen, and available plant nutrient levels) differ in areas with and without Amur honeysuckle encroachment, will provide further research exploring the role of these properties in the prediction of non-native species invasions, and/or the impact of non-native species invasions on these properties. In turn, this information would facilitate a more accurate discussion about how white oak regeneration and recruitment might be impacted in invaded sites by any potential differences in dynamic soil properties and altered resource competition dynamics (Dey 2002; Wilson et al. 2013).

2.6 DISPERSAL MECHANISMS INFERRED THROUGH POPULATION GENETICS: INVASION MODES AND POTENTIAL PATHWAYS OF AMUR HONEYSUCKLE

Most hypotheses regarding plant invasion biology rely on the assumption that the improved success of the invaders outside their native range is made possible by various unique evolutionary and ecological dynamics found in their newly established range (e.g. Novel Weapons Hypothesis, Evolution of Invasiveness Hypothesis, etc.) (Parker et al. 2013). There are, however, a few studies that have found large differences in the invaders' native and newly established habitats, but no significant difference in their performance from one to the other; thereby providing support for an alternative

hypothesis wherein the success is due to the interactions between inherent individual traits of the invasive species and the novel conditions of the environment invaded (Parker et al. 2013). Inherent traits possessed by successful plant invaders often include better resistance to pathogens and pests, higher net primary productivity, more rapid growth rates, higher phenotypic plasticity, higher fecundity, and longer range seed dispersal as compared to their native counterparts (Luken 1997b; Reichard and Hamilton 1997; Collier et al. 2002; Lieurance 2004). Long-distance dispersal events are important features of populations, especially influential to the biological aspects of non-native plant species invasions, such as the metapopulation dynamics, diversity and dynamics of ecological communities, population dynamics, evolution of populations, and colonization probabilities (Ouborg et al. 1999; Cain et al. 2000).

As rapid biodiversity loss continues, understanding the general geographic and evolutionary patterns and relationships associated with invasive species population range expansions has become increasingly important in targeting potential source populations, and in developing effective management strategies that maximize limited conservation resources (Whitlock and Mccauley 1999; McNutt 2010; Barriball 2012; Castellano and Gorchov 2013; Gorchov et al. 2014; Barriball et al. 2015). Once the mechanisms by which invasive species spread to their current range distributions can be understood, then predictions about where and in what way that species might spread in the future can be made, which can ultimately inform management strategies meant to prevent future invasions (Castellano and Gorchov 2013). If, for example, an invasive species is spreading through local dispersal through an expanding front, and

subsequent propagule recruitment continually occurs from outside the newly established patch from neighboring populations, then management strategies would be best served targeting the edge of the invasive specie's current range (Gorchov and Henry 2013). If, on the other hand, an invasive species is spreading through long-distance dispersal, and subsequent propagule recruitment occurs from the matured individuals that have established themselves within the new patch after the initial long-distance dispersal event, then management strategies would be best served targeting individual colonists; preferably before they begin to propagate after establishment (Gorchov and Henry 2013).

Amur honeysuckle possess a few of the traits identified as being beneficial for invasive species, including long-range seed dispersal, the absence of a seed dormancy phase, and year-round germination abilities (Luken and Thieret 1996; Bartuszevige et al. 2006; Wilson et al. 2013). Evidence suggests that Amur honeysuckle spreads from multiple locations through stratified diffusion (coined by Hengeveld in1989), which means that it relies on both long-distance dispersal between towns early in the invasion and short distance dispersal between woodlots and other suitable habitats as propagule recruitment accelerates from within the newly established population via white-tailed deer, rodents, and birds, specifically: European starlings (*Sturnus vulgaris*), American robins (*Turdus migratorius*), hermit thrushes (Catharus guttatus), cedar waxwings (*Bombycilla cedrorum*), and northern mockingbirds (*Mimus polyglottus*) (Williams et al. 1992; Collier et al. 2002; Bartuszevige and Gorchov 2006; Bartuszevige et al. 2006; McNutt 2010; Barriball 2012; Castellano and Gorchov 2013; Gorchov and Henry 2013;

Gorchov et al. 2014; Orrock et al. 2014). The proportion of edge in a landscape, along with forest connectivity (> 0%; contrary to findings of Bartuszevige et al. 2006) and cover (> 5%) were observed as being positively correlate with the abundance of Amur honeysuckle, while large agricultural fields, tree basal area, leaf litter accumulation, and woody species diversity might act as barriers to its spread, given their negative correlation with Amur honeysuckle distribution and density (Hutchinson and Vankat 1998; Wilson et al. 2013). Subsequent to the dispersal and establishment of Amur honeysuckle in a new area, they were found to have high physiological and morphological plasticity in response to environmental changes (Luken et al. 1995; Wilson et al. 2013).

Introduction of invasive species are usually accelerated by human dispersal and expansion of disturbed habitats (Collier et al. 2002). Given the history of Amur honeysuckle, human dispersal has played a role in its spread over long distances, as specimens and seeds were exchanged and shared between herbaria, commercial nurseries, and distributed by the USDA Section of Foreign Seed and Plant Introduction (Luken and Thieret 1996). Understanding the mode by which invasive species, like Amur honeysuckle, spread into the United States and identifying populations that act as a seed source can potentially aid management strategies, in that they can be targeted for *in situ* removal, as a way to prevent the further spread of the invasive species (Bartuszevige et al. 2006). Unfortunately, even in light of its importance to invasion dynamics, long-distance dispersal is frequently ignored in the literature, or only addressed anecdotally, due to the logistical and technical difficulties associated with

physically monitoring and measuring it (i.e. expensive, difficult to directly observe, time-consuming) (Whitlock and Mccauley 1999; Cain et al. 2000).

Huebner (2003) found that herbarium and land classification data alone were insufficient and unreliable in fully predicting the spread and distribution patterns of nine invasive species, including Amur honeysuckle. Age structure assessments have been successfully used to infer invasion patterns of Amur honeysuckle, but are limited in their ability to assess whether the founding individuals of each population stem from single or multiple source populations (Gorchov et al. 2014). Genetic methods on the other hand provide a general approach to monitoring and estimating long-distance dispersal (Cain et al. 2000). Furthermore, genetic methods have been successfully used in a variety of studies inferring plant demographic processes (Davis and Shaw 2001; Diochon et al. 2003; DeWoody et al. 2004; Hu et al. 2010), including studies specifically on Amur Honeysuckle (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015). Ultimately, Cain et al. (2000) argues that utilizing genetic methods are more beneficial to the scientific community than taking a defeatist attitude and assuming that long-distance dispersal is just too difficult to measure.

With specific relevance to invasive species, like Amur honeysuckle, landscape genetic population structure analyses that identify geographic and genetic differentiation and variation between populations, can be used to estimate dispersal distances, colonization patterns, and infer potential sources of both founding and newly established individuals (Cain et al. 2000; DeWoody et al. 2004; Hu et al. 2010). Moreover, populations of Amur honeysuckle in Ohio have been successfully analyzed

using microsatellite primers specifically designed for Amur honeysuckle in genetic population structure analyses (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015).

Based on the data obtained from fragment analyses, samples can be arranged along a geographic gradient, and the geographic distribution of likelihoods can be used to describe the probability that the focal population belongs to each population along that gradient (Barriball 2012; Barriball et al. 2015). This is possible because the number and source of individuals establishing new populations, along with gene flow (or pattern of dispersal) and geographic distance, determine the extent of genetic differentiation between populations at a landscape level (Whitlock and McCauley 1999). Ultimately, the combination of genetic methods and geographic knowledge in the research presented in this dissertation promotes the integration of spatial scientists and geographers in interdisciplinary research. More research that utilizes the known invasion history of Amur honeysuckle and redefines our understanding of long-distance dispersal with regard to potential anthropogenic influences is necessary, in order to more accurately determine the general geographic and evolutionary patterns associated with Amur honeysuckle's range expansions throughout the eastern and central United States, as well as the location of potential source populations for use in targeted *in situ* removal management strategies.

CHAPTER 3: STUDY SITE AND SPECIES

3.1 STUDY AREA

3.1.1 INTRODUCTION

Lee County was established in 1839 and is located in north-central Illinois, USA, around 41° north latitude and between 88° and 89° west longitude (Lee County, Illinois: History Outline of Lee County 2010) (Figure 3). This study focuses on the North-Central portion of Lee County, specifically within Nachusa Township, situated in the Rock River Hill Country of the Till Plains section within the Central Lowland providence of the Interior Plains physiographic division (Figure 4). The Major Land Resource Area (MLRA) associated with Lee counties is called the Central Feed Grains and Livestock Region, also known as Region M. The geographic extent of Region M is large, extending from Minnesota to Oklahoma and Nebraska to Ohio (United States Department of Agriculture 2006). In total, Region M comprises 282,450 square miles of the Midwest (United States Department of Agriculture 2006). More specifically, Lee County is located within the Illinois and Iowa Deep Loess and Drift, East-Central Part of Region M, also known as MLRA 108B, and therefore will be the focus of the general study area description (United States Department of Agriculture 2006) (Figure 5). This part is contained entirely within Illinois and makes up 7,450 square miles, or about 2.6% of Region M (United States Department of Agriculture 2006).

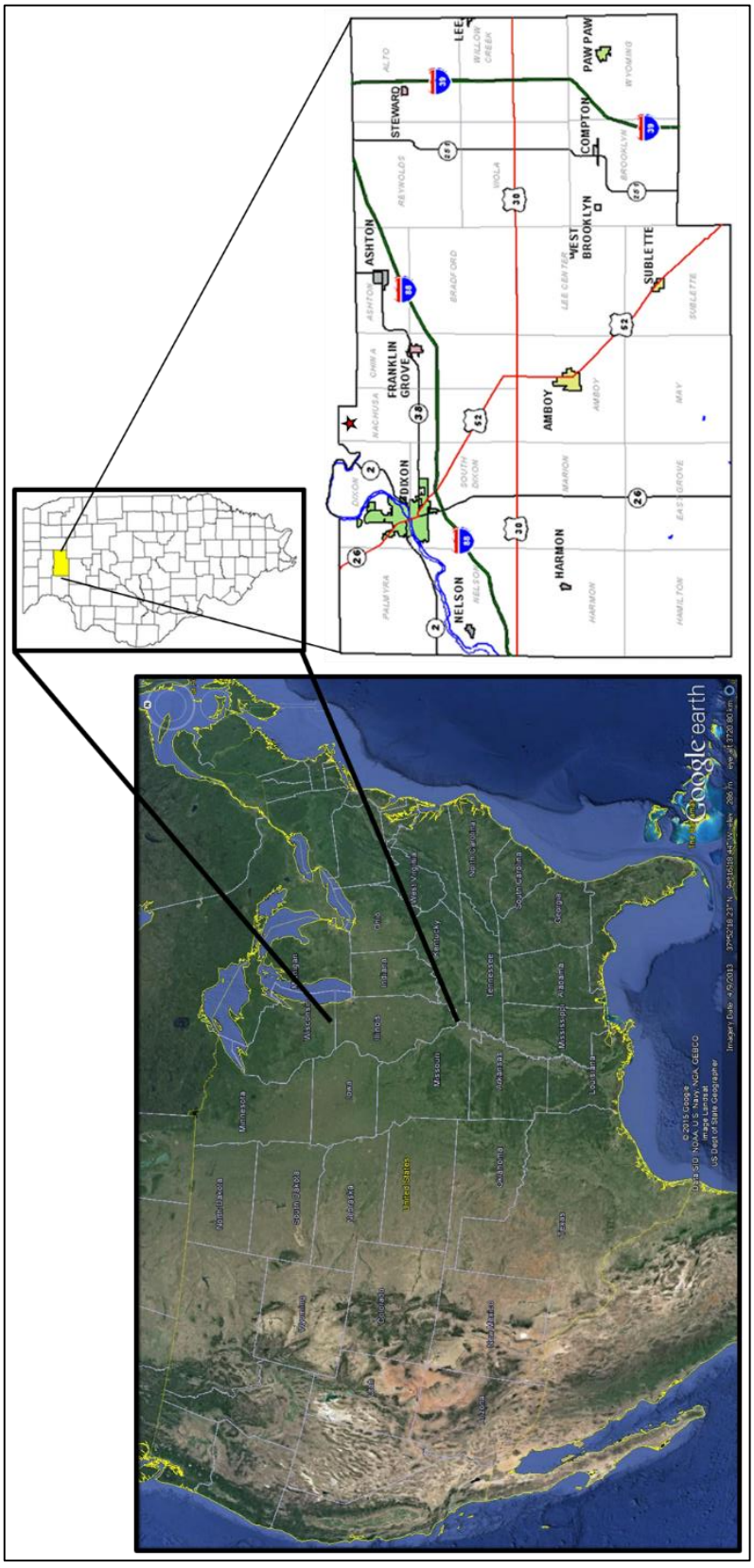

Figure 3. Location of the study area: Lee County (highlighted yellow) in north-central Illinois, USA. Red star indicates approximate location of oak savanna restoration study site within Nachusa Township at Nachusa Grasslands. Maps modified from Google Earth and Lee County GIS Portico Website (2015).

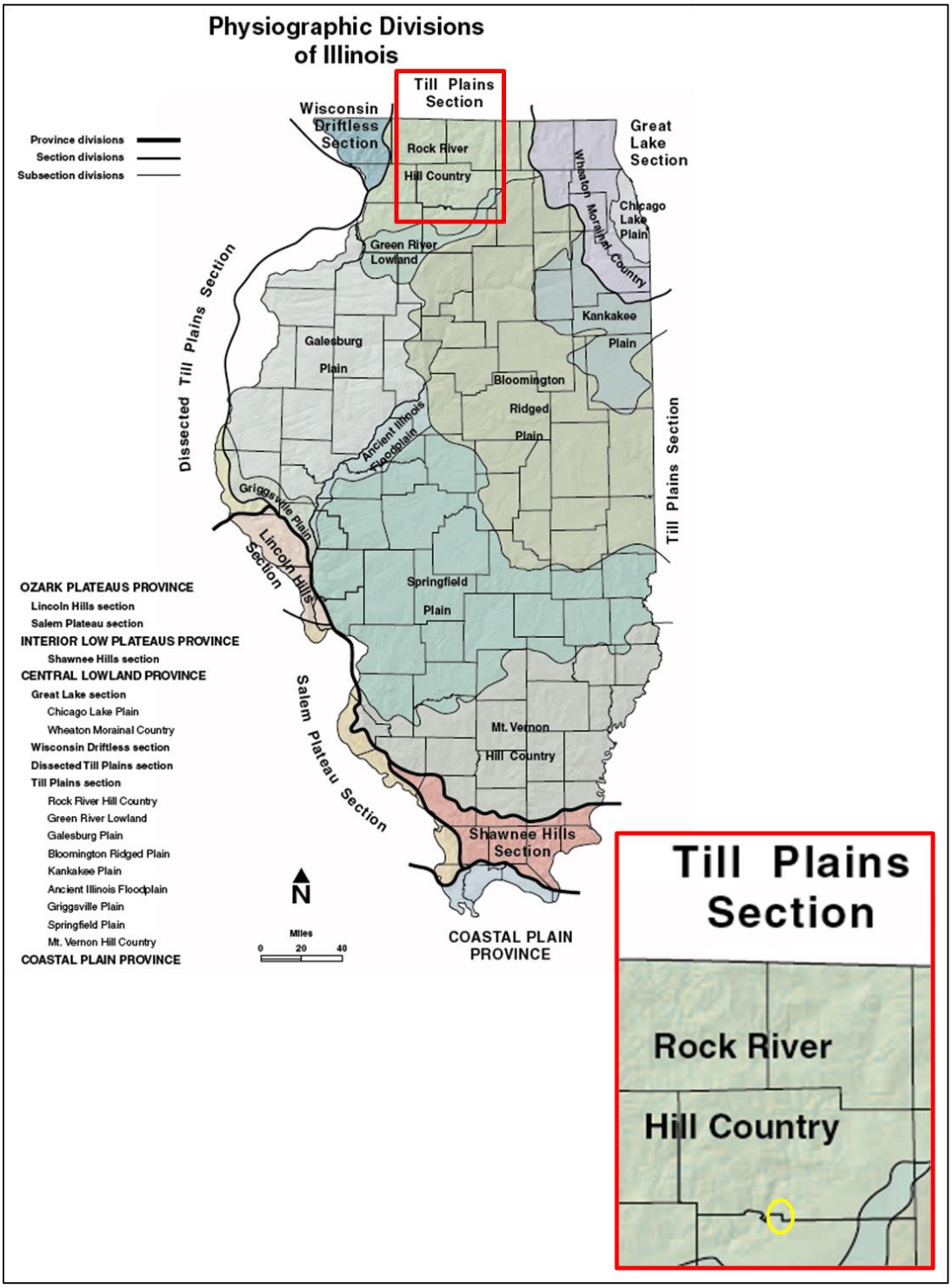

Figure 4. Map of the Physiographic Divisions of Illinois. Inset shows enlarged Till Plains Section in order to identify site location within the Rock River Hill Country. Circle represents approximate location of the site that is the focus for this report. (Mckay 2009).

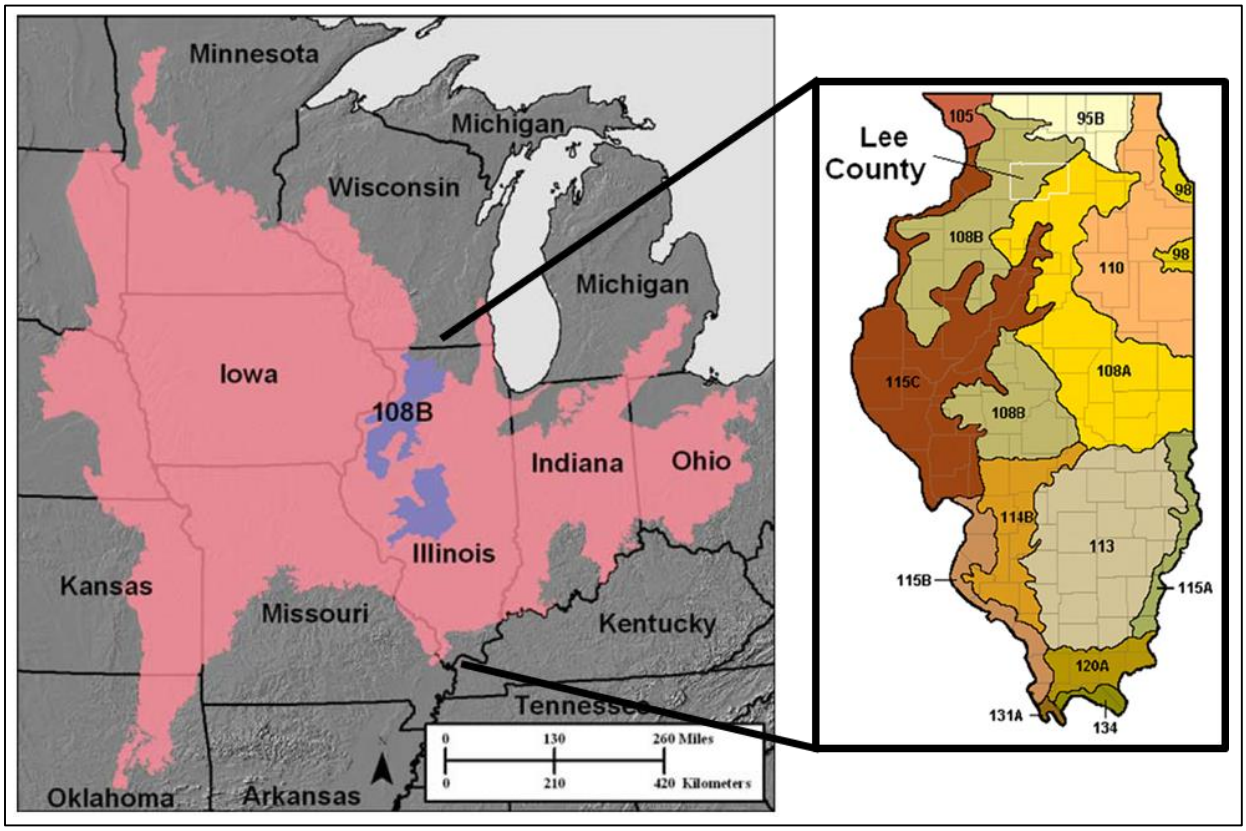

Figure 5. Map depicting the geographic extent of MLRA 108B in Region M (pink), as well as the location of Lee County within MLRA 108B (United States Department of Agriculture 2006).

3.1.2 TOPOGRAPHY AND GEOLOGY

Having been glaciated, the northern part of MLRA 108B is found on a fairly young rolling plain that has been moderately to strongly dissected with an elevation of around 985 feet with maximum local reliefs ranging from 3–10 feet on the broad, flat uplands to about 160 feet along major streams (United States Department of Agriculture 2006). Throughout the Lee County, the slopes range between 0 to 35 percent (Elmer and Zwicker 2003). The underlying geology for the northern part of MLRA 108B consists of Ordovician and Silurian limestone, while Pennsylvanian shale, siltstone, and

limestone are found in the southern and western parts (United States Department of Agriculture 2006). Loess, till – calcareous in nature, outwash deposits, eolian deposits, lacustrine deposits, alluvium, organic material, paleosols, and residuum from sandstone and limestone are the primary material within which the soils of Lee County developed (Elmer and Zwicker 2003). Illinoian glacial till covers the entire MLRA 108B area, except bluffs found along major streams (United States Department of Agriculture 2006). In addition to the Illinoian till, the glacial drift is also composed of Wisconsin aged sorted, stratified outwash (United States Department of Agriculture 2006).

3.1.3 SOILS

Topography affects the soils temperature, susceptibility to erosion, and drainage (Elmer and Zwicker 2003). All soils have mixed mineralogy with drainage and depths range from moderately deep to very deep and somewhat poorly drained to well drained (United States Department of Agriculture 2006). The excessively drained soils are primarily found on sandy ridge-tops, while the very poorly drained soils are found in depressions (Elmer and Zwicker 2003).

In general, the MLRA 108B falls within the mesic soil temperature regime, often having either an aquic or udic soil moisture regime (United States Department of Agriculture 2006). Soils found within aquic moisture regimes tend to have periodic or continuous reduction and saturation, which often requires artificial drainage by techniques such as subsurface tiles for certain land uses, especially agriculture (Soil Survey Staff 1999). Soils found in udic moisture regimes, on the other hand, tend to receive well distributed rainfall with enough precipitation and stored soil moisture in the

summer to equal or exceed the amount of evapotranspiration and enough precipitation in the winter to recharge the stored soil moisture (Soil Survey Staff 1999).

Within the MLRA 108B, most soils are silty or clayey Udalfs or Udolls, with the dominant soil orders therefore being Alfisols, Mollisols , in addition to sporadic Entisols (United States Department of Agriculture 2006). More specifically, Udalfs are freely drained Alfisols having a mesic or warmer temperature regime and are usually associated with having supported deciduous forest vegetation during their development, while Udolls are freely drained Mollisols having a thermic or warmer temperature regime and are commonly associated with tall grass prairie vegetation at the time of settlement (Soil Survey Staff 1999). Alfisols are mineral soils having a moderate to high base saturation, with an argillic horizon, and an ochric epipedon, and are commonly associated with mixed vegetation cover or forests in moist to semiarid areas (Soil Survey Staff 1999). Mollisols are mineral soils that are typically base-rich and very dark in color with a mollic epipedon and a range of temperature and soil moisture regimes (Soil Survey Staff 1999). Entisols, on the other hand, are soils with little or no evidence of pedogenic horizon development as a result of inadequate time or high disturbance (Soil Survey Staff 1999). Entisols can have any mineral parent material, but tend to only have an ochric epipedon with a few rare exceptions (Soil Survey Staff 1999).

The Alfisols found in the United States frequently form a belt between the Inceptisols and Spodosols in locations with very humid climates and the Mollisols of the prairies (Figure 6) (Soil Survey Staff 1999). Most North American Mollisols are found in subhumid to semiarid locations on the plains between the Spodosols or Alfisols of

humid climates and the Aridisols of arid climates, and although they primarily developed under grassland vegetation, some may have been associated with areas that were historically forested (Figure 7) (Soil Survey Staff 1999). Entisols can form under any aged vegetation, and is typically found on active glacial outwash or flood plains and steep, eroding slopes within a range of temperature and moisture regimes (Figure 8) (Soil Survey Staff 1999).

Organisms, particularly plants, played a key role in forming the soils within Lee County (Elmer and Zwicker 2003). Fungi, earthworms, and bacteria were also identified as factors affecting Lee County soils (Elmer and Zwicker 2003). The soils within the study area initially supported prairie vegetation, in addition to a few hardwood forests on scattered upland sites (United States Department of Agriculture 2006). Most of the level soils within Lee County formed under prairie grasses, while the steeper, sloping soils formed under forests composed of primarily oak and hickory trees (Elmer and Zwicker 2003).

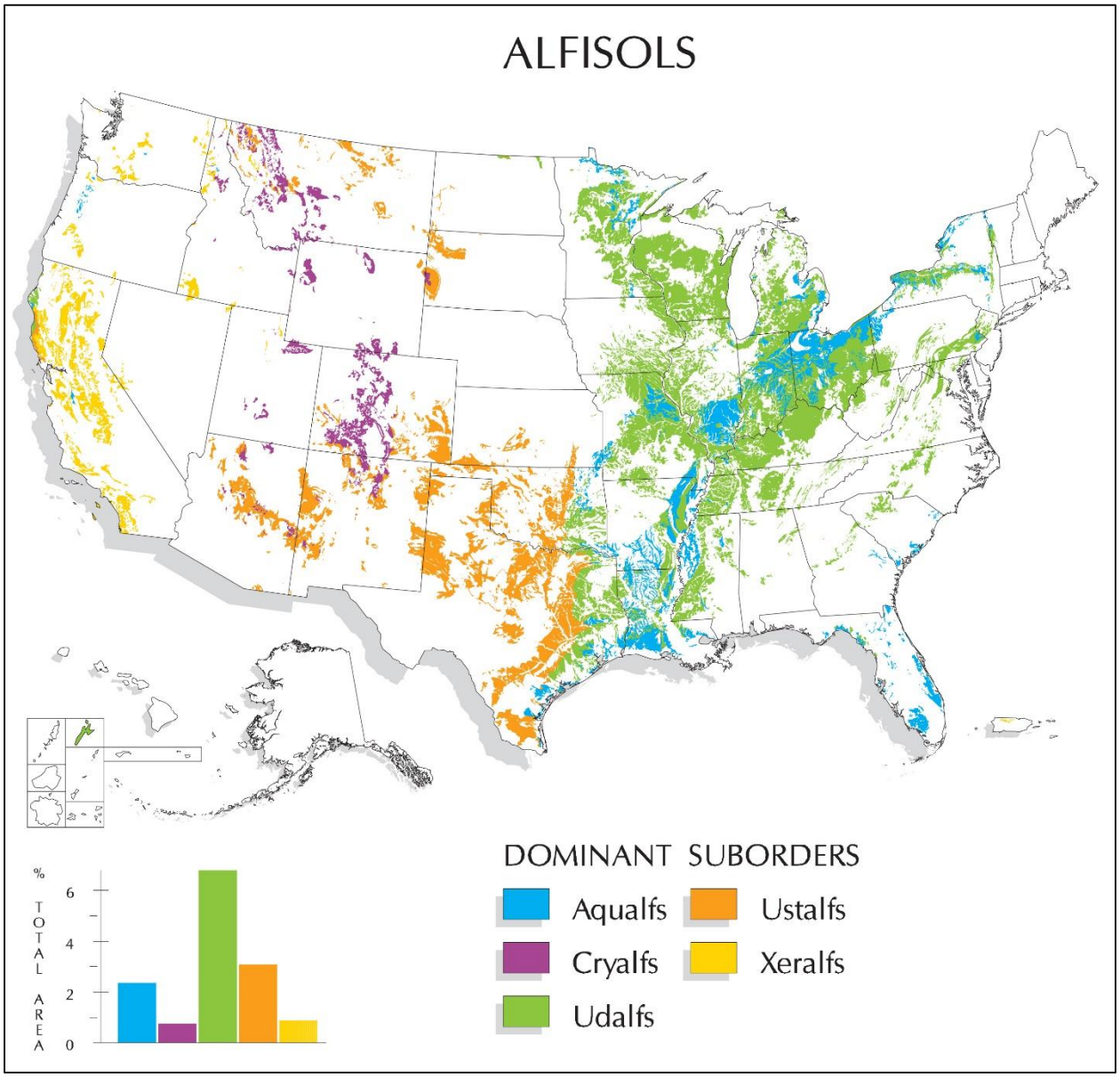

Figure 6. Alfisols soil distribution map with percent total area graph of associated dominant suborders for the United States of America (United States Department of Agriculture 2015a).

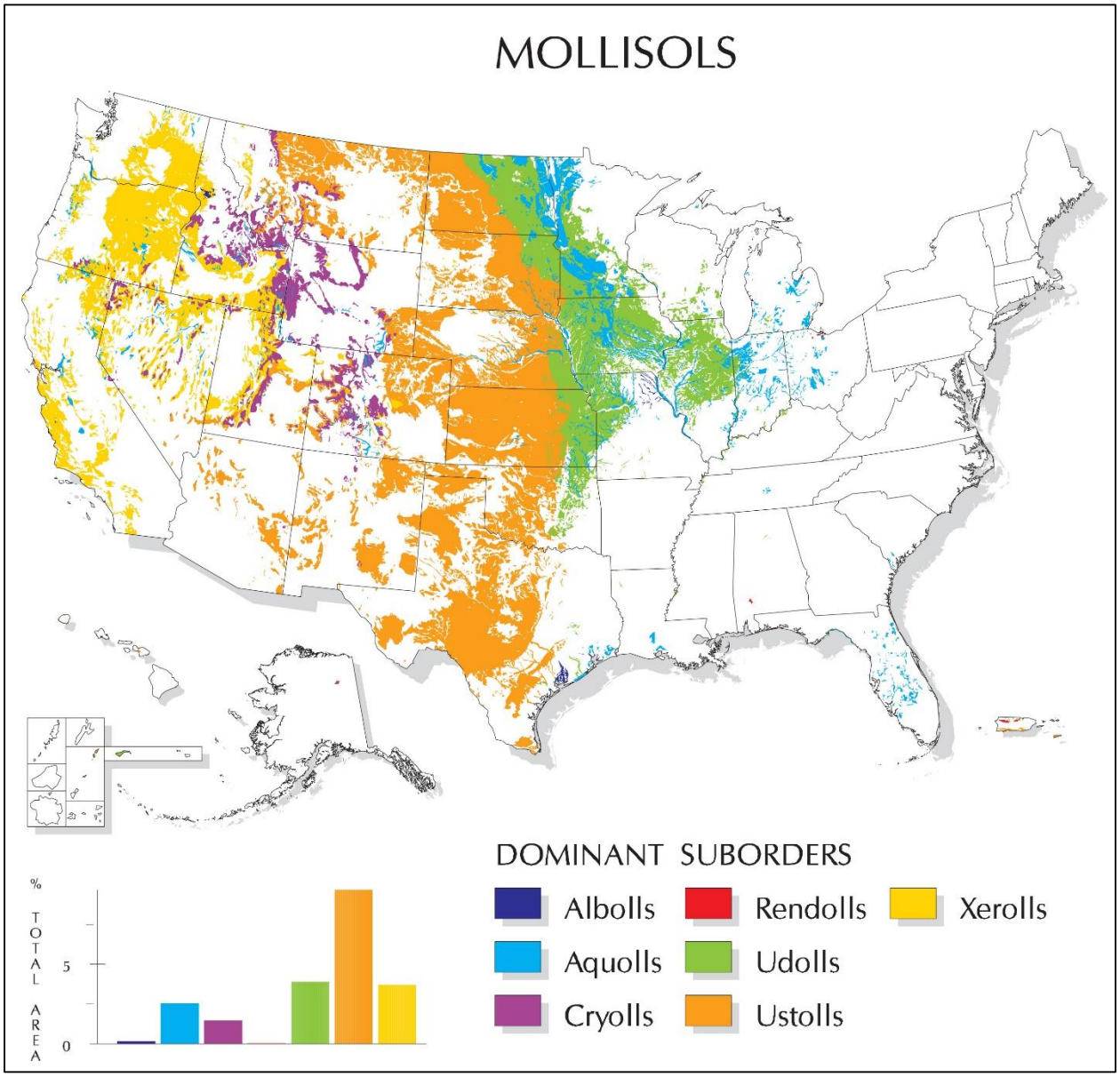

Figure 7. Mollisols soil distribution map with percent total area graph of associated dominant suborders for the United States of America (United States Department of Agriculture 2015b).

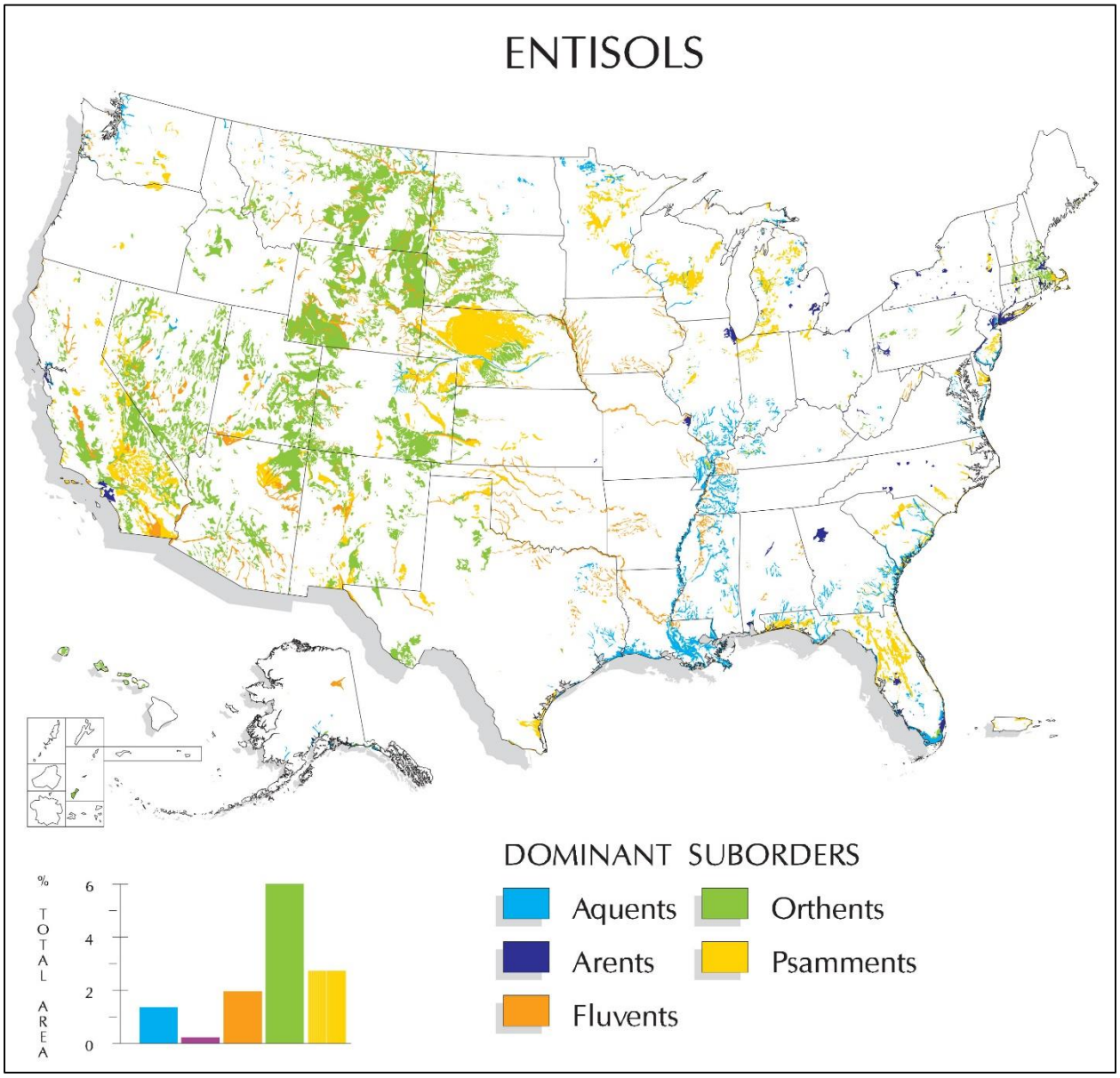

Figure 8. Entisols soil distribution map with percent total area graph of associated dominant suborders for the United States of America (United States Department of Agriculture 2015c).

3.1.4 CLIMATE

The climate within Lee County is temperate and humid (Elmer and Zwicker 2003). Broadly, the average total annual precipitation within MLRA 108B ranges between 838.2 mm and 990.6 mm, while the average annual temperature fluctuates between 8.3 °C and 12.2 °C with freeze-free periods averaging about 185 days (United States Department of Agriculture 2006). Specifically, the average total annual precipitation normals (1981-2010) for Lee County is 965.3 mm, with January having the least precipitation (40.39 mm) and June having the highest precipitation (121.03 mm) (Amboy, IL US and Dixon 1 W, IL US NOAA Stations) (Figure 9). The average annual temperature normals (1981-2010) for Lee County is 9 °C, with January having the lowest mean monthly temperature (-6.6 °C) and July having the highest mean monthly temperature (22.6 °C) (Dixon 1 W, IL US NOAA Station) (Figure 9).

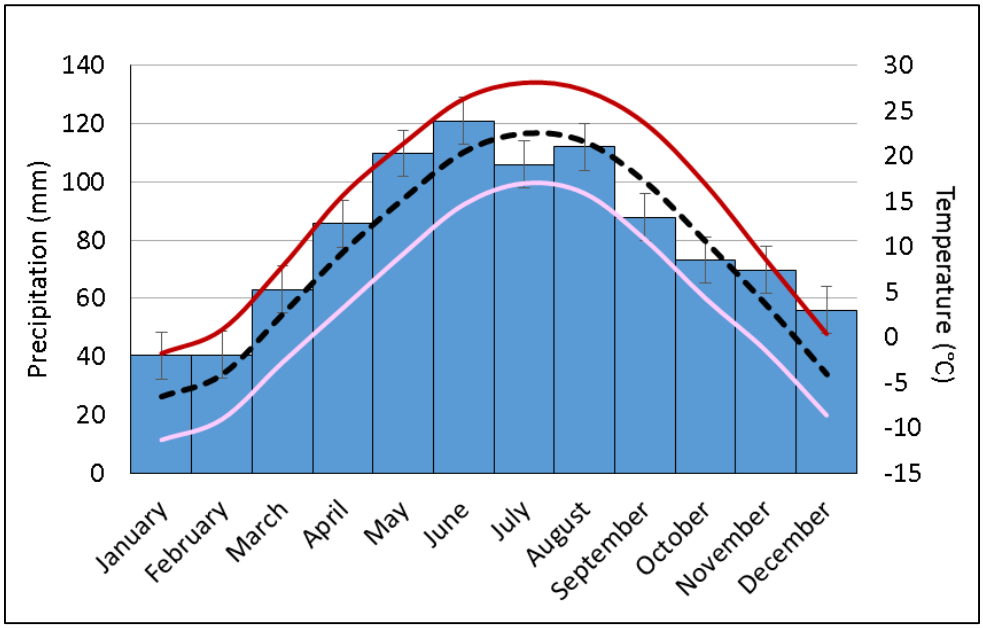

Figure 9. Mean monthly precipitation values (bars), mean maximum monthly temperature (dark red, top line), mean monthly temperature (black dash line), and mean minimum monthly temperature (pink, bottom line) for Lee County, Illinois, USA, 1981-2010. Error bars represent 95% confidence interval.

3.1.5 LAND USE

Currently, land use in the MLRA 108B region is dominated by cropland (79%) – particularly cash-grain crops, so it is not surprising that a majority of the area is made up of privately owned farms (United States Department of Agriculture 2006). The rest of the area is made up of privately owned grasslands with both native and introduced grasses (7%), privately owned forests (5%), private urban developments (6%), water (1%), and other privately owned land (2%) – including a few surface-mined and underground coal-mining areas (United States Department of Agriculture 2006). Conservation practices used in MLRA 108B to combat resource concerns (i.e. wind and water erosion, as well as maintenance of organic matter and productivity of soils) are predominantly systems meant to manage crop residue (i.e. cover crops, no-till systems, windbreaks, nutrient management, and vegetative wind barriers) (United States Department of Agriculture 2006).

3.2 *QUERCUS ALBA*: WHITE OAK

Quercus alba L. (white oak) (Figure 10) is a tree in the taxonomic family Fagaceae (Beech family) within the order Fagales. Most active in the spring and summer, white oak grow slowly, has a long lifespan (USDA 2015d), and is found throughout eastern and central United States (Figure 11). White oak is adapted to all soil textures except fine textured soils and does not require cold stratification for growth (USDA 2015d). Other growth requirement characteristics for white oak include: a medium drought tolerance, the ability to persist in locations with low fertility, a medium moisture usage, a pH range of 6.8 to 4.5, and an intermediate shade tolerance (USDA

2015d). White oak bloom in mid spring and produce a high abundance of acorns that mature in a single season beginning in summer and ending in fall (Koenig and Knops 2014; USDA 2015d). The fate of white oak flowers (i.e. survival or death) were reported as being determined post pollination, shortly after fertilization, with around 80% of the flowers resulting in mortality (Cecich and Sullivan 1999). Ultimately, Cecich and Sullivan (1999) found that the number of acorns produced were positively correlated with the number of fertilized flowers in early July.

The success and abundance of the oak regeneration layer is influenced by environmental and site characteristics, in addition to inter-species competition and seed predation (Gazol and Ibanez 2010). White oak acorns contain less tannins (a phenolic chemical compound produced by plants as a defense against herbivory, competition, and diseases) than other oak species (Thomas 2014). The acorns are produced irregularly in masting events, defined as the synchronized and intermittent production of seed crops that oversaturate the area with seed, so as to counteract the impact of herbivores (i.e. predator satiation) (Silvertown 1980; Pearse et al. 2013; Thomas 2014). The masting events tend to be heavily correlated with climate, particularly temperature, from up to as many as two years prior to the acorn crop development (Thomas 2014). For example, white oak in east-central Missouri were found to have a three year reproduction cycle that was impacted in part by summer drought (negative influence) and spring temperature (positive influence), with an acorn crop size that was negatively correlated with prior year (i.e. 1, 2, and 4 year) crop sizes and positively correlated with the third prior year acorn crop size (Sork et al. 1993). Furthermore, the number of days

in which it hails and maximum temperatures were found to negatively influence acorn production (Cecich and Sullivan 1999).

Oak acorns undergo hypogeal germination, whereby the cotyledon remains below ground and therefore does not photosynthesize, while the shoot survives off of the large energy reserves in the seed and grows above ground to eventually produce photosynthesizing true leaves (Thomas 2014). Once established, after all the seed reserves from the initial germination year have been used completely and functional true leaves and roots have developed, oak seedlings have a relatively short window of time to accumulate an adequate amount of resources (e.g. light, nutrients, water, etc.) to survive and recruit to the next life cycle phases, as compared to some of the competing species that can persist in the understory as a seedling for multiple years before recruiting to the canopy layer (Gazol and Ibanez 2010; Thomas 2014). In the end, oak seedling mortality often exceeds successful establishment (Albrecht and McCarthy 2006; Thomas 2014). During the 20th century, white oak has experienced a decline in regeneration and recruitment, defined as the ability to transition into subsequent life stages (i.e. seedling to sapling) (Abrams 2005; Brudvig and Evans 2006; Wang and Bauerle 2006; McEwan et al. 2011).

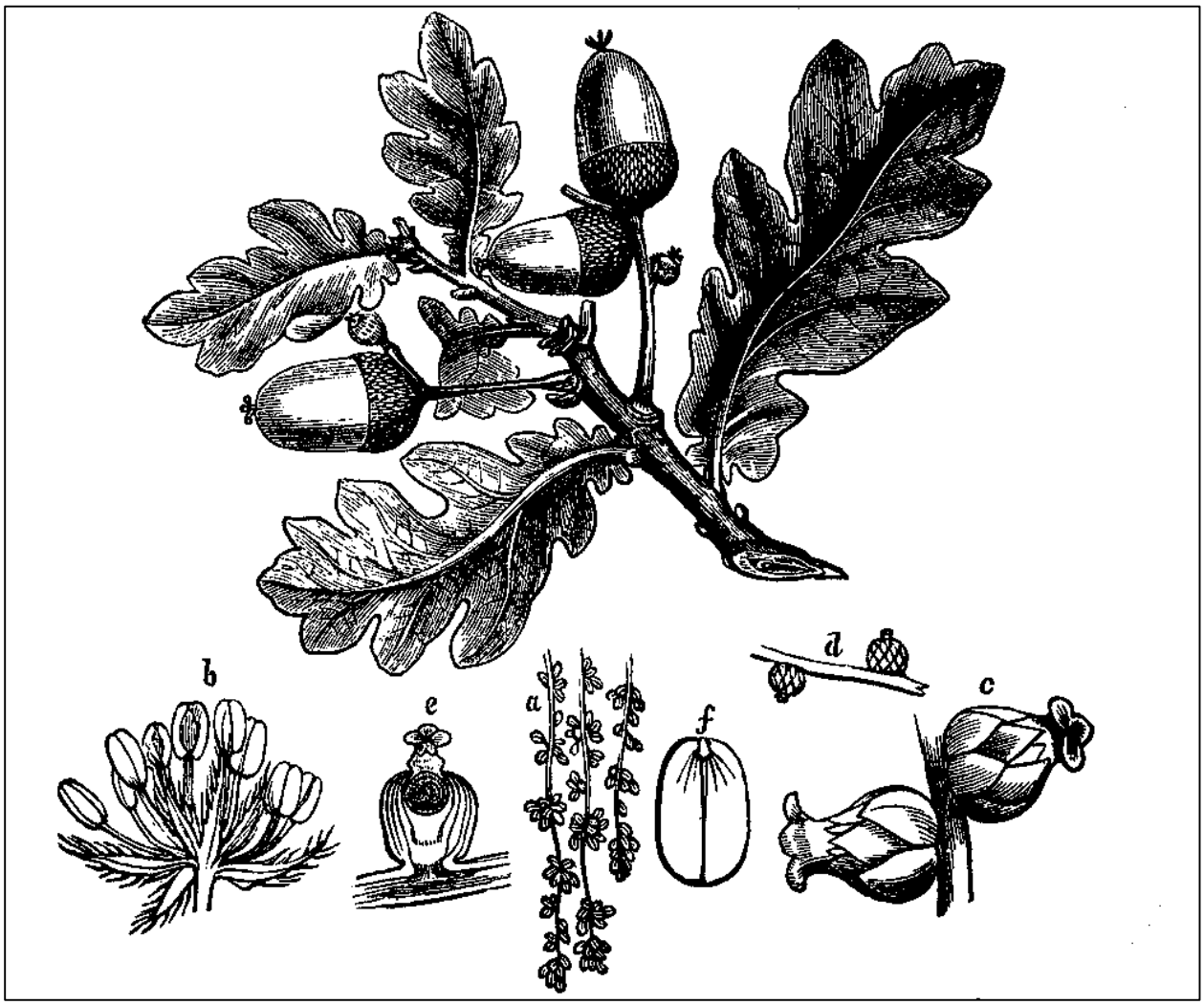

Figure 10. Foliage, staminate catkins (a), magnified staminate flower (b), pistillate flower with stigmas magnified (c), acorn in embryo (d), young acorn section (e), and cotyledons with radicle (f) of *Quercus alba* (white oak) (http://www.swsbm.com/Illustrations/Quercus_alba.gif).

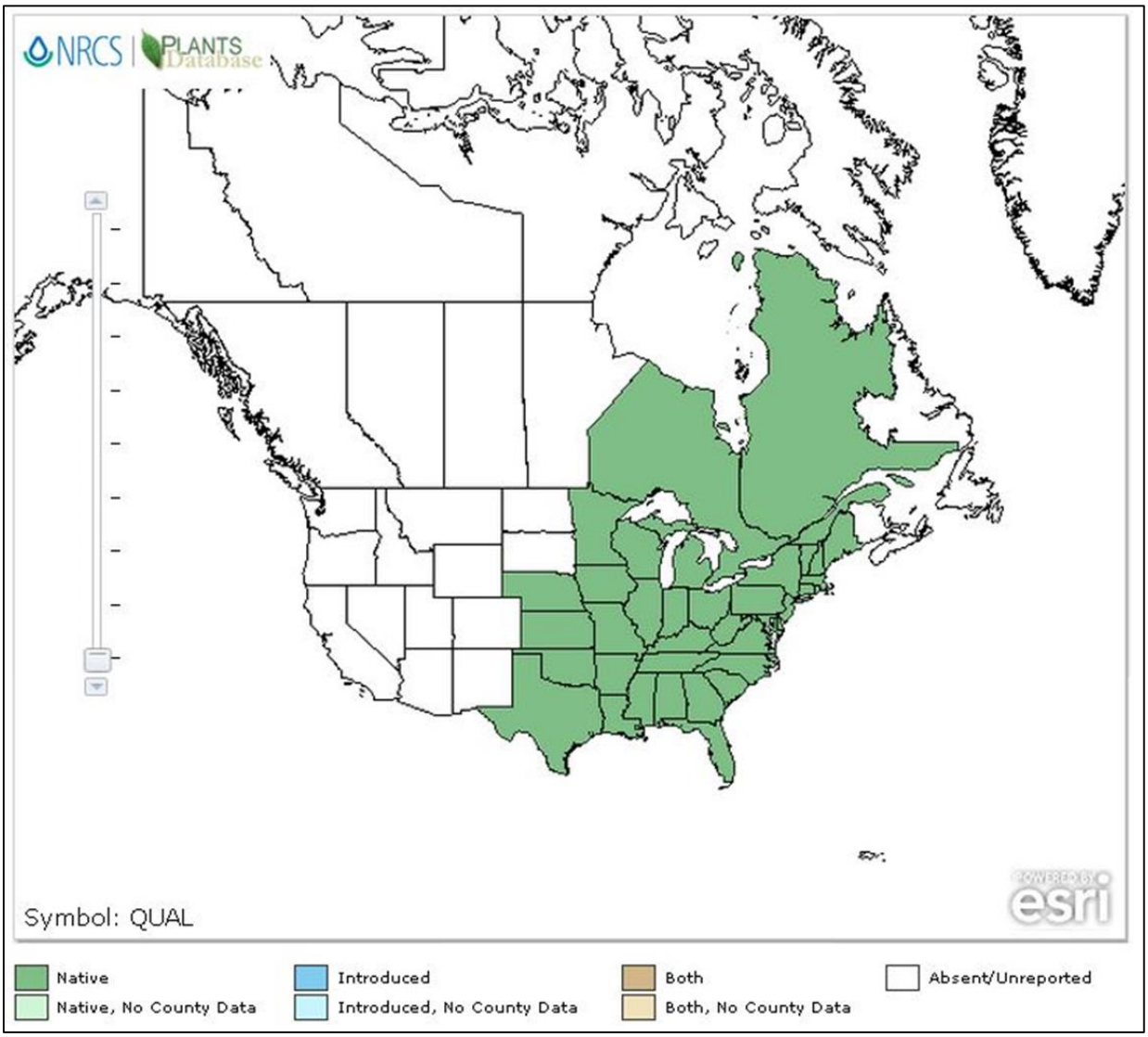

Figure 11. Distribution of *Quercus alba* (white oak) throughout eastern and central United States according to the Natural Resources Conservation Services.

3.3 *LONICERA MAACKII*: AMUR HONEYSUCKLE

Native to the former Manchuria region in East Asia, *Lonicera maackii* (Rupr.) Maxim (Amur honeysuckle) (Figure 12) is an upright, deciduous, multi-stemmed shrub in the taxonomic family Caprifoliaceae (Honeysuckle family) within the order Dipsacales. Amur honeysuckle sprouts from its base and can grow to be as tall as six meters, although shrubs ranging between four to five meters are more common in North America (Luken and Thieret 1996; Collier et al. 2002) (Figure 13). Amur honeysuckle leaves taper to a slender point from a broad ellipses or lance head shape (Luken and Thieret 1996) (Figure 14).

Amur honeysuckle shrubs take three to five years to become reproductively mature, at which time they produces numerous bright red, globose fruits (3.5-8.5 mm in diameter) that mature in early autumn, unlike the fruit of most of the other *Lonicera* species, which mature in the summer (Luken and Thieret 1996; Collier et al. 2002; Deering and Vankat 1999; Bartuszevige et al. 2006; Castellano and Gorchov 2013). The peduncles (or fruit stalk) is one of the defining morphological characteristics differentiating *Lonicera maackii* from other *Lonicera* spp (Figure 15). According to Swink and Wilhelm (1994, pg. 472), *L. maackii* has: "Flowers and fruits paired in the axils of free, usually petiolate, leaves; habits various. Plant erect shrubs. Leaves strongly long-acuminate at the tip; flower clusters sessile or subsessile in the leaf axils; peduncles minute or up to 5 mm long, shorter than the petioles of their subtending leaves." Methanol extracts of Amur honeysuckle leaves have been identified as containing phenolic metabolites (predominantly comprised of two major flavones,

apigenin and luteolin, along with their glucoside derivatives, apigenin-7-glucoside and luteolin-7-glucoside), which act as allelochemicals (Cipollini et al. 2008).

Within each berry, there are on average 4.6 seeds (Castellano and Gorchov 2013) (Figure 16). The fruits provides browsers with a low quality food source when other resources become scarce, since Amur honeysuckle fruits often persist through winter (Ingold and Craycraft 1983; Bartuszevige and Gorchov 2006; Bartuszevige et al. 2006). Common consumers of Amur honeysuckle fruits include: white-tailed deer (*Odocoileus virginianus* Zimmerman; hereafter 'deer'), rodents, and both resident and migrating birds (Williams et al. 1992; Ingold and Craycraft 1983; Bartuszevige and Gorchov 2006; Bartuszevige et al. 2006; Castellano and Gorchov 2013; Orrock et al. 2014). Amur honeysuckle seed viability was found to increase when removed from the fruit, which occurs during the digestive process after having been consumed (Bartuszevige and Gorchov 2006). Since its introduction to North America in 1896 (Luken and Thieret 1996), Amur honeysuckle has spread throughout the Midwest and eastern United States and can now be found in 29 of the lower 48 United States (Figure 17), making it one of the most aggressive, abundant, and problematic non-native invasive species (Luken and Thieret 1996; Hutchinson and Vankat 1997; Collier et al. 2002; McNutt 2010; Barriball 2012; Castellano and Gorchov 2013; Wilson et al. 2013).

Figure 12. Flowering branch (a), abaxial leaf surface section (b), and bracts, bracteoles, and magnified calyx tubes of *Lonicera maackii* (Amur honeysuckle) (Image modified from *http://flora.huh.harvard.edu/FloraIllustration/foci19/foci19-482.jpg*)

Figure 13. Image depicting the upright, multi-stemmed nature of the *Lonicera maackii* (Amur honeysuckle) shrub (Image taken at Arnold Arboretum at Harvard University by S. McCarragher).

Figure 14. Lonicera maackii (Amur honeysuckle) leaves (Image by S. McCarragher).

Figure 15. Image highlighting the difference between the peduncle and subtending leaf petiole, which represents the defining morphological feature for differentiating *L. maackii* from other *Lonicera* spp. (Image taken by S. McCarragher).

Figure 16. Seeds of *Lonicera maackii* (Amur honeysuckle) (Image: Craves and Wloch 2012).

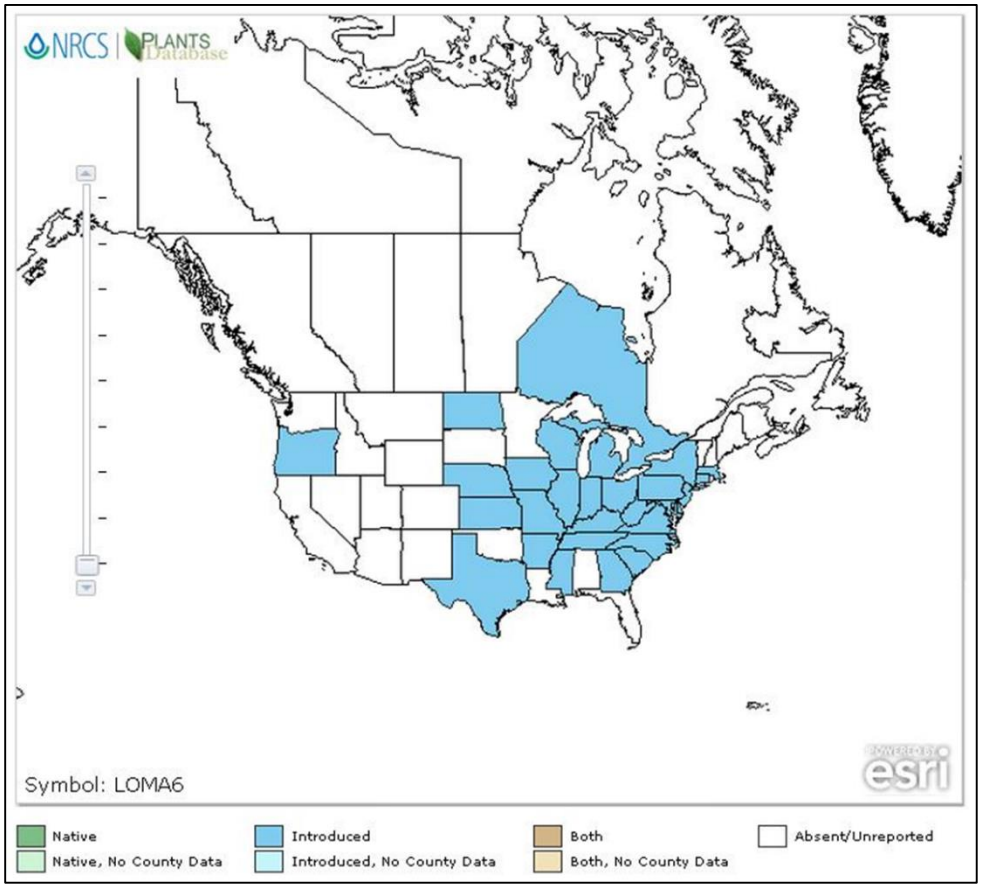

Figure 17. Distribution of *Lonicera maackii* (Amur honeysuckle) throughout the United States according to the Natural Resources Conservation Services.

3.4 STUDY SITE: NACHUSA GRASSLANDS

3.4.1 INTRODUCTION

The field work for this project was conducted in Nachusa Grasslands, one of The Nature Conservancy's "greatest ongoing success stories" (TNC 2010). The Nature Conservancy (TNC), founded in 1951, is a major non-profit conservation organization renowned for its large membership base (more than one million members) and exemplary efforts to protect ecologically important regions world-wide, having operations within all 50 of the United States as well as in 30 countries (TNC 2010). To date they manage about 100 global marine conservation projects and have protected about 5,000 miles of rivers as well as about 119 million acres of land worldwide (TNC 2010).

Nachusa Grasslands is a 1,255 hectares prairie, wetland and woodland preserve located in north-central Illinois straddling the border of Ogle and Lee Counties (Figure 18). Nachusa Grasslands began as a 100 hectare matrix of agricultural fields and remnant prairies, first purchased in 1986 by The Nature Conservancy (TNC 2010; Saxton 2012). Beyond the 1,255 hectares of land owned by Nachusa Grassland, an additional 293 acres are also protected through easements, which grants the land Stewarts the right to use and manage the property even though the title to the land is retained by the original owner (TNC 2010). Much time and effort has been spent on various restoration projects within the preserve, including multiple oak savanna restoration projects. An oak savanna restoration, approximately 29 hectares in size and located in the northwest corner of the Nachusa Grasslands property was used as the

specific study site for this research (41°53’49.06” N, 89°22’11.22” W) (Figure 18). The Nature Conservancy obtained this area in two separate purchases, one in 2005 for 13 hectares (eastern tract) and the other in 2008 for the remaining 16 hectares (western tract) (Saxton 2012).

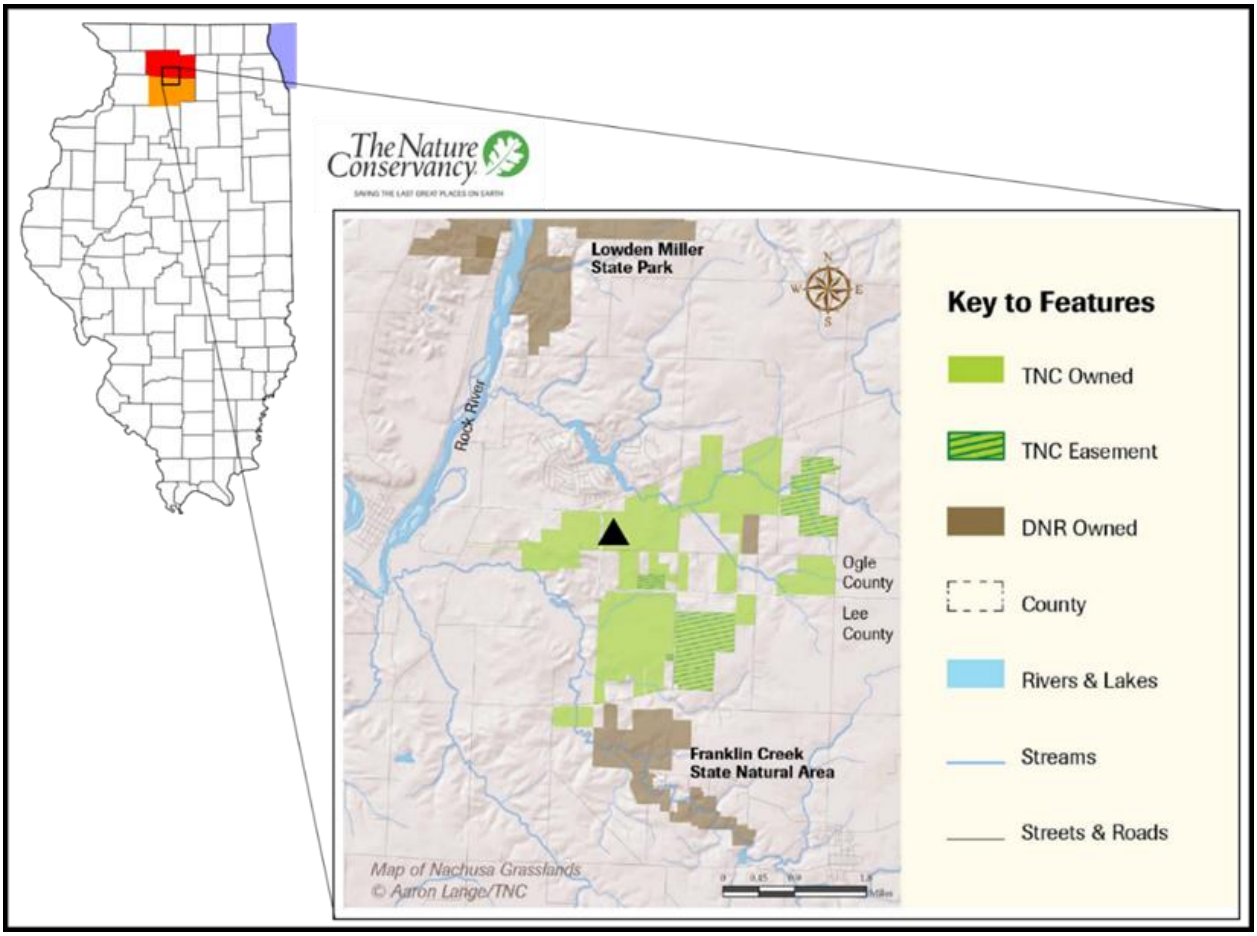

Figure 18. Map illustrating the location (Nachusa Township in north-central Lee County, Illinois) and extent of Nachusa Grasslands (green), owned by The Nature Conservancy. Black triangle depicts approximate location of the oak savanna restoration study site within Nachusa Grasslands.

3.4.2 GEOLOGY AND SOILS

According to the current soil survey, the dominant parent materials in the oak restoration study site are sandstone, till, limestone, and a small amount of eolian sand (Figure 19) (Soil Survey Staff 2015a). Furthermore, the current soil survey classifies the majority of the soils in the oak restoration study site as Mollic Alfisols and Entisols, with Boone, Whalan, Coloma, and Eleva being the dominant soil types (Figure 19) (Soil Survey Staff 2015a). The study site elevation ranges between 225m and 250m (Soil Survey Staff 2015a). The excessively drained soils in the Boone series are primarily found on hills with slopes ranging from 1 to 90 percent and form in 50 to 100 centimeters of siliceous sandy residuum from the underlying sandstone bedrock, in addition to siliceous sandy colluvium or slope alluvium (Soil Survey Staff 2015b). The soils in the Whalan series are well drained, moderately deep and are found primarily on dissected glaciated uplands with between 0 to 25 percent slopes, forming in thin layers of clayey residuum from limestone bedrock and a mantle of loamy drift or glacial till (Soil Survey Staff 2015b). The Coloma series of soils are somewhat excessively drained all the way to excessively drained and are very deep, forming in sandy drift on deltas, stream terraces, moraines, and outwash plains with slopes between 0 to 70 percent (Soil Survey Staff 2015b). Finally, the soils in the Eleva series are somewhat excessively drained to well drained and are moderately deep, forming on slopes ranging from 1 to 60 percent in 50 to 102 centimeters of loamy deposits over sandstone (Soil Survey Staff 2015b).

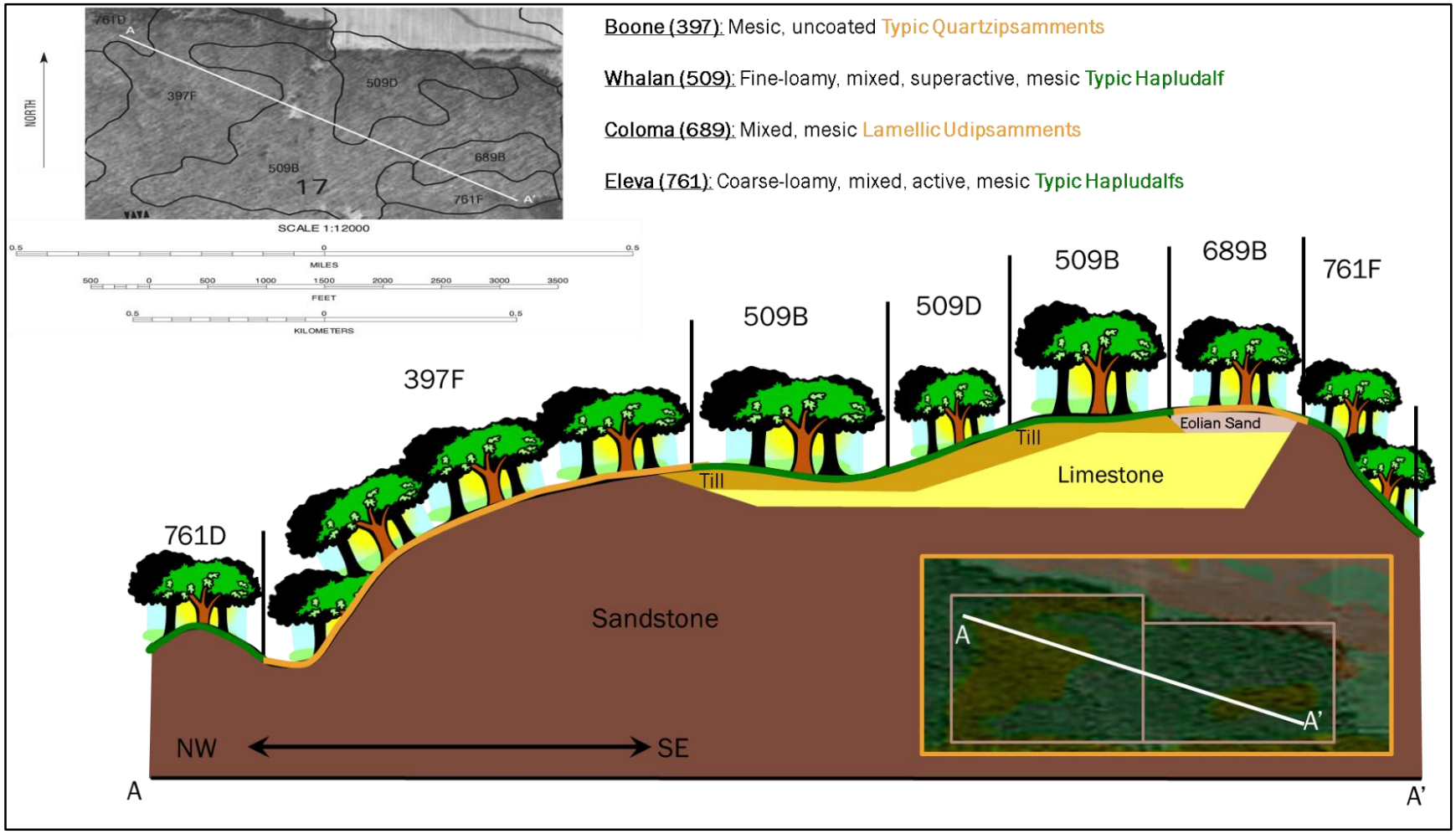

Figure 19. Soil Survey classifications of soil in study site, along with a cross-section depicting the elevation and surficial geology of the oak savanna study site at Nachusa Grasslands, IL, USA (vertical exaggeration 13 meters; not to scale).

3.4.3 CLIMATE

The 50 year Climate Normals (1965-2014) for Dixon 1 NW (the closest climate station to the study site), show the mean annual air temperature as being 9.22 ± 3.08 °C, varying from -6.67 °C in January to 22.88 °C in July. The mean total annual precipitation normal is 967.38 mm, varying from 40.81 mm in February to as much as 129.84 mm in June, with an overall mean annual precipitation normal of 80.62 ± 8.08 mm. Fifty year seasonal Climate Normals were calculated for April through October, in order to characterize the climate conditions of the leaf phenology stage in which all leaves of white oak seedlings and Amur honeysuckle shrubs were fully open and green and therefore the most photosynthetically active. The mean seasonal air temperature normal for this region is 17 °C ± 0.1 °C (Figure 20a), with 1992 having the lowest seasonal temperature (15.3 °C) and 2010 having the highest seasonal temperature (18.4 °C). The mean total seasonal precipitation normal for the study site is 700 mm ± 23.4 mm (Figure 20b), with 1988 having the lowest total seasonal precipitation (375.2 mm) and 1970 having the highest total seasonal precipitation (986.0 mm).

Normal climate variability was defined in this study as any mean seasonal temperature or precipitation that fell outside of one standard deviation from each respective mean (0.7 °C and 165.3 mm). Therefore, normal variability range for seasonal temperature was 16.3 °C to 17.7 °C, while normal variability range for seasonal precipitation was 534.7 mm to 865.3 mm. When the mean temperatures and mean total precipitations for each season within the study period (2011-2014) were placed on an ogive graph with the last 50 years of mean seasonal temperature and

mean total seasonal precipitation data, only 2012 fell outside the realm of normal variability for both temperature (18 °C; 90th percentile) and precipitation (458.7 mm; 10th percentile) (Figure 20). The total seasonal precipitation experienced during 2012 was 241.3 mm less than the mean total seasonal study site Climate Normals, while the mean seasonal temperature was 1 °C above the mean seasonal study site Climate Normals. These climate anomalies simulated a naturally occurring experiment representing the conservative regional climate change projections. One other season, 2014, fell just outside of normal variability, but only for temperature (16.2 °C; 14th percentile), which was 0.8 °C less than the mean (Figure 20a). All other mean seasonal temperatures and precipitations for the study period fell within the normal range of climate variability, with 2014 having the highest total seasonal precipitation (844.1 mm), followed by 2011 and 2013, respectively (811.3 mm and 775.2 mm) (Figure 20b). The mean seasonal temperature of 2011 (17.2 °C) was the next highest after 2012, followed by 2013 (16.8 °C), with 2014 having the lowest mean seasonal temperature (Figure 20a).

Based on data collected in this study, a microclimate was detected within the oak savanna restoration study site understory in relation to temperature. More specifically, a t-test revealed that the overall three year average (2012-2014) *in situ* air temperature measured within the understory of the study site at two meters above the ground was significantly lower (8.8 ± 0.6 °C) than the overall three year average *in situ* air temperature measured within the understory of the oak savanna restoration study site at ground level (9.6 ± 0.5 °C) ($p<0.0001$). Additionally, the temperatures measured at two

meters above the ground and at ground level were highly positively correlated with one another (0.98). Out of the three years for which general study site temperatures were collected, 2013 was the only individual year within the study time period that when analyzed using a t-test was found to have a significantly lower average *in situ* air temperature at two meters (8.9 ± 0.6 °C) than at ground level (9.2 ± 0.6 °C) ($p<0.0001$), with 2012 and 2014 showing no significant differences.

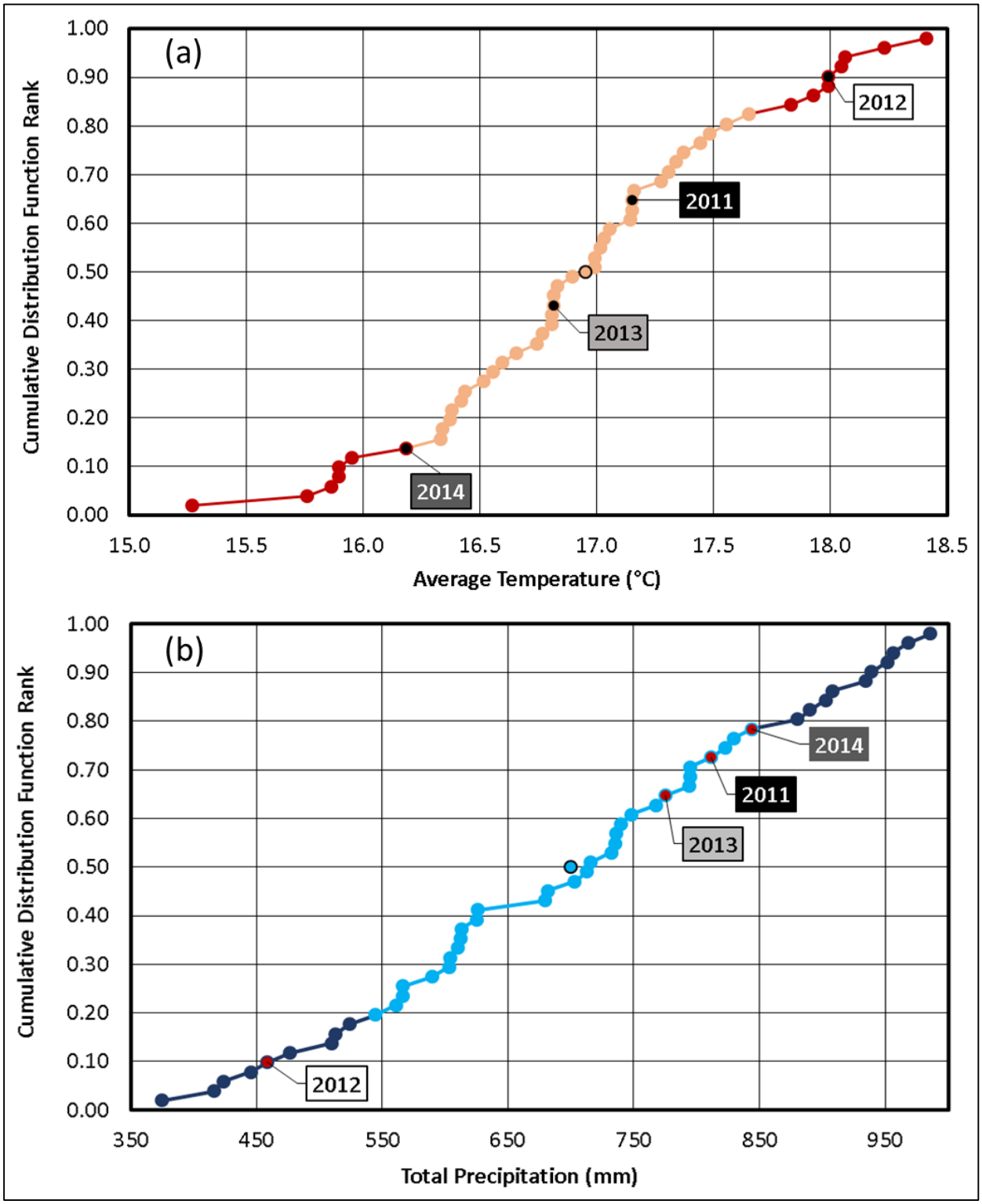

Figure 20. Ogive graph displaying ranked mean seasonal (April to October) temperatures (a) and precipitations (b) for the last 50 years (1965-2014). The peach (temperature) and light blue (precipitation) colors represent one standard deviation from the respective means, depicted by the outlined center dots. The dark red (temperature) and navy blue (precipitation) colors represent the years that fall outside of normal variability. The mean seasonal temperatures and total precipitation for the study period years are labeled.

3.4.4 VEGETATION

Historic 1939 aerial imagery of the oak restoration study site displays a landscape with partially patchy tree canopy cover and partially dense forest canopy (Figure 21). The Federal Township Plat for the area depicts the area that is now Nachusa Grasslands as being situated on the boundary between forested lands classified as timber and open grasslands classified as prairie (Figure 22). According to Bill Kleiman, the project manager at Nachusa Grasslands, the owner from which they purchased the eastern tract bought the land in the early 1980s, and at the time he could see clearly through the trees on his property (Saxton 2012). By the time The Nature Conservancy purchased the eastern tract, in 2005, dense thickets of mature Amur honeysuckle had established in the understory (Saxton 2012). Active management strategies were initiated on the eastern tract shortly after its acquisition. The management techniques applied included annual spring prescribed fires, brush management of invasive species (i.e. cut, removal, and herbicide use), thinning of overpopulated native tree species, and seeding with 160 lbs. of seed composed of 63 native herbaceous species (personal communications with Bill Kleiman; Saxton 2012).

Although the second, adjacent western tract was purchased only three years after the first tract in 2008, contractual agreements hindered active management on the property until January 1, 2012. As a result, mature Amur honeysuckle populations and mesophytic trees dominated and thrived on this tract without active management and the western tract developed a dense closed canopy (Figure 23). Beginning January 1, 2012, steps were taken to mechanically and chemically remove much of the mature

Amur honeysuckle population and the management strategies being used in the eastern tract were initiated in the western tract.

Nachusa Grasslands is home to about 180 species of birds and 700 native plant species (TNC 2010). Within the oak savanna restoration study site, white oak, *Carya ovata* (shagbark hickory), *Ulmus rubra* (slippery elm), *Quercus rubra* (red oak), *Prunus serotina* (wild black cherry), and *Celtis occidentalis* (hackberry) dominate the overstory tree canopy. There is a dense understory of herbaceous plants found throughout the oak savanna restoration study site that includes around 75 species from 43 taxonomic families (Saxton 2012). The following are examples of some understory species commonly found throughout the oak savanna study site: *Sanicula gregaria* E.P. Bicknell (clustered black snakeroot), *Cryptotaenia canadensis* (L.) DC. (honewort), *Ageratina altissima* (L.) R.M.King & H.Rob. (white snakeroot), *Galium concinnum* Torr. & A.Gray (shining bedstraw), *Galium triflorum* Michx. (sweet-scented bedstraw), *Hackelia virginiana* (L.) I.M. Johnst. (stickseed), *Phryma leptostachya* L. (lopseed), *Polygonum virginianum* L. (woodland knotweed), in addition to a variety of sedges and grasses.

According to previous germination studies, the soil seed bank within the oak savanna restoration study site is dominated by about 34 species from 24 taxonomic families, with *Pilea pumila* (clearweed), *Verbascum thapsus* (mullein), and *Acalypha virginica* (three-seeded mercury) representing about 56 percent of the germinants recorded (Saxton 2012). Of the 13 known savanna plant specialist species identified by Henderson (1995), six appear on the Nachusa Grasslands Plant Inventory. Three are

classified as uncommon (*Triosteum perfoliatum* L. (horse gentian), *Eupatorium sessilifolium* L. (bonset or sessile-leaved eupatorium), and *Ceanothus americanus* L. (New Jersey tea)), one is classified as threatened (*Gentiana alba* Muhl. (cream gentian)), and one is classified as endangered (*Asclepias purpurascens* L. (purple milkweed) (Henderson 1995).

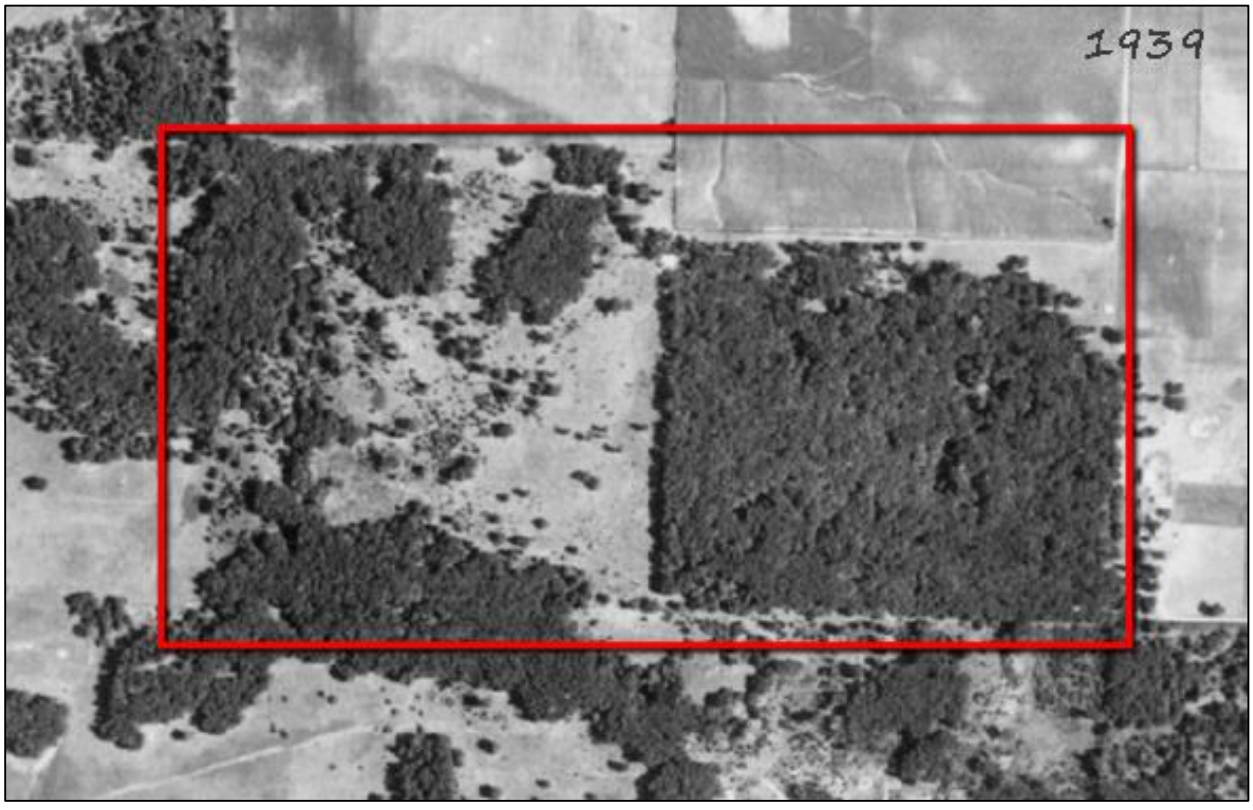

Figure 21. Historic 1939 aerial imagery of the oak restoration study site in Nachusa Grasslands, Lee County, Illinois, USA, denoted by rectangle (Google Earth image).

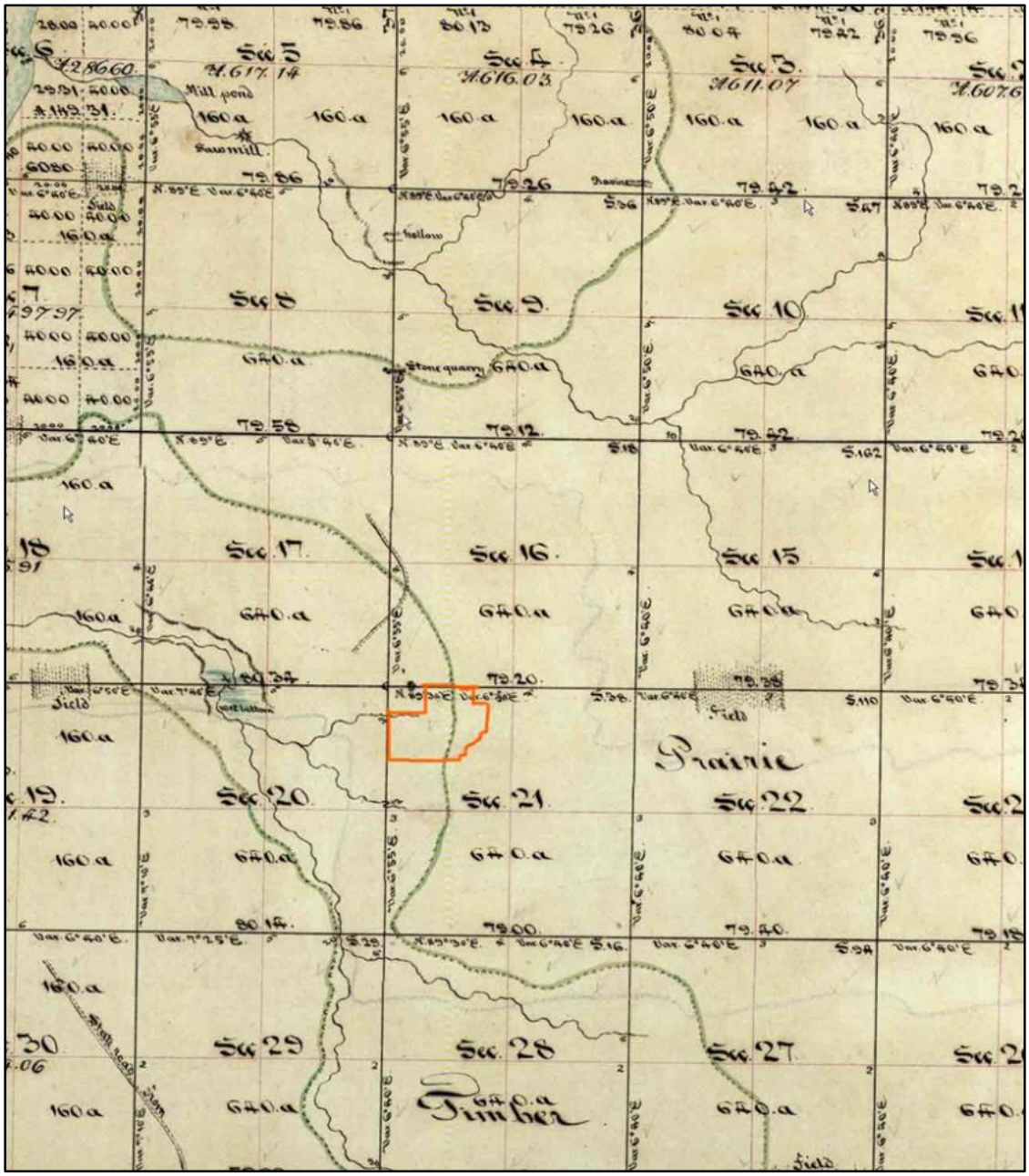

Figure 22. Partial Federal Township Plat for the area that now contains Nachusa Grasslands, Lee County, Illinois, USA (depicted by polygon on map).

Figure 23. Current Google Earth image illustrating the dense current canopy cover of the oak savanna restoration study site in Nachusa Grasslands, Lee County, Illinois, USA (denoted by red rectangle).

CHAPTER 4: METHODS

This interdisciplinary research integrates methodologies from physical geography, conservation biogeography, and population genetics to explore the ecological impacts and underlying evolutionary mechanisms associated with the spread of one of the most aggressive and abundant invasive species throughout the Midwest: Amur honeysuckle. To better understand the demographic and invasive processes occurring within the oak savanna restoration study site vegetation community, past and present characteristics of the white oak and Amur honeysuckle populations must be obtained (Rigg 1998, 1999). In addition to sampling and analyzing the community vegetation at the oak savanna restoration study site, various other environmental and evolutionary variables were explored including understory light environments, soil dynamic properties, and the population genetics of Amur honeysuckle using microsatellites to infer dispersal and colonization patterns.

This methods chapter begins first with a description of field methods conducted in the oak savanna restoration study site, including plotless and plot sampling techniques, environmental data logging stations, leaf phenology observations, photosynthetic efficiency measurements, and soil sampling. Next, Amur honeysuckle leaf tissue collection techniques for the genetic population structure analysis are described. Followed by a description of lab methods, including soil lab methods and

genetic lab methods used in this research. The last section in this chapter describes how all data were analyzed.

4.1 FIELD METHODS IN OAK SAVANNA RESTORATION STUDY SITE

There are a variety of standard quantitative methods that have been designed to measure forest structure and composition parameters via both plot-based and plot-less techniques (Cottam et al. 1953; Kent 2011; Bonham 2013). Plot-based techniques establish areas of a known size (e.g. fixed-area plots (FAP)) within which characteristics of concern are measured for each plant, while plotless techniques (e.g. point-center quarter method (PCQ)) establish transects along which characteristics of concern and distances are recorded for a random sample of trees (Mitchell 2010). All field sampling and observations took place between August 2010 and December 2014.

4.1.1 Plotless Sampling of Tree Stand Structure. General site and species specific population densities, frequencies, and cover for the tree layer at the oak savanna restoration study site were quantified during the summer of 2010 and 2011 using the accepted forest sampling method: point-center quarter (PCQ) (Cottam and Curtis 1956; Kent 2011; Bonham 2013). The PCQ method is based on an empirical formula developed from Cottam et al. (1953) that can use distance data to infer population density estimates. Previous studies have compared various plot-less techniques (i.e. the nearest neighbor, the random pairs, the closest individual and the PCQ method) and verified that the most accurate, least labor and equipment intensive, and quickest was the PCQ method (Cottam and Curtis 1956; Beasom and Haucke 1975). Mitchell (2010) addresses modifications, adaptations, applications, and practical

considerations of the PCQ method since its introduction, which were adopted by this study.

PCQ sampling points for this study were placed 20 meters apart along parallel, linear, north-south transects, with the first node beginning 50 meters from the edges of the site. Transects were spaced 20 meters apart and when possible, the center point locations were recorded with a global positioning system (GPS) unit to ensure no overlap or sampling duplication. Cardinal compass directions delineated the quarters at each of the 250 points and within each quarter, the distance to and the diameter at breast height (defined as 130 centimeters (D_{130}) as per Mitchell 2010) of the closest living tree (defined as > 5 centimeters at D_{130}) was measured and recorded.

4.1.2 Plot Sampling of Understory Stand Structure. Ten randomly placed 5 m x 5 m temporary plots were established between September and October 2011 to measure the understory density of the oak savanna restoration study site near the end of a growing season (Kent 2011; Bonham 2013). Each plot was delineated into quarters. Stem counts were recorded within each quarter for all tree seedlings (individuals < 30 cm in height from the ground to the tip of the apical bud (Diochon et al. 2003)) and saplings (individuals ≥ 30 cm in height and < 5 cm D_{130} (Rigg 1998, 1999)), and woody shrub seedlings (< 1 m) and saplings (≥ 1 m) including Amur honeysuckle, to

characterize understory stand density (Figure 24). Percent estimated crown cover of Amur honeysuckle was also recorded in each plot.

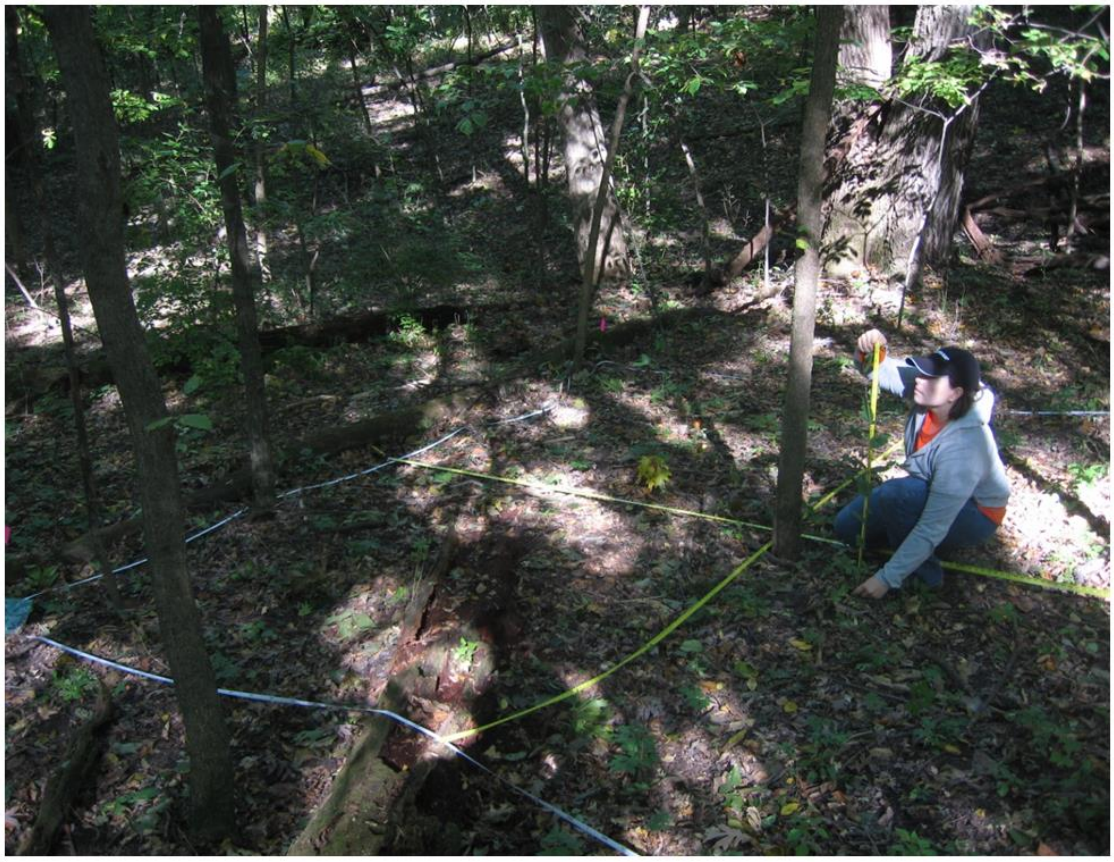

Figure 24. Image showing one of the 10 randomly placed 5x5 m plots used to describe the regeneration layer and Amur honeysuckle stand densities at the oak savanna restoration study site in Nachusa Grasslands, IL, USA (Picture by J. Halpern-Givens).

4.1.3 Environmental Data Logging Stations. In total, 11 environmental data logging stations were established throughout the center of the oak savanna restoration study site (Figure 25), and one environmental data logging station was established just south of the oak savanna restoration study site near the Nachusa Grasslands headquarters to measure general local environmental variables (n=12).

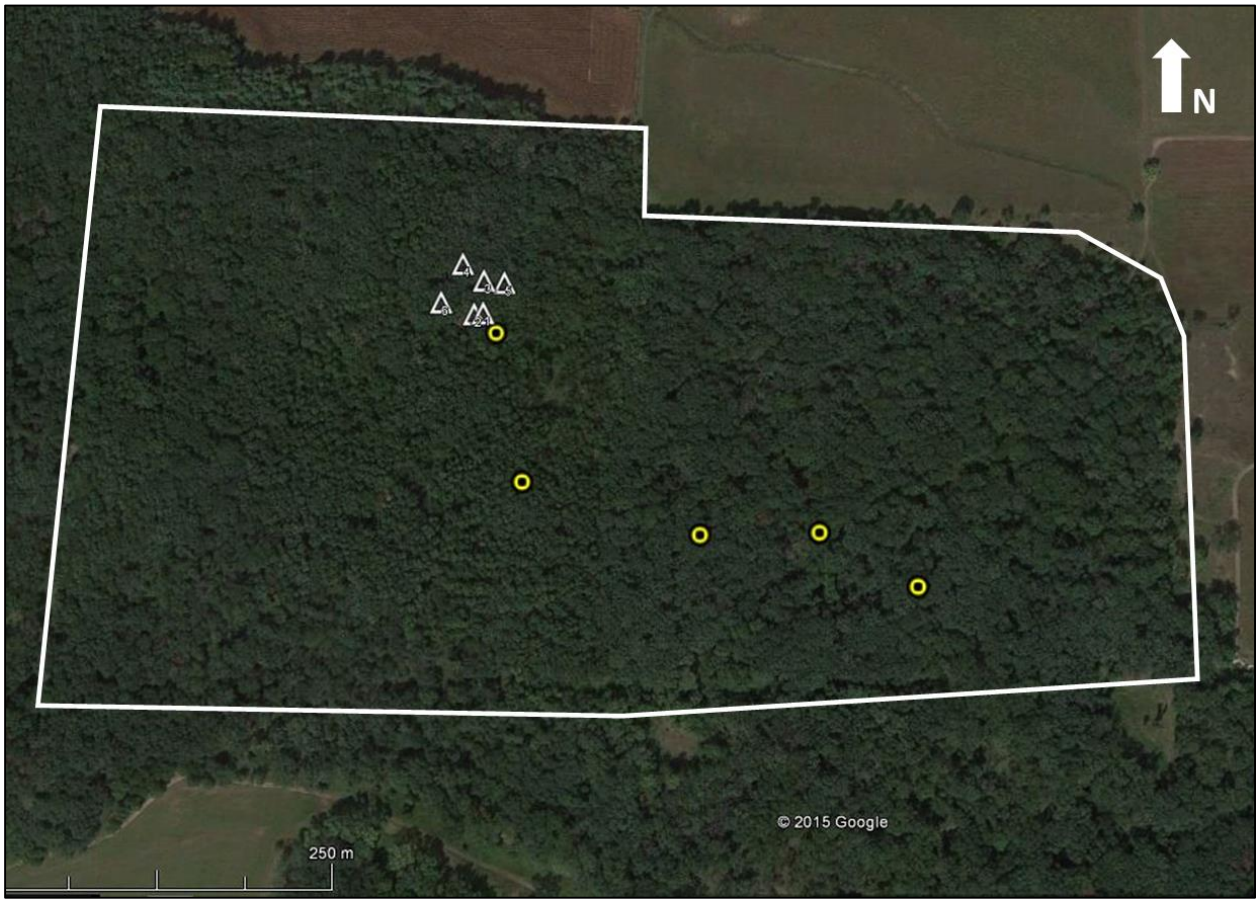

Figure 25. Locations of 11 environmental logging stations established throughout the center of the oak savanna restoration study site in Nachusa Grasslands, IL, USA. The six small triangles denote the location of the environmental logging stations collecting only soil moisture and temperature data associated with and without Amur honeysuckle encroachment. The five circles denote the location of the environmental logging stations collecting PAR, air temperature, relative humidity, as well as general soil moisture and temperature data.

Six of the 11 environmental data logging stations in the oak savanna restoration study site (denoted by triangles in Figure 25) only contained soil probe sensors (n=30; five in each station) (ECH_2O EC-TM, Decagon Devices, Pullman, Washington, USA) placed within the first 5 cm of the soil, to measure both soil moisture (m^3/m^3 VWC) and soil temperature (°C) in areas with and without Amur honeysuckle encroachment. Of the five soil probe sensors in each of the six soil environmental logging stations, one was placed as far away from any Amur honeysuckle shrub as possible (ranging from 64 cm to 147 cm) (control) (n=6), two were placed under Amur honeysuckle shrubs near the

stems (n=12), and two were placed near the driplines (i.e. edge of the canopy) of Amur honeysuckle shrubs (n=12). The six soil probe logging stations were clustered in one part of the study site so as to reduce the impact of inherent soil variability. Soil temperatures (°C ± 1°C) and volumetric soil water content (m^3/m^3 VWC ± 0.03 m^3/m^3) were collected every 30 min year round between May 2013 and December 2014. The mineral soil factory calibration was used for the Decagon soil sensors (Pullman, Washington, USA), which automatically employed the Topp equation (Θ $m^3/m^3 = 4.3 \times 10^{-6} * \varepsilon^3 - 5.5 \times 10^{-4} * \varepsilon^2 + 2.92 \times 10^{-2} * \varepsilon - 5.3 \times 10^{-2}$, where Θ is volumetric water content of soil; Topp et al. 1980) to calculate VWC using dielectric constant of the soils, independent of soluble salt content, soil temperature, and soil type (Decagon Devices, Inc., 2015).

When compared against two other volumetric water content measuring devices in a study assessing forest soils of the Pacific Northwest, the low-cost ECH_2O device from Decagon Devices (Pullman, Washington, USA) was found to have only a small difference in performance and was therefore recommended, given that the low-cost could ultimately facilitate the deployment of a larger number of devices (Czarnomski 2005). Furthermore, the results obtained by ECH_2O soil sensors were found to be repeatable and reliable across a range of mineral soils types, and have a low sensitivity to soil environmental factors that could potentially confound the results (i.e. temperature), with the highest performance occurring when operated at a measurement frequency of 70 MHz (Campbell 2001; Kizito 2008).

The five remaining environmental data logging stations in the oak savanna restoration study site (denoted by circles in Figure 25), as well as the logging station established near the Nachusa Grasslands headquarters (n=6), contained a variety of environmental data sensors meant to measure general site characteristics. Each of those logging stations contained between one to five Photosynthetically Active Radiation Photon Flux Sensors (n=20) (PAR Photon Flux Sensors, Model QSO-S, Decagon Devices, Pullman, Washington, USA) measuring photosynthetic photon flux (µmol $CO_2 \cdot cm^{-2} \cdot s^{-1}$ ± 5%) with a 180 degree field of vision, to characterize *in situ* light environments at varying heights (i.e. 30 cm, 1 m, and 2 m) (Figure 26a). Only the PAR sensors placed at a height of 30 centimeters (n=8) and one meter (n=8) were used for this analysis, so as to best represent the seasonal light levels received by white oak seedling and Amur honeysuckles in the study site understory, respectively. Wünsche et al. (1995) concluded that sites with upright vegetation canopies require several light readings at different times of the day under clear skies. Therefore, PAR data (µmol $CO_2 \cdot cm^{-2} \cdot s^{-1}$) were continuously collected every 30 min, year round for three growing seasons (2011 to 2013) until downloaded, to capture the inherent variability found in understory light at the oak savanna restoration study site. From the continuous data, daily PAR totals were calculated in mol/m^2 (Kwit et al. 2010).

In total, four different light environments were quantified between March 2011 and December 2014: 1) an open, full-sun light environment with no overstory tree canopy (referred to as “full sun” from this point on); 2) the Amur honeysuckle (HS) understory light environment in the study site at 1 meter (referred to as “HS light” from

this point on); 3) the white oak seedlings understory light environment in the study site at 30 cm without Amur honeysuckle encroachment (i.e. no Amur honeysuckle shrub within 3 meters of the light sensor; referred to as “no HS encroachment” from this point on); and 4) the white oak seedlings understory light environment in the study site at 30 cm with Amur honeysuckle encroachment (referred to as “HS encroachment” from this point on).

In response to the high frequency at which wildlife mastication resulted in wire damage, a logging station enclosure design was devised and implemented in 2012, whereby each PAR sensor was fully enclosed within a weatherized square metal electrical box, with only the eye protruding slightly out of an opening in the top (Figure 26a). The wires of each PAR sensor were then threaded through metal lined conduit into a large heavy-duty PVC electrical box (Figure 26f) that housed a Decagon EM50 data loggers (Decagon Devices, Pullman, Washington, USA) into which each sensor was plugged. In the logging stations that were composed of five PAR sensors, small PVC connection boxes were used to create fully enclosed split lines with the metal lined conduit to ensure that the sensors were positioned far enough apart from one another. Ultimately, this unique enclosure design eliminated wire damage, costly equipment replacement purchases, and gaps in the data record from the mastication of PAR sensor wires without decreasing the quality of the data collected.

Four of the six environmental data logging stations with PAR sensors (including the station near the headquarters) also contained air temperature (°C) sensors (n=4) (Figure 26b), relative humidity (%) sensors (n=2) (Figure 26c), precipitation sensor

(n=1), and additional ECH$_2$O EC-TM soil probe sensors measuring both soil moisture (m^3/m^3 VWC) and soil temperature (°C) (n=11) (Figure 26d) (Decagon Devices, Pullman, Washington, USA). All environmental data collected within each environmental logging stations were stored on Decagon EM50 data loggers (Decagon Devices, Pullman, Washington, USA; Figure 26e). Each EM50 data logger had five sensor ports for gathering continuous environmental data and one com port to which a laptop equipped with the ECH$_2$O Utility Software was connected (Decagon Devices, Pullman, Washington, USA), to set timing of data measurements, sensor types plugged into each sensor port, logger clock and name, as well as to manually download data.

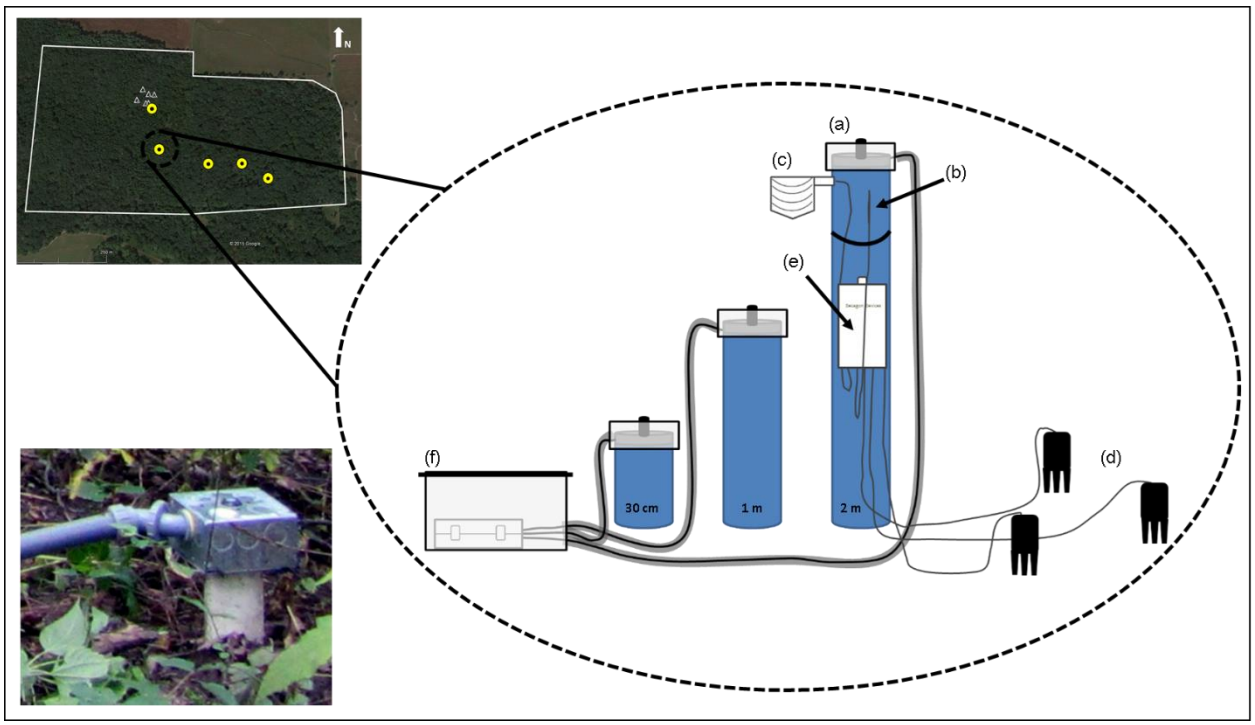

Figure 26. Example diagram of an environmental data logging station located within the oak savanna restoration study site (not drawn to scale). The enlarged insert illustrates a typical layout of a station containing three PAR sensors (a); an air temperature sensor (b); a relative humidity sensor (c); three soil moisture/temperature probes (d); and two EM50 data loggers (e) (not drawn to scale). The PAR sensors pictured (a) are fully armored against mastication damage (see also photo insert; Picture by S. R. McCarragher).

4.1.4 Leaf Phenology Observations. Leaf phenology of dominant tree species (≥ 5 cm D_{130}; April 2011 to November 2014; n=35), white oak seedlings (≤ 30 cm (Rigg et al. 1998, 1999); September 2012 to November 2014; n=10-20) and Amur honeysuckle shrubs (April 2011 to December 2014; n=13-30) growing within the oak savanna restoration study site were recorded using an adapted ordinal scale (Kriebel and Wang 1962; McEwan et al. 2009; Fridley 2012; Fridley and Craddock 2013) (Table 1). More specifically, the leaf phenology of three *Carya cordiformis* (Wangenh.) K.Koch (Bitternut Hickory), six *Carya ovata* (Mill.) K.Koch (Shagbark Hickory), two *Ulmus rubra* Muhl. (Slippery Elm), five *Celtis occidentalis* L. (Hackberry), five *Prunus serotina* Ehrh. (Wild Cherry), and six *Quercus alba* L. (White Oak) trees were observed. The development of the entire plant was taken into consideration when assessing leaf phenology. Half integers were recorded only for spring phenology, when the most advanced stage of the plant represented less than 50% of the entire individual's development stage. For example, if some buds on a white oak tree were breaking (<50%), but the majority of the buds remained swollen, a 2.5 was recorded as the leaf phenology stage. When the most advanced stage of a plant represented greater than or equal to 50% of the entire individual's development stage, full integers were recorded. For example, if ≥50 % of the buds on a white oak tree were breaking, a 3 was recorded as the leaf phenology, representing that the individual had reached bud break phase. In the end, the average leaf phenology for each dominant tree species, as well as for all the white oak seedlings and Amur honeysuckle shrubs were used to represent their overall leaf phenology stages throughout the four growing seasons.

Table 1. Modified spring leaf development/emergence and autumn leaf senescence scale used to record the leaf phenology stages of the dominant tree species, white oak seedling s, and Amur honeysuckle shrubs in the oak savanna restoration study site at Nachusa Grasslands, IL, USA.

Spring Leaf Development/Emergence Scale	Autumn Leaf Senescence Scale
1 – No bud swell (dormant; closed fibrous or woody scales, no growth of naked buds)	**6 – Color transition** (leaves exhibit color change/chlorosis – senescence initiated)
2 – Bud swell (active; engorgement of bud, scale development)	
3 – Bud break (loosening of bud structure, tips of first leaves exposed)	**7 – Leaf senescence** (all leaves exhibit full color change/chlorosis - senescence complete, leaves dead)
4 – Leaves unfolding (broken; leaf slightly emerged from bud: apex and margins visible, lamina slightly exposed)	
5 – Leaves open (flushed; leaves taking on mature form, may not be fully expanded; lamina surface of leaf is visible and mostly exposed; leaf margins may be curled; often corresponds with stem elongation)	

4.1.5 Photosynthetic Efficiency Measurements. Throughout four growing seasons (2011-2014), *in situ* photosynthetic efficiency measurements were taken on white oak seedlings (n=35) and Amur honeysuckle shrubs (n=39); inferred by measuring real-time CO_2 uptake (A), transpiration (E), leaf conductance (g_1), and the intercellular CO_2 mole fraction (C_i) using a LI-6400 Portable Photosynthesis System (LI-COR, Inc., Lincoln NE, USA) (Long and Bernacchi 2003). Prior to measuring the leaf-level CO_2 assimilation rate of each plant, the LI-6400 sensor head was clamped onto an attached leaf with the light source shut off (Figure 27). The leaf section fully enclosed in the sensor head (6 cm^2), was then kept in the dark for five minutes so as to manually dark adapt the leaf prior to subjecting it to varying light levels (Kwit et al. 2010). After manual dark adaption, three

Figure 27. LI-6400 sensor head clamped onto a white oak seedling leaf in the oak savanna restoration study site at Nachusa Grasslands, IL, USA (Picture by S. R. McCarragher).

measurements were recorded and later averaged to obtain one dark respiration rate for each plant. After the manual dark adaption measurements were recorded, the same leaf section was then gradually acclimated to a saturating light level for approximately 15 minutes using a warm-up program (750, 1250, 750, 1500, 1800 µmol PAR·cm^{-2}·s^{-1}) before initiating the automated light curve program, as per standard methodology (Herrick and Thomas 1999; Kwit et al. 2010). A nocturnal sample of white oak seedling (n=15) and Amur honeysuckle (n=15) dark respiration rates were collected in October 2013, to verify the accuracy of the manually dark adapted measurements.

In situ leaf-level CO_2 assimilation rates (µmol CO_2·cm^{-2}·s^{-1}), were measured for each plant using an automated light curve program that performed stepwise drops in photosynthetic photon flux densities (1800, 1600, 1400, 1200, 1000, 800, 600, 400, 200, 150, 75, 25, 10, 0 µmol PAR·cm^{-2}·s^{-1}), while ambient environmental conditions (i.e. relative humidity, CO_2 levels, and air temperature) were maintained around the leaf section being measured (LI-COR Biosciences Inc.; Kwit et al. 2010). CO_2 assimilation rates were measured in the spring, summer, and/or autumn of each growing season as able. More specifically, white oak seedlings were surveyed in July, September, and October (n=7), while Amur honeysuckle shrubs were surveyed in August and November (n=11) in 2011. White oak seedlings (n=7) and Amur honeysuckle (n=8) shrubs were surveyed in July and September in 2012. White oak seedlings were surveyed in May and September (n=7), while Amur honeysuckle shrubs were surveyed in May, October, and November (n=6) in 2013.Lastly, white oak seedlings were surveyed in May, June,

July, and September (n=14), while Amur honeysuckle shrubs were surveyed in May, July, and September (n=14) in 2014.

4.1.6 Soil Sampling. Accounting for inherent variations in soil data is important to any study assessing soil dynamic properties (Petersen and Calvin 1996; van Es 2002). Therefore, variability in general A horizon (top layer) soil characteristics (i.e. moisture content, texture, carbon/nitrogen ratios, pH, nutrient levels, below-ground respiration levels, and aggregate stability) in the oak savanna restoration study site were assessed at 40 equally spaced systematic sampling points along a superimposed grid, in order to obtain a random sample throughout the entire site while avoiding edge environments (Petersen and Calvin 1996; de Gruijter 2002) (Figure 28). Geographic coordinates (i.e. latitude and longitude) for each grid point were used to find the sampling point in the field (Table 2). At each sampling point, four scoops of A horizon soil (top layer; approx. 0-15 cm) from around the grid point location were combined into a large Ziploc bag, air dried, and then mixed thoroughly so as to reduce total error (Allmaras and Kempthorne 2002).

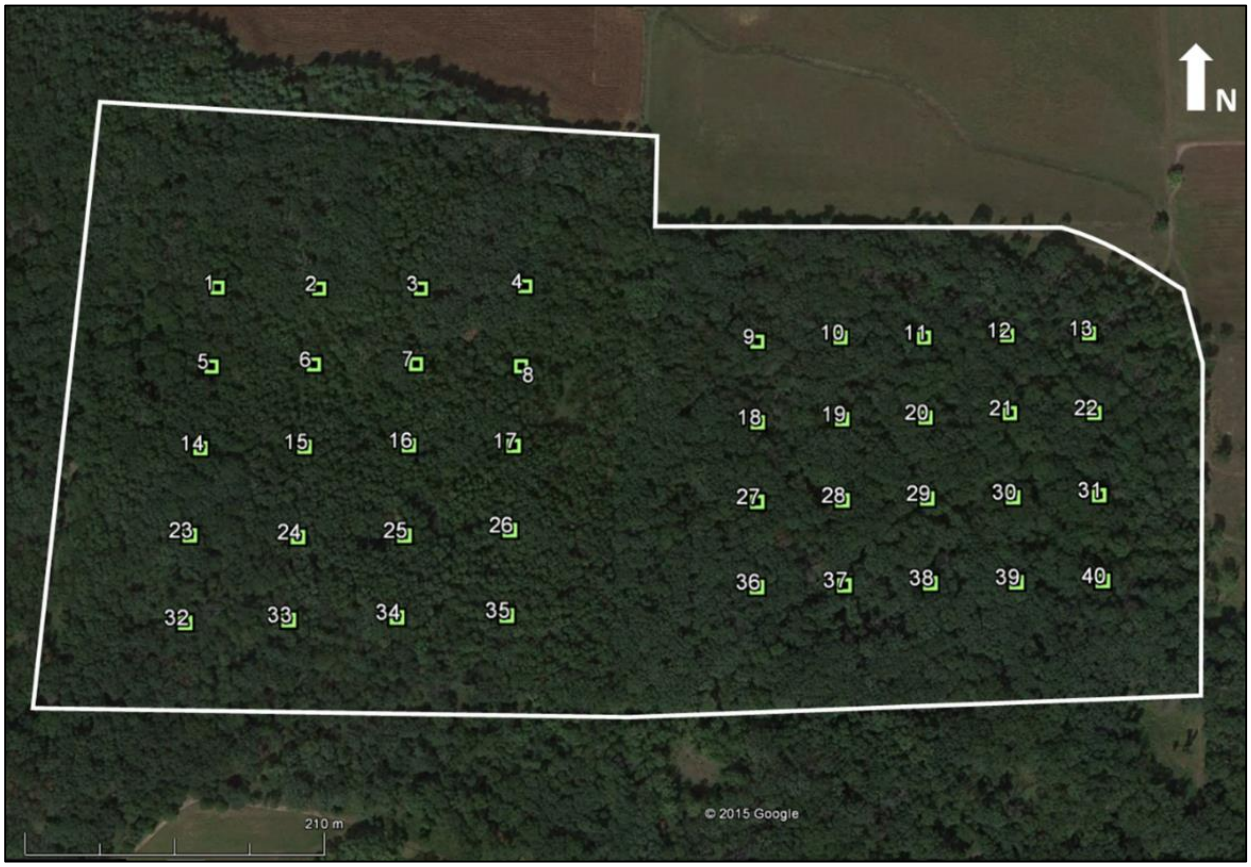

Figure 28. Location of the 40 equally spaced points along a superimposed grid at which the top soil was sampled in the oak savanna restoration study site at Nachusa Grassland, IL, USA.

An additional subset of soil samples were collected from within the western half of the oak savanna restoration study site for use in determining whether various soil dynamic properties (i.e. carbon/nitrogen ratios, nutrient levels, and wet aggregate stability) differ under and away from Amur honeysuckle (n=20). More specifically, the soil samples (each being a mixture of four scoops of A horizon soil from the sampling location) were collected from adjacent sites within the western half of the study site, so as to ensure that they had similar land-use histories. Areas with a high abundance of Amur honeysuckle encroachment were targeted for the first soil sample in the pair that was meant to represent soil characteristics with Amur honeysuckle present (n=10),

while the second soil sample in the pair was taken from the nearest adjacent area having no Amur honeysuckle within at least three meters of the sampling location (n=10). It was important to collect the soil samples from adjacent sites with similar land-use histories, to more accurately determine whether a non-native invasive species was successful in a particular site as a result of: 1) historical land uses altering the site's soil nutrient characteristics in a way that would later facilitate the invasion; 2) pre-existing, unaltered soil nutrient characteristics that make the site more vulnerable to the invasion; or 3) a post-invasion modification to the site's ecosystem processes affecting its soil nutrient characteristics by the non-native invasive species, as a result of the invasion (Kourtev et al. 1998; Ehrenfeld 2003; Wilson et al. 2013).

Table 2. Geographic coordinates (i.e. latitude and longitude) for all 40 systematically placed random grid sampling points in the oak savanna restoration study site at Nachusa Grasslands, IL, USA.

Soil Sampling Point	Geographic Coordinates
1	41°53'52.62"N, 89°22'25.78"W
2	41°53'52.59"N, 89°22'22.52"W
3	41°53'52.57"N, 89°22'19.24"W
4	41°53'52.64"N, 89°22'15.92"W
5	41°53'50.72"N, 89°22'25.82"W
6	41°53'50.74"N, 89°22'22.51"W
7	41°53'50.73"N, 89°22'19.25"W
8	41°53'50.68"N, 89°22'15.94"W
9	41°53'51.31"N, 89°22'08.51"W
10	41°53'51.38"N, 89°22'05.88"W
11	41°53'51.40"N, 89°22'03.22"W
12	41°53'51.44"N, 89°22'00.60"W
13	41°53'51.50"N, 89°21'57.98"W
14	41°53'48.76"N, 89°22'25.88"W
15	41°53'48.78"N, 89°22'22.59"W
16	41°53'48.81"N, 89°22'19.34"W
17	41°53'48.79"N, 89°22'16.07"W
18	41°53'49.35"N, 89°22'08.50"W
19	41°53'49.42"N, 89°22'05.87"W
20	41°53'49.47"N, 89°22'03.26"W
21	41°53'49.57"N, 89°22'00.62"W
22	41°53'49.57"N, 89°21'57.99"W
23	41°53'46.74"N, 89°22'25.92"W
24	41°53'46.70"N, 89°22'22.58"W
25	41°53'46.73"N, 89°22'19.31"W
26	41°53'46.85"N, 89°22'16.08"W
27	41°53'47.50"N, 89°22'08.52"W
28	41°53'47.53"N, 89°22'05.90"W
29	41°53'47.58"N, 89°22'03.28"W
30	41°53'47.61"N, 89°22'00.63"W
31	41°53'47.65"N, 89°21'58.00"W
32	41°53'44.78"N, 89°22'25.96"W
33	41°53'44.84"N, 89°22'22.70"W
34	41°53'44.90"N, 89°22'19.41"W
35	41°53'44.94"N, 89°22'16.08"W
36	41°53'45.57"N, 89°22'08.53"W
37	41°53'45.61"N, 89°22'05.88"W
38	41°53'45.66"N, 89°22'03.27"W
39	41°53'45.68"N, 89°22'00.65"W
40	41°53'45.71"N, 89°21'58.03"W

Supplementary study site soil information was also obtained by describing and analyzing soil cores collected throughout the eastern half of the oak savanna restoration study site using a trailer mounted Giddings HDGSRPT-#25 hydraulic soil coring machine (Giddings, Windsor, CO, USA) (Figure 29). Two, five centimeter in diameter cores were taken at each of the twenty grid points in the eastern half of the study site (n=40) to five meters deep, or to bedrock, for primary use in a separate chronosequence study as a control when assessing soil carbon sequestration in sites with various restoration status at Nachusa Grasslands (Osterloh 2013). The soil cores using the hydraulic soil coring machine were only collected in the eastern half, because of accessibility and maneuverability constraints present in the western half of the study site as a result of the different management histories (i.e. too many small trees obstructing the entrance of the trailer mounted Giddings hydraulic soil coring machine).

Figure 29. Image showing the trailer mounted Giddings HDGSRPT-#25 hydraulic soil coring machine (Giddings, Windsor, CO, USA) used to collect the 5 meter soil cores (n=40) in the eastern tract of the oak savanna restoration study site at Nachusa Grasslands, IL, USA (Picture by M. Konen).

4.2 AMUR HONEYSUCKLE LEAF TISSUE COLLECTION

A total of 22 locations were initially selected as potential leaf collection sites, including the oak restoration study site at Nachusa Grasslands (subsets were collected from both the western half (n=30) and eastern half (n=40) of the study site, so as to capture the variability in Amur honeysuckle age throughout the study site resulting from differences in management regulations). Two of the other 21 potential collection sites (New York Botanical Garden, NY and Morton Arboretum, IL) were chosen based on historical records that documented the spread of Amur honeysuckle through the procurements and distributions between national arboretum and botanical gardens (Luken and Thieret 1996). The remaining 19 collection locations were selected based on the current crowd-sourced sighting records of the Invasive Plant Atlas of New England (IPANE) published by the Center for Invasive Species and Ecosystem Health at the University of Georgia (EDDMapS 2015). The New York Botanical Garden (Bronx, NY), supplied 40 Amur honeysuckle leaf samples via mail (J. L. Peter, Plant Records Manager, The New York Botanical Garden). Of the other 20 potential collection locations, Amur honeysuckle were only found and manually collected from 11 sites. In total, this study obtained leaf tissue samples from 408 Amur honeysuckle individuals from 14 sites, including both halves of the oak savanna restoration study site at Nachusa Grasslands (Table 3).

Leaf tissue was only sampled from well-established populations of Amur honeysuckle for use in the genetic structure analysis in this study, to infer Amur honeysuckle dispersion patterns across eastern and central United States. At each

collection site, leaf tissue samples were acquired from between 8-40 mature Amur honeysuckle individuals (defined in this study as Amur honeysuckle individuals that have reached reproductive maturity and have evidence of flowering and/or fruit development) from well-established populations (Table 3). Each individual shrub sampled was at least five meters from other individuals, to reduce the probability of sampling close relatives or clonal offsets (McNutt 2010; Barriball 2012). Upon collection of the leaf material, it was stored in a Ziploc plastic bag with silica desiccant (Chase and Hills 1991) and then frozen to preserve the integrity of the DNA until extraction.

Table 3. Table listing all 14 locations (populations) from which Amur honeysuckle leaf tissue samples were collected, with approximate geographic coordinates of the site, the number of individual shrubs sampled, and the assigned population ID.

Site	Geographic Coordinates	Sample Size	Population ID
Study Site at Nachusa Grasslands (West), IL	41°53’48.55”N 89°22’20.81”W	30	NGW.IL
Study Site at Nachusa Grasslands (East), IL	41°53’48.25”N 89°22’04.40”W	40	NGE.IL
Morton Arboretum, IL	41°48’43.57”N 88°05’00.16”W	40	MA.IL
Hidden Springs State Forest, IL	39°18’54.44”N 88°41’17.13”W	30	HS.IL
Trail of Tears State Forest, IL	37°29’06.04”N 89°21’53.76”W	8	TT.IL
Iron Horse Park, OH	39°39’22.06”N 84°08’22.98”W	30	IH.OH
Black Oak Park, OH	39°37’56.40”N 84°07’33.70”W	30	BO.OH
Bill Yeck Park, OH	39°37’31.18”N 84°07’03.88”W	30	BY.OH
Sugarcreek MetroPark, OH	39°37’05.30”N 84°05’50.93”W	30	SC.OH
Green Ridge State Forest, MD	39°39’59.85”N 78°26’35.21”W	30	GR.MD
Tuscarora State Forest, PA	40°15'48.00"N, 77°33'44.30"W	28	TU.PA
Tiadaghton State Forest, PA	41°17‘03.56"N, 77°19'27.63"W	30	TI.PA
New York Botanical Garden, NY	40°51’43.54”N 73°52’38.73”W	40	NYBG
Arnold Arboretum at Harvard University, MA	42°17’55.46”N 71°07’30.90”W	12	AA.MA
	TOTAL	408	

4.3 LAB METHODS

4.3.1 Soil Lab Methods. The soil lab methods described in this section were conducted at Northern Illinois University (Geography Department), to obtain general soil characteristics (i.e. soil order via soil core descriptions, moisture content, texture, carbon/nitrogen ratios, pH, nutrient levels, below-ground respiration levels, and wet aggregate stability) in the oak savanna restoration study site. Soil order was determined based on the soil descriptions of 20 soil cores from the eastern half of the study site. All other general site characteristics were quantified using the A horizon bulk soil samples collected throughout the entire site (n=40).

Soil Core Descriptions. One of the two five meter cores collected in the eastern half of the study site (n=20) was used to measure and describe the soil horizons, specifically: depth intervals (cm), matrix color, redox features (color, quantity, size, contrast), soil structure (grade, size, and shape), coatings (type, color, abundance, thickness, contrast, and location), continuity, presence and size of roots, effervescence, and soil boundary (distance and shape). The other five meter core (n=20) was used to measure bulk density (mass of dry soil divided by volume of total soil, including solid particles and pore spaces), soil pH, and assess individual carbon/nitrogen stocks within each soil horizon. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

Moisture Content. Water content, or the amount of water present in soil, was assessed using the standard procedure described by Gardner (1986) for all soil

samples (n=60) (including those collected to assess whether Amur honeysuckle impacts soil properties). Measuring soil water content is important, since the moisture content of a soil impacts the organic compounds found within that soil (Papiernik and Yates 2002). Clean and dry 50 milliliter beakers were weighed empty using a balance readable and accurate to 0.0001 gram. From each A horizon bulk soil sample, a spoonful of air dried and ground (< 2 mm) soil was placed in a beaker and weighted to the nearest 0.0001 gram. The beakers with the soil samples were then placed in a thermostatically controlled oven at 105 °C overnight. After removal of the beakers from the oven, they were placed in a desiccator to cool and then weighed to the nearest 0.0001 gram. Moisture content was expressed as a percentage that defined the ratio of the mass of water in a soil sample to the mass of solids in a soil sample (Gardner 1986).

Soil Texture. The soil particle size-class (i.e. size distribution of individual soil particles) of each A horizon soil sample (n=60) (including those collected to assess whether Amur honeysuckle impacts soil properties) was determined using particle-size analysis (PSA) conducted by means of the standard direct sampling pipetting technique with fleakers (Gee and Bauder 1986; Indorante et al. 1990; Gee and Or 2002). This method relies on Stokes' Law to calculate the settling time for clay particles (<2 µm) depending on the temperature of the water in which the particles are suspended, to determine subsampling depths and times used to measure the density of a soil solution, and to ultimately quantify the amount of sand (2-0.05 mm), silt (0.05-0.002 mm), and clay particles (<0.002 mm) present within that solution. Sand fraction proportions were determined after completing the pipetting technique, based on a modified protocol as

described by Gee and Bauder (1986) and Gee and Or (2002). More specifically, sand fraction proportions were determined in this research by: 1) pouring the remaining suspended soil solutions through a 32 µm sieve; 2) washing the sand particles (2-0.05mm) on the sieve; 3) transferring the sand into beakers, which were then place in an oven at 105 °C and dried; 4) shaking the dried sand through a nest of sieves (i.e. 2-1 mm, 1-0.5 mm, 0.5-0.25 mm, 0.25-0125 mm, 0.125-0.063 mm, 0.063-0.053 mm, 0.053-0.032 mm, respectively) for one minute; and 5) weighing each sieve with the sand. In the end, the PSA pipetting method has a precision of ± 1% for determining clay fractions (Gee and Bauder 1986; Gee and Or 2002). Standard USDA soil texture classification schemes for each sample were identified using the soil texture triangle based on Soil Survey Staff (1975, 1999).

Total Carbon/Nitrogen Ratios. Organic carbon is an important chemical component of organic matter and is often quantified along with inorganic carbon in mineral soil samples by measuring the proportion of total organic carbon (Nelson and Sommers 1996; Schumacher 2002). The amount of total organic carbon found in a soil plays an essential role in how chemicals react in the soil and can be present in three different forms of carbon: organic (i.e. decomposed animal and plant material), inorganic (i.e. parent material and/or geologic sources, typically carbonate minerals), and/or elemental (i.e. geologically sourced or anthropogenically dispersed soot, charcoal, and graphite) (Nelson and Sommers 1996; Schumacher 2002). According to Bremner (1996), most cultivated soils contain between 0.06 and 0.5% nitrogen in the surface soil horizon. For the purpose of this study it was important to quantify how much

nitrogen was generally present throughout the never cultivated oak savanna restoration study site. Total soil carbon and nitrogen contents were measured in approximately 500 mg of soil from each A horizon sample (n=60) (including those collected to assess whether Amur honeysuckle impacts soil properties) using the standard instrument parameters and oxygen methods in an automated Elementar CNS macro elemental analyzer (Elementar Analysensysteme GmbH, Hanau, Germany).

Soil Nutrients and Soil pH. A subsample of the 40 A horizon soil samples (n=10) collected from throughout the oak savanna restoration study site at the systematically placed random sampling gird points were selected based on the national soil survey data (selected samples within the same soil orders) and were sent via mail to the University of Wisconsin-Madison Soil Testing Laboratories (Madison, WI, USA; http://uwlab.soils.wisc.edu/) for nutrient analysis. The soil samples from beneath (under canopy near stem) and away from (≥ one meter) Amur honeysuckle collected within the western half of the oak savanna (n=20) were sent via mail to a commercial soil lab in Macomb, IL (Key Agricultural Services, Inc) for nutrient analysis. Key Agricultural Services soil lab was used for the nutrient analysis of the soil samples only because the UW-Madison soil lab discontinued their nutrient analysis services. In both nutrient analyses, available phosphorous (P), exchangeable potassium (K), calcium (Ca), and magnesium (Mg) were quantified using the standard lab procedures followed by each commercial lab.

Soil pH has been identified as one of the most informative measurement in determining the characteristics of a soil, such as soil toxicity and essential nutrient

availability (Thomas 1996). Soil pH can also impact the rate of chemical reactions that occur within a soil (Papiernik and Yates 2002). For this study, soil pH was quantified using soil from each A horizon sample (n=60) (including those collected to assess whether Amur honeysuckle impacts soil properties) based on the standard procedure of both commercial labs (UW-Madison Soil lab and Key Agricultural Services, Inc).

Below-Ground Soil Respiration. Soil respiration was measured at 20-25 randomly selected permanent points (marked with PVC collars having approximately a 4 cm interior diameter and inserted into the ground between three to four centimeters) every three weeks throughout the growing season using both a 6400-09 Soil CO_2 Flux Chamber attached to the sensor head of the LI-6400 and a fully automated measurement protocol (LI-COR, Inc., Lincoln NE, USA) (n=45) (Figure 30). A soil temperature probe attached to the LI-6400 was used to integrate soil temperatures (approx. 15 cm below the surface) into the soil respiration data sets (LI-COR, Inc., Lincoln NE, USA) (Figure 30). The automated measurement protocol was run for a total of 4 cycles at each point. Random sampling points were used to capture the spatial variability associated with the soil microbial activity throughout the oak savanna restoration study site (Curiel Yuste et al. 2007). Any plants found growing inside the collars were removed with care, so as to not disturb the soil, while all plants growing on the outside of the collar were left alone (Tang and Baldocchi 2005). Following each soil respiration measurement, the intermediate flux data was automatically fit with a regression, which was then used to compute the soil CO_2 flux (μmol m^{-2} $s^{-}1$) for the target ambient CO_2 concentration (LI-COR Biosciences Inc. 2015).

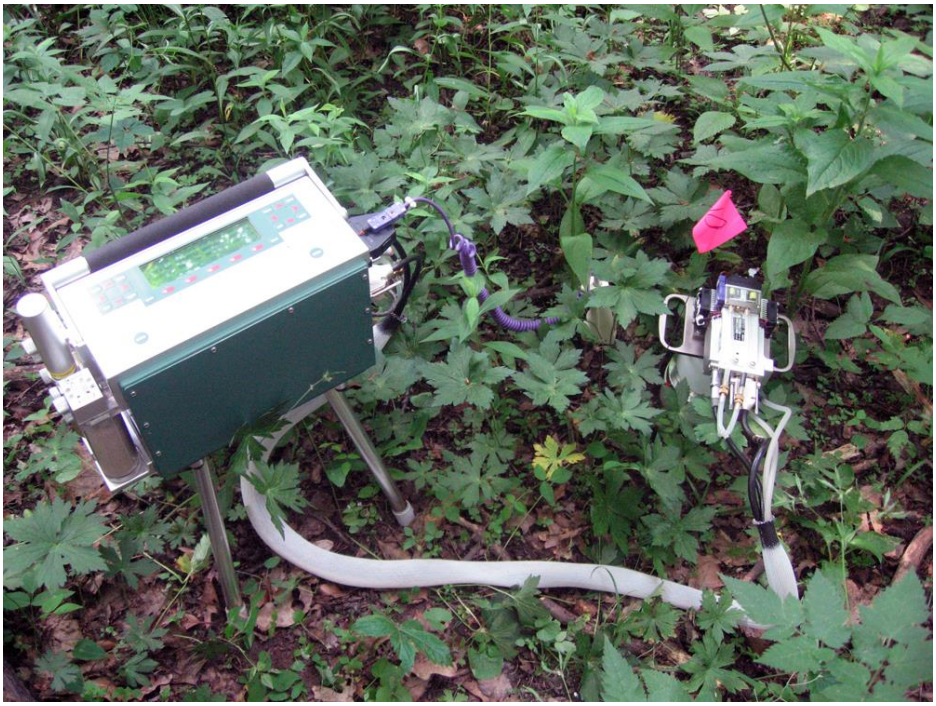

Figure 30. 6400-09 Soil CO_2 Flux Chamber attached to the sensor head of the LI-6400 with the attached soil temperature probe measuring soil temperature at approximately 15 cm below ground.

Wet Aggregate Stability. Wet aggregate stability represents how vulnerable a soil is to water erosion and infers soil quality, since the stability of a soil aggregates (i.e. cohered soil particles) is a function of cohesiveness strength associated with organic compounds when disruptive forces or disturbances are introduced (Kemper and Rosenau 1986). To date, aggregate stability has been widely used as a physical indicator of erodibility and there have been a number of methods proposed to successfully measure soil aggregate stability (Kemper and Rosenau 1986; Yang and Wander 1998; Amezketa 1999; Soil Quality Institute Staff 1999; Herrick et al. 2001; Patton et al. 2001; Bird et al. 2002; Bird et al. 2007; Yoo et al. 2011; Nciizah and Wakindiki 2015). For this study, wet aggregate stability was assessed on the 40 A horizon soil samples (collected at each grid point throughout the oak savanna

restoration study site), as well as the 10 A horizon soil samples (n=20) (collected for use in detecting differences associated with the presence and absence of Amur honeysuckle). All wet aggregate stability samples (n=60) were analyzed according to a modified method described by Kemper and Rosenau (1986) and Bird et al. (2007).

More specifically, between 30-60 g of soil aggregates (<4 mm, >2 mm) from each sample were placed on top of four nested stainless steel mesh test sieves (2 mm, 1mm, 0.5 mm, and 0.25 mm) positioned just above water level inside two large paint buckets for 10 min. This first step was conducted to ensure that the capillaries in the soil aggregates would slowly absorb water, so as to reduce the pressure and not burst the aggregates before each experiment. After the 10 min. capillary soak, the nested sieves were lowered into the buckets and vertically agitated (one and a half centimeter stroke) at a consistent speed (one cycle every two seconds) for an additional 10 min. using a motorized platform built by M. Wander and M. Konen (as per Kemper and Rosenau 1986) (Figure 31). All soil samples remained fully immersed in water throughout the 10 min. agitation period, as per Bird et al. (2007). Soil aggregates remaining on the sieves after the agitation period were washed into pre-weighed tins and placed in an oven at 105 °C until dry. Once dry each tin was immediately weighed to record the proportion of the total soil sample that was comprised by each total aggregate size fraction, including any sand particles present. To determine what proportion of the original samples were sand-free wet stable aggregates, about five milliliters of 5% sodium hexametaphosphate (calgon) was added to each oven dried/weighted sample, and washed through its respective sieve (i.e. 2 mm, 1mm, 0.5 mm, and 0.25 mm) (Bird et al. 2007). Any

remaining sand particles left on the sieve were washed back into the pre-weighed tin and placed in an oven at 105 °C until dry. Once dry each tin was immediately weighed again, to record the proportions of the total soil samples that were comprised by sand-free stable wet aggregate size fraction (hereafter referred to as stable aggregates) (Bird et al. 2007).; values were calculated following Kemper and Rosenau (1986). When possible two to four replicates were run for each sample point, so as to capture any variability.

Figure 31. Image showing the motorized platform built by M. Wander and M. Konen (as per Kemper and Rosenau 1986), used to agitate the soil samples to measure wet aggregate stability (Picture by S. McCarragher).

4.3.2 Molecular Methods. The molecular methods described in this section were conducted at Northern Illinois University (Biology Department, DeKalb, IL, USA), to obtain genetic diversity data for Amur honeysuckle subpopulations throughout Illinois (n=5; including the samples collected from the western and eastern half of the oak savanna restoration study site) and the eastern coast of the United States (n=2) (Table 4), based on microsatellite analyses conducted at Yale University (DNA Analysis Facility on Science Hill, New Haven, CT, USA). The total number of individual Amur honeysuckle samples (n=80) and subpopulations (n=7) used in this analysis were constrained by existing research resources and therefore did not include all 408 collected samples from all 14 sampled subpopulations (as described in section 4.2). All genetic data obtained from this study were used to assess the general geographic and evolutionary patterns associated with Amur honeysuckle's historic range expansion throughout the eastern and central United States, with implications for identifying past and future invasion pathways and potentially redefining long distance dispersal events with regard to invasive species.

Table 4. Table listing the seven locations (subpopulations) from which Amur honeysuckle DNA were analyzed by Yale University's DNA Analysis Facility on Science Hill using fragment analyses. Approximate geographic coordinates of each site are also listed, along with the number of samples analyzed from each location, and the assigned population ID.

Site	Geographic Coordinates		Sample Size	Population ID
Study Site at Nachusa Grasslands (West), IL	41°53'48.55"N	89°22'20.81"W	12	NGW.IL
Study Site at Nachusa Grasslands (East), IL	41°53'48.25"N	89°22'04.40"W	12	NGE.IL
Morton Arboretum, IL	41°48'43.57"N	88°05'00.16"W	12	MA.IL
Hidden Springs State Forest, IL	39°18'54.44"N	88°41'17.13"W	12	HS.IL
Trail of Tears State Forest, IL	37°29'06.04"N	89°21'53.76"W	8	TT.IL
New York Botanical Garden, NY	40°51'43.54"N	73°52'38.73"W	12	NYBG
Arnold Arboretum at Harvard University, MA	42°17'55.46"N	71°07'30.90"W	12	AA.MA
		TOTAL	80	

Deoxyribonucleic Acid (DNA) extraction. The PowerPlant® Pro DNA Isolation Kit and protocol were used to extract genomic DNA from each sample following the manufacturer's instructions (MO BIO Laboratories, Inc., Carlsbad, CA, USA). Genetic variation patterns were inferred using five microsatellite marker loci (Table 5) with primer pairs specifically developed for Amur honeysuckle (Rocha et al. 2014; Barriball et al. 2015; Sigma/Genosys, The Woodlands, TX, USA), using a modification of the protocol described by Rocha et al. (2014), Barriball (2012), and Barriball et al. (2015). More specifically, as per the MoBIO PowerPlant® Pro DNA Isolation Kit protocol for each DNA extraction, about 50 mg of crushed, dried Amur honeysuckle leaf tissue was combined with proprietary solutions (including a Phenolic Separation Solution, since Amur honeysuckle contains phenolic metabolites in their leaves; Cipollini et al. 2008) into a provided 2 ml PowerPlant® Bead Tube and vortexed for 2 cycles of 60 sec. at 5 m/s using a FastPrep®-24 Instrument (MP Biomedicals, LLC, Santa Ana, California, USA). The samples were then centrifuged at 13,000 x *g* for 2 min. using a Micromax RF Thermo IEC Centrifuge (GMI, Ramsey, MN, USA), after which the supernatant was transferred to a clean 2 ml Collection Tube, combined with additional proprietary solution and mixed using a vortex mixer for 5 sec., and incubated in a refrigerator at 4°C for 5 min. After incubation, each sample was centrifuged again at 13,000 x *g* for 2 min., transferred to another clean 2 ml Collection Tube and combined with additional proprietary solution and mixed using a vortex mixer for 5 sec. In three separate steps, each sample lysate was loaded onto a provided Spin Filter and centrifuged at 10,000 x *g* for 30 sec. allowing the DNA to bind to the spin filter and all unwanted salt and impurities to flow through the spin filter membrane. After discarding the flow-through in

each of the previous steps, the spin filter is centrifuged again at 16,000 x *g* for 2 min. to remove any remaining proprietary solution and then placed in a clean 2 ml Collection tube. Finally, 50 µl of reverse osmosis, autoclaved water was added to the center of the filter membrane and incubated at room temperature for 10 min., after which the sample was centrifuged at 10,000 x *g* for 30 sec. and the spin filter was discarded. This protocol produced 50 µl of ready-to-use DNA, which was stored frozen until use. Prior to freezing, the concentrations of 1 µl of all extracted DNA samples were measured using a NanoDrop 1000 Spectrophotometer (Thermo Fisher Scientific, NYSE: TMO).

Table 5. Table listing the five Lonicera maackii microsatellite loci used in this study, along with their associated GenBank accession numbers (Rocha et al. 2014), primer sequences (Rocha et al. 2014; Barriball et al. 2015), number of alleles, allele sizes, and annealing temperatures (T_a).

Locus	GenBank Accession No.	Repeat Motif	Primer Sequences (5'-3')	No. of Alleles	Allele Size Range (bp)	T_a (°C)
Maack-Di3 F	KF463291	$(CA)_9$	[6-FAM] AAAAGGCAAAGAAGCTCTTGGCA	5	216-226	57
Maack-Di3 R			AGAAAAGAAGTCAGACTCTGCA			
Maack-Di4 F	KF463292	$(CT)_{19}$	[5HEX]CTCATTCAGTCAAGTCCAAGT	24	102-182	57
Maack-Di4 R			CGATGCTACATCATAATTAACAG			
Maack-Di19 F	KF463294	$(CT)_{12}$	[6-FAM]CGTGTTCCCCTTCTCTCACT	8	245-269	57
Maack-Di19 R			CGGGGCTGCTTATCTTCTTC			
Maack-Tet21 F	KF463298	$(GTAT)_6(GTAT)_7$	[5HEX]GCCTCCACCGATCTACTTCA	12	134-202	57
Maack-Tet21 R			TCGGACGGTCGTTATGTGTA			
Maack-Tri8 F	KF463299	$(GAA)_{15}$	[6-FAM]TCAAACGAGCTCCTAGATTGTAA	11	133-189	57
Maack-Tri8 R			GTTAGCGTGTTGCGTTCACT			

Polymerase Chain Reaction (PCR). Type-it Microsatellite polymerase chain reaction (PCR) Kits (Qiagen Inc., Valencia, CA, USA) were used to prepare DNA samples for the polymerase chain reactions (Yale Institute for Biospheric Studies 2015a), performed using an Applied Biosystems 2720 96-well thermal cyclers (Thermo Fischer Scientific, Inc., Life Technologies, Rockford, IL, USA). Prior to conducting

PCRs, all reagents and tubes were placed in a Spectrolinker™ XL-1000 UV Crosslinker (Spectronics Corporation Westbury, NY, USA) that covalently binds nucleic acid sequences to reduce amplification of contaminants. As per the Type-it kit Multiplex PCR protocol for Amplification of Microsatellite Loci Using Q-Solution, each PCR reaction was a 25 µl solution comprised of 12.5 µl (final concentration: 1x) of 2x Type-it Multiplex PCR Master Mix (containing 3 mM $MgCl_2$, Taq-polymerase, buffer and dNTPs), 0.2 µM of each primer pair , 2.5 µl of Q-Solution (final concentration: 0.5x), 4 µl of RNase-free water, and 1 µl of template DNA (≤200 ng/reaction) (Qiagen 2009). The PCR program provided in the Type-it Microsatellite PCR Handbook was used, which included: a five minute initial activation step for the HotStarTaq and DNA polymerase at 95 °C; 28 cycles of the following three steps: denaturation (95 °C for 30 seconds), annealing (57 °C for 90 seconds), and extension (72 °C for 30 seconds); and a final extension step at 60 °C for 30 minutes (Qiagen 2009). All reverse primers were unlabeled, while all the forward primers were labelled with either the 6-FAM or 5HEX fluorescent dyes from the standard DS-30 dye set (Eurofins Genomics, Huntsville, AL) (Table 4). Negative control reactions were run with each PCR experiment to verify sample quality.

Gel Electrophoresis Screening. Following the PCR step, samples were separated using gel electrophoresis to verify that the PCR conditions yielded correctly sized amplicons and were therefore appropriate for this analysis. In total, over 140 gel electrophoresis screening experiments were conducted, each testing between four to sixteen PCR samples (>2000 samples in total). Both a Mini-Sub® Cell GT Horizontal Electrophoresis System gel box (Bio-Rad Laboratories, Inc., Hercules, CA, USA) and a

FisherBiotech™ Midi-Horizontal Electrophoresis Systems gel box(Fisher Scientific Company, Ottawa, Ontario, Canada) were used with standard 1% Molecular Biology grade agarose gels (Fisher Scientific Company, Ottawa, Ontario, Canada). Two power supplies were used interchangeably, as available: 1) E-C Apparatus Corporation EC250-90 (American Laboratory Trading, Inc., East Lyme, CN) and 2) PowerPac™ Universal Power Supply (Bio-Rad Laboratories, Inc., Hercules, CA, USA).

Large gels (200 ml) were loaded with 8 µl of each PCR product (including positive and negative controls) that was combined with 2 µl of Promega 5X Green GoTaq™ Flexi Buffer (Fisher Scientific Company, Ottawa, Ontario, Canada). After adding DNA ladder (4 µl), the large gels were run at 65V for 10 min. followed by an additional 150 min. at 78V. Large gels were then transferred to about 300 ml of deionized water with 15 µl of Ethidium Bromide solution (used to stain the gel to visualize the amplicons) and gently agitated on a Lab-Line Orbital Shaker (Labline Instruments, India) for 20 min.

Small gels (50 ml) were loaded with between 3-5 µl of each PCR product (including positive and negative controls) that was combined with 1 µl of Promega 5X Green GoTaq™ Flexi Buffer (Fisher Scientific Company, Ottawa, Ontario, Canada). After adding DNA ladder (2 µl), the small gels was run at 100V for 60 min. Small gels were then transferred to about 50 ml of deionized water with 5 µl of Ethidium Bromide solution and gently agitated on a Lab-Line Orbital Shaker (Labline Instruments, India) for 14 min.

Following agitation, the gels were transferred to a KODAK Gel Logic 200 Imaging System (Eastman Kodak Company, Rochester, NY, USA) to visualize the amplicons using UV trans-illumination. KODAK Molecular Imaging Software (KODAK MI Software) was used to digitally capture images of each gel for documentation purposes.

This analysis rotated between using the following three different DNA ladders based on availability: 1) GeneRuler ™ Express ready-to-use DNA Ladder (5000, 3000, 2000, 1500, 1000, 750, 500, 300, and 100 bp) (Thermo Fisher Scientific, Life Technologies, NYSE: TMO); 2) GeneRuler ™ Mix ready-to-use DNA Ladder (10000, 8000, 6000, 5000, 4000, 3500, 3000, 2500, 2000, 1500, 1200, 1000, 900, 800, 700, 600, 500, 400, 300, 200, and 100 bp) (Thermo Fisher Scientific, Life Technologies, NYSE: TMO); and 3) GeneRuler ™ Low Range ready-to-use DNA Ladder (700, 500, 400, 300, 200, 150, 100, 75, 50, 25 bp) (Thermo Fisher Scientific, Life Technologies, NYSE: TMO).

Fragment Analysis. Capillary electrophoresis on an automated, genetic analysis system (3730xl 96-Capillary Genetic Analyzer, Applied Biosystems, San Francisco, CA, USA) was used to genotype all samples at the DNA Analysis Facility on Science Hill at Yale University. An initial dilution series (full strength, 1:50 dilution of PCR, 1:100 dilution of PCR, and 1:250 dilution of PCR) was used to optimize the intensities for each locus (Yale Institute for Biospheric Studies 2015b). Based on the results of the dilution series, the 1X PCR product was identified as performing best for all loci. Four of the five loci were multiplexed post-PCR to reduce analysis cost (i.e. Di3/Di4 and Di19/Tet21). Each post-PCR multiplexed sample was prepared for capillary electrophoresis by

adding 8 µl of Hi-Di Formamide and 1 µl of each PCR product (total 2 µl of PCR product) to their respective wells within a MicroAmp® Fast Optical 96-Well Reaction Plate (0.1 mL; Thermo Fischer Scientific, Inc.). The samples associated with the non-multiplexed locus (Tri8) were prepared for capillary electrophoresis by adding 9 µl of Hi-Di Formamide and 1 µl of PCR product to their respective wells within a MicroAmp® Fast Optical 96-Well Reaction Plate (0.1 mL; Thermo Fischer Scientific, Inc.). All samples sent to Yale University had an initial volume of 10 µl to which the DNA Analysis Facility on Science Hill at Yale University added Gel Company (San Francisco, CA, USA) Rox-500 size standard (containing 25 single-stranded labeled fragment of: 70, 80, 90, 100, 120, 140, 160, 180, 190, 200, 220, 240, 260, 280, 300, 320, 340, 360, 380, 400, 425, 450, 475, 490, and 500 bp), to identify the fragments based on their mobility and size (Yale Institute for Biospheric Studies 2015a). Final results were received electronically from Yale University via the GeneSifter interface in raw .fsa file format following each successful run.

4.4 DATA ANALYSIS

4.4.1 Descriptive Analysis of Oak Savanna Restoration Study Site.

Confidence intervals and point estimates were calculated for population densities of the tree canopy layer (e.g. white oak and other dominant trees), as well as the understory layer (e.g. white oak seedlings, Amur honeysuckle, and other species). Relative measures of density, size, and distribution (frequency) were calculated, and ultimately combined to determine a measure of relative importance for each species as per Mitchell (2010). The relative importance value is identified as an objective way of measuring tree

dominance and contributes to the understanding of the successional stages of a vegetation community (Mitchell 2010). Five measures of stand structure were estimated based on the standard PCQ method described by Mitchell (2010) for the general canopy and understory layer in the oak savanna restoration study site, as well as specifically for individual species found comprising the canopy and understory layer at the study site in Nachusa Grasslands, IL, USA. More specifically: 1) a*bsolute density* - the number of trees per hectare or the expected number of trees of a given species per hectare, often expressed as stems per hectare; 2) *relative density* - the percentage of total observations for a given species; 3) *cover* – defined as absolute density divided by average species basal area and expressed as meters squared per hectare for all trees combined, as well as for individual species; 4) *absolute frequency* - the percentage of PCQ sample points at which a given species is observed; and 5) *relative frequency* - normalized absolute frequency, so that total proportions add up to 100%.

4.4.2 Modeling Seasonal Carbon Assimilation. Raw photosynthetic data obtained from the LI-6400 Portable Photosynthesis System (LI-COR, Inc., Lincoln NE, USA) were analyzed using SigmaPlot statistical software (Jandel Scientific Software, Corte Madera, CA, USA), following procedures described by Goudriaan (1982) and Kwit et al. (2010). Ultimately, average light response curves were produced for the active growth periods defined in this study to represent an average white oak seedlings' CO_2 uptake (*A*) (i.e photosynthetic CO_2 assimilation ($\mu mol\ CO_2 \cdot cm^{-2}_{leaf\ area} \cdot s^{-1}$) in relation to the level of absorbed photosynthetic active radiation (α_{PAR}, $\mu mol_{photons} m^{-2}_{leaf\ area} s^{-1}$) (Long et al. 1996; Long and Bernacchi 2003; Kwit et al. 2010) (Figure 32). Key physiological elements of

the light response curves were calculated, including dark respiration levels ($\mu mol \cdot m^{-2} \cdot s^{-1}$), light compensation point ($\mu mol \cdot m^{-2} \cdot s^{-1}$) (i.e the PAR level at which the plant begins to photosynthesize), quantum use efficiency of the photosystems ($(\mu molCO_2) \cdot (\mu molPAR)^{-1}$), light saturation point ($\mu mol \cdot m^{-2} \cdot s^{-1}$) (i.e. the PAR level at which 90% of A_{max} is reached; Avola et al. 2008), and maximum assimilation rate (A_{max}; $\mu mol \cdot m^{-2} \cdot s^{-1}$).

The light response curves and their variables were then used to estimate *in situ* carbon assimilation rates based the PAR levels measured *in situ*, to predict daily and seasonal carbon gains of the white oak seedlings and Amur honeysuckle using the exponential rise to maximum curve equation: $A_n = R_d + (A_{max}-R_d)(1-exp^{-(Q*PAR)/(Amax-Rd)})$, where A_n is CO_2 assimilation, R_d is the dark respiration rate, A_{max} is the maximum assimilation rate, *Q* is the quantum use efficiency of the photosystems, and PAR is the photosynthetically active radiation measured *in situ* at Nachusa Grasslands (Kwit et al. 2010) (Figure 32). More specifically, white oak *in situ* carbon assimilation rates were calculated based on the full sun, no HS encroachment, and HS encroachment light scenarios, while Amur honeysuckle *in situ* carbon assimilation rates were calculated based on the HS light scenario. In all cases, carbon assimilation rates were isolated using the knowledge that carbon is ~27% of the total molar mass of CO_2 (44.01 g/mol).

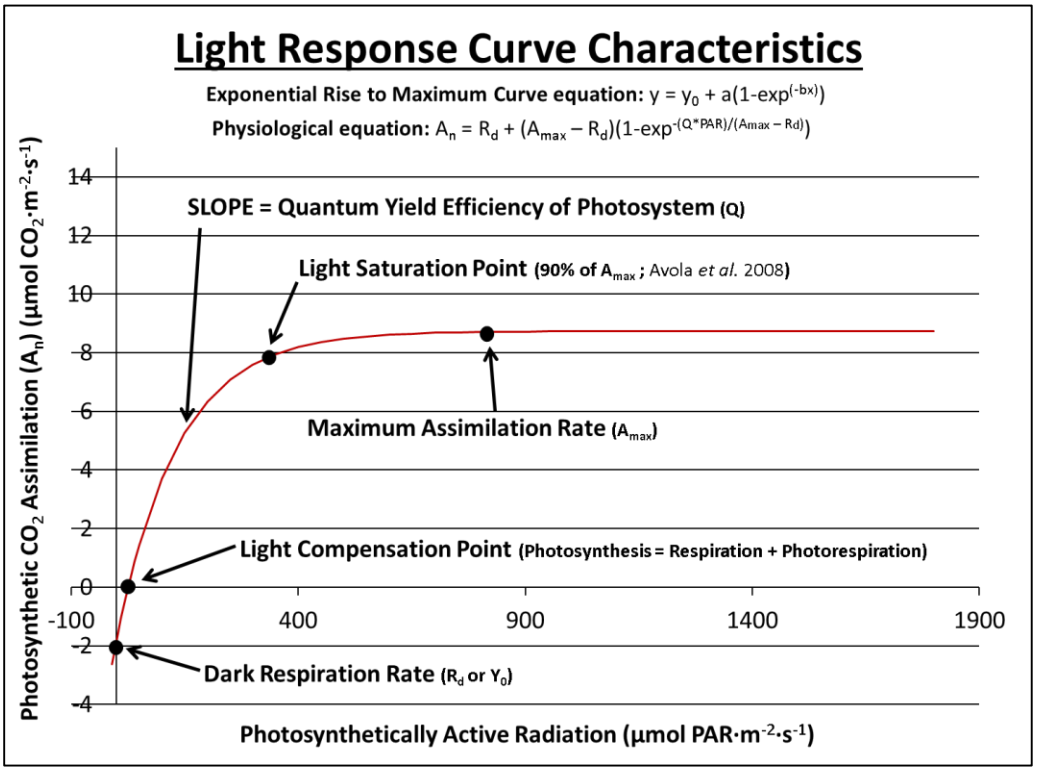

Figure 32. Light response curve example. Important variables and characteristics of the curve are defined (i.e. maximum assimilation rate, light saturation point, quantum yield efficiency, light compensation point, and dark respiration). Both the exponential rise to maximum curve and the physiologic equivalent equation are provided.

Ultimately, daily white oak seedling photosynthetic carbon assimilation rates under the three light scenarios were calculated for each growing season using the four year average PAR values from each light environment scenario and averaged annual light curve variables. In the end, the light response curves were also used to isolate a strongest (i.e. highest photosynthetic efficiency identified by highest light curve) and weakest (i.e. lowest photosynthetic efficiency identified by lowest light curve) white oak and Amur honeysuckle shrub each year to calculate carbon assimilation rates associated with different photosynthetic efficiencies, so as to illustrate the range in which carbon assimilation may occur given the different photosynthetic efficiencies. Particular light levels at which white oak seedlings and Amur honeysuckle achieve

optimal photosynthetic efficiency and productivity were identified based on the light saturation point (LSP) of the light curves produced for both species. These light levels can in turn be used to guide management strategies for increasing the light availability within encroached ecosystems, so as to promote optimal photosynthetic productivity of white oak seedlings and better understand how Amur honeysuckle is competing for light resources in these invaded environments. Ultimately, the nonparametric Kruskal-Wallis test (combined with the nonparametric Tukey-type multiple comparisons post-hoc test) and the nonparametric Mann-Whitney U test were used to determine statistical differences between seasonal light levels, light curve variables, and seasonal carbon assimilation totals (Zar 1999).

4.4.3 Soil Data Analyses. All soil data obtained from the soil methods described in section 4.3 were used to describe general study site soil characteristics (i.e. soil order via soil core descriptions, moisture content, texture, carbon/nitrogen ratios, pH, nutrient levels, below-ground respiration levels, and wet aggregate stability), as well as to assess differences in soils characteristics found below and away from Amur honeysuckle (i.e. soil moisture, soil temperature, soil nutrients, soil acidity, and wet aggregate stability) in the western half of the oak savanna restoration study site, as this half contained a higher abundance of mature Amur honeysuckle. More specifically, a nonparametric Kruskal-Wallis test was performed on soil moisture and soil temperature data from near the stems of Amur honeysuckle, at the dripline of Amur honeysuckle, and at least three meters from any Amur honeysuckle (Zar 1999). Percent total carbon, percent total nitrogen, nutrient levels, soil pH, and wet aggregate stability of soil

collected under and away from Amur honeysuckle were compared using the Mann-Whitney U test (Zar 1999).

4.4.4 Molecular Data Analyses. This research used a modification of procedures previously described for specific use in examining the genetic variation within and between Amur honeysuckle populations (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015), to quantify genetic diversity for each locus (n=5) and sampled population site (n=7) in this study. More specifically, the observed heterozygosity (H_o), Nei's expected heterozygosity (H_e), the mean number of alleles per locus (*Na*), and the effective number of alleles per locus (*Ne*) were calculated using GeneAlEx 6.501 software (Peakall and Smouse 2006, 2012) (Nei 1973). Shannon Diversity Indices were also calculated using GeneAlEx 6.501 software (Peakall and Smouse 2006, 2012), as they provide a useful measure of differentiation among subpopulations and possess ideal statistical properties for analyzing biological information across multiple scales (Sherwin et al. 2006; Rossetto et al. 2008; Peakall and Smouse 2006, 2012). Genetic differentiation was determined using the infinite allele model F_{ST} (Wright 1965; Weir and Cockerham 1984; McNutt 2010). Ultimately, the genetic analysis software GenAlEx 6.501 software (Peakall and Smouse 2006, 2012; http://biology-assets.anu.edu.au/GenAlEx/Welcome.html) was also used to perform an analysis of molecular variance (AMOVA) to determine the level of differentiation between sampled populations of Amur honeysuckle (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015).

4.5 CONCLUSION

This chapter has described the field methods conducted in the oak savanna restoration study site, including plotless and plot sampling techniques, environmental data logging stations, leaf phenology observations, photosynthetic efficiency measurements, and soil sampling. The chapter also outlined the Amur honeysuckle leaf tissue collection techniques for the genetic population structure analysis, as well as the lab methods conducted in this study, including both soil lab methods and genetic lab methods. Finally, this chapter concluded by describing how all data collected in this research were analyzed. In the end, this interdisciplinary research integrates methodologies from physical geography, conservation biogeography, population genetics and explores the ecological impacts and underlying evolutionary mechanisms associated with the spread of Amur honeysuckle, one of the most aggressive and abundant invasive species throughout the Midwest. The ultimate goal of this research is to contribute to the conservation of white oak by better understanding the geographic spread and ecological impact of Amur honeysuckle encroachment.

CHAPTER 5: RESULTS

ECOLOGICAL IMPACTS RELATED TO LIGHT AND CARBON ASSIMILATION

5.1 INTRODUCTION

One of the overarching goals of this research was to better understand how the encroachment of Amur honeysuckle impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration study site located at Nachusa Grasslands in Lee County, Illinois, with particular focus on ecological mechanisms required for successful oak regeneration and recruitment. More specifically, the first research objective of this research was to assess the impact of extended leaf phenology and invasive encroachment of Amur honeysuckle on understory light environments and seasonal carbon assimilation rates within the oak savanna restoration study site. This results chapter addresses the following questions, which are directly associated with the first objective of this research: What role does the extended leaf phenology of Amur honeysuckle play in its leaf-level seasonal carbon gain? What are the existing *in situ* light levels above and below Amur honeysuckle canopies and do those light levels inhibit the ability of *in situ* white oak seedlings to maintain a positive net leaf-level seasonal carbon balance?

At the time of this study, the overstory canopy in the oak savanna restoration site was fairly dense (Figure 33). The land composing the study site was originally purchased in two tracts. The eastern half of the study site was purchased by The Nature

Conservancy in 2003 (Figure 33), after which an active management regime was initiated, including annual spring prescribed fires, brush management of invasive species including Amur honeysuckle (i.e. cut, removal, and herbicide application), thinning of small mesophytic tree species not historically associated with an oak savanna community, and seeding with 160 lbs. of seed composed of 63 native herbaceous species (Saxton 2012). The western half of the study site was purchased in 2006 with contractual agreements hindering any active management on the property until January 1, 2012 (Figure 33). As a result, mature Amur honeysuckle populations and mesophytic trees abundant in the western half of the study site without active management. Beginning January 1, 2012, steps were taken to mechanically and chemically remove much of the mature Amur honeysuckle population and a near annual fire regime was initiated in the western half. Given the historical differences in management between the two halves of the oak savanna study site, the stand structure results in this chapter will be reported as a whole for the entire site, as well as separately for both the western and eastern half of the study site.

Figure 33. Current Google Earth image illustrating the dense current canopy cover of the oak savanna restoration study site in Nachusa Grasslands, Lee County, Illinois, USA (denoted by red rectangle). Dotted line depicts the separation of the western (left) and eastern (right) half of the whole study site, based on the individual purchases made by The Nature Conservancy.

5.2 TREE STAND STRUCTURE OF OAK SAVANNA RESTORATION STUDY SITE

Based on a point centered quarter stand structure analysis, the average tree density of the entire oak savanna restoration study site was 589 stems/ha with a total basal area of 38.7 m^2/ha. Relative density and relative frequency were used to assess species composition and distribution throughout the oak savanna restoration study site. *Ulmus rubra* (slippery elm; 165 stems/ha – 28.1% relative density, 26.2 % relative frequency), *Carya ovata* (shagbark hickory; 155 stems/ha – 26.5% relative density, 23.0% relative frequency), and *Quercus alba* (white oak; 102 stems/ha – 17.5% relative density, 15.9% relative frequency) had the three highest densities (stems/ha) and relative frequencies (proportion of PCQ points at which a given species is observed, normalized to add to 100%) in the oak savanna study site (Figure 34). Beyond having the highest species density of all trees found in the study site, slippery elm trees had a relatively low cover (absolute density divided by average species basal area; 3.3 m^2/ha – 8.6% relative cover). White oak trees, on the other hand, had the highest cover (18.4 m^2/ha – 47.2% relative cover) of all the trees surveyed in the study site. *Quercus rubra* (red oak) had the next highest cover (9.5 m^2/ha – 24.5% relative cover) in the study site, but also had a relatively low density (29.7 stems/ha) and relative frequency (6.6%). Overall, white oak trees were found to be the dominant and most important species throughout the study site (based on relative density, relative cover, and relative frequency).

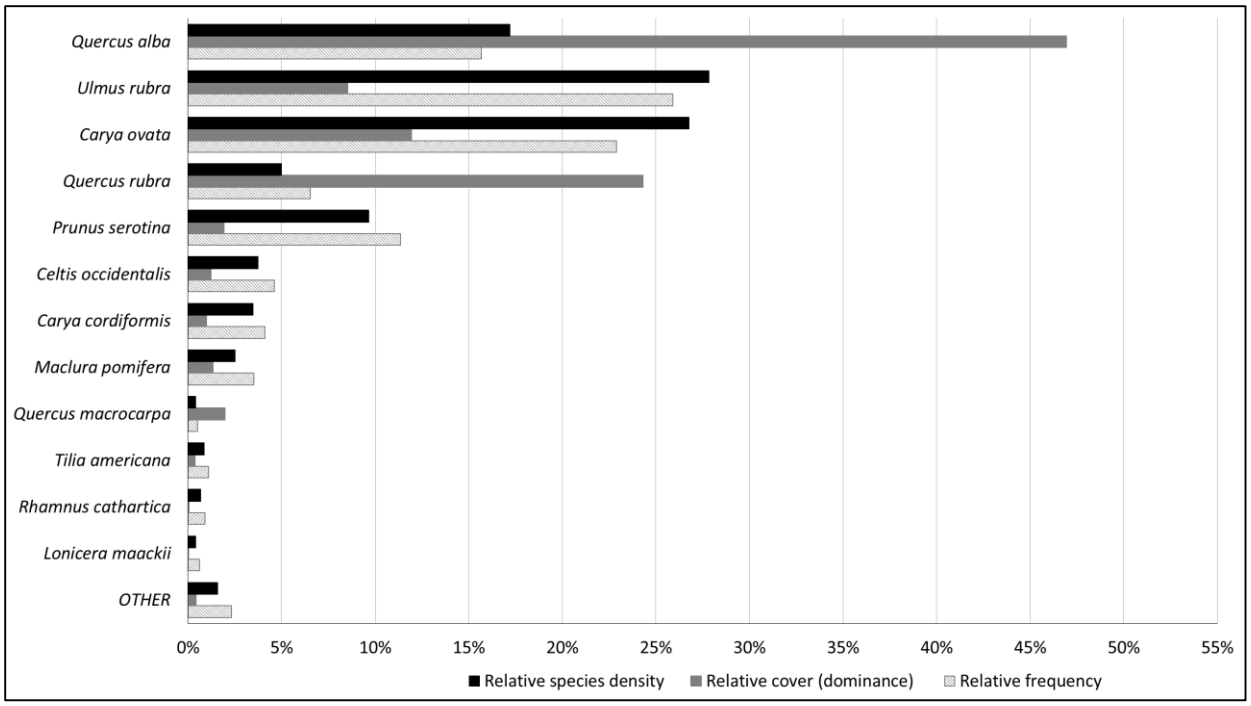

Figure 34. Relative species density (proportion of total stems/ha), cover (dominance; proportion of total basal area/ha), and frequency (distribution; proportion of PCQ points at which a given species is present) of the tree species observed in the canopy layer of the oak savanna restoration study site as a whole, sorted based on importance value (top-high to bottom-low; calculation of importance value factors all three relative stand structure variables).

The size distribution of the canopy layer trees found in the oak savanna restoration study site are represented in Figure 35 using five cm size-classes (n=1500). More than half (922 individuals or 61%) of the trees recorded in the study site measured between ten to twenty cm in diameter at breast height (dbh) (Figure 35). Most (87%) of the white oak trees (n=262) found in the oak savanna restoration study site had sizes between 35 to 60 cm at dbh (average: 46.4 cm ± 0.7 cm standard error (SE); minimum: 7.1 cm; maximum: 107.9 cm) (Figure 35), while all of the mature, large Amur honeysuckle (≥ 5 cm dbh; n=6) found in the study site had sizes between five to 10 cm at dbh (average: 5.4 cm ± 0.1 cm SE; minimum: 5 cm; maximum: 5.7 cm). Most (72%) of red oak trees (n=76) found in the oak savanna restoration study site were sized between 55 to 85 cm at dbh (average: 60.2 cm ± 2.5 cm SE; minimum: 6.1 cm;

maximum: 94.8 cm) (Figure 35). The average size of shagbark hickory (15.8 cm ± 0.6 cm SE; n=398), slippery elm (13.4 cm ± 0.4 cm SE; n=422), and *Prunus serotine* (black cherry) (11.4 cm ± 0.5 cm SE; n=146) found in the oak savanna restoration study site were smaller than those of the oaks (Figure 35).

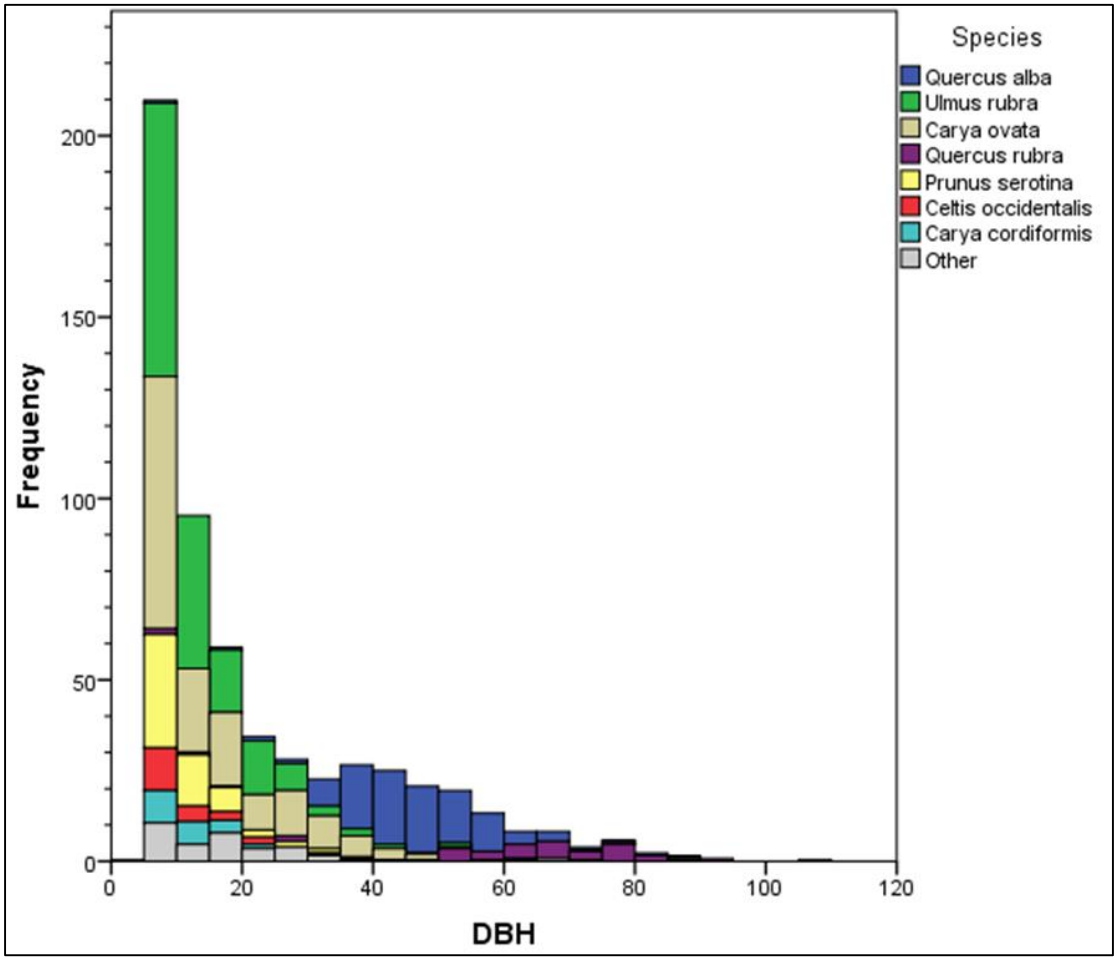

Figure 35. Size-structure diagram of trees (based on diameter at breast height; dbh) surveyed throughout the oak savanna restoration study site in Nachusa Grasslands, IL. Top seven species with the highest overall importance values are highlighted in the diagram and listed in the legend in the order of importance, with Quercus alba having the highest and Carya cordiformis having the lowest importance value.

When the stand structure for both halves of the oak savanna restoration study site were analyzed separately, the western half was found to have a density of 858 stems/ha with a total cover (absolute density divided by average species basal area) of 15.2 m^2/ha (Figure 36), while the eastern half had a density 483 stems/ha with a total cover of 41.7 m^2/ha (Figure 37). The five tree species with the highest importance values (based on relative density, relative cover, and relative frequency) found in the western half of the study site included: shagbark hickory (37.1% relative density, 82.0% relative cover, 42.2% relative frequency), slippery elm (28.8% relative density, 16.2% relative cover, 40.1% relative frequency), white oak (5.2% relative density, 46.1% relative cover, 9.7% relative frequency), black cherry (12.4% relative density, 4.0% relative cover, 20.7% relative frequency), and *Maclura pomifera* (osage orange) (5.6% relative density, 11.1% relative cover, 11.8% relative frequency), respectively (Figure 38). The five tree species with the highest importance values (based on relative density, relative cover, and relative frequency) found in the eastern half of the study site included: white oak (24.7% relative density, 52.1% relative cover, 21.0% relative frequency), slippery elm (27.8% relative density, 8.5% relative cover, 25.4% relative frequency), shagbark hickory (20.3% relative density, 4.3% relative cover, 19.7% relative frequency), red oak (6.9% relative density, 28.4% relative cover, 8.7% relative frequency), and black cherry (8.2% relative density, 1.9% relative cover, 9.9% relative frequency), respectively (Figure 39). More specifically, there were more midsized shagbark hickory in the western half of the study site as compared to the eastern half, while the eastern half was dominated primarily by mature, large white oak.

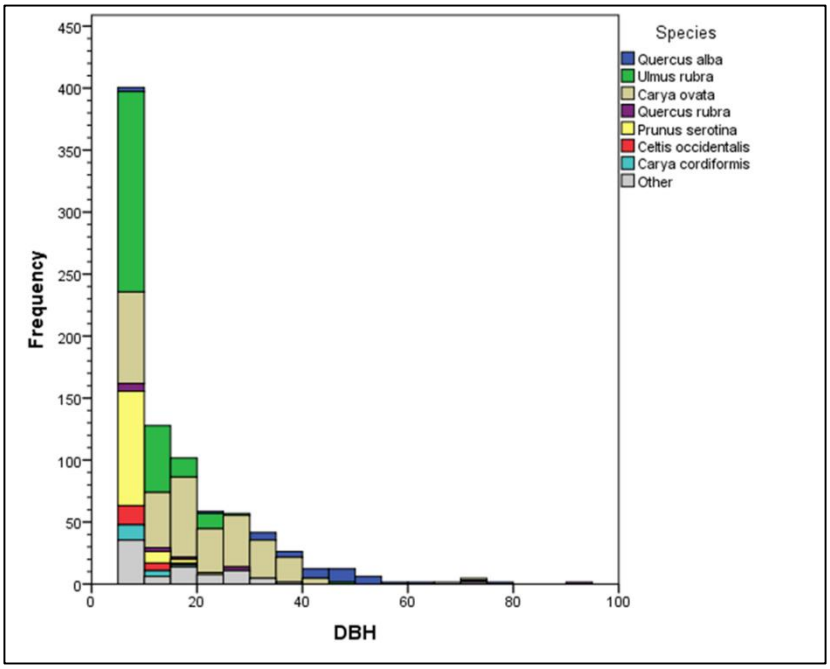

Figure 36. Size-structure diagram of trees (based on diameter at breast height; dbh) surveyed throughout the western half of the oak savanna restoration study site in Nachusa Grasslands, IL. The seven species highlighted in the diagram represent the top seven species with the highest importance values for the entire study site, listed in the legend in the order of importance, with Quercus alba having the highest and Carya cordiformis having the lowest importance value.

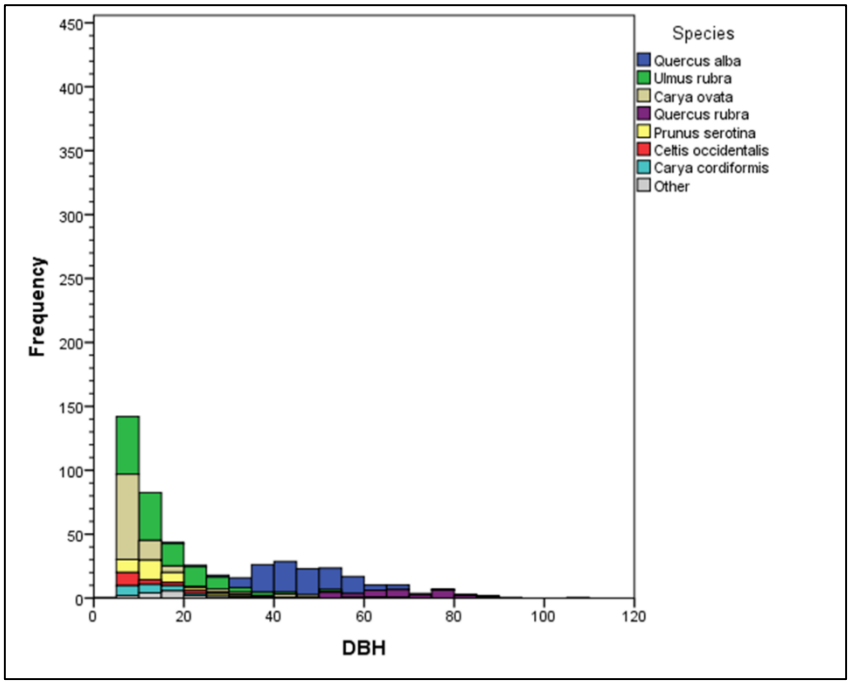

Figure 37. Size-structure diagram of trees (based on diameter at breast height; dbh) surveyed throughout the eastern half of the oak savanna restoration study site in Nachusa Grasslands, IL. The seven species highlighted in the diagram represent the top seven species with the highest importance values for the entire study site, listed in the legend in the order of importance, with Quercus alba having the highest and Carya cordiformis having the lowest importance value.

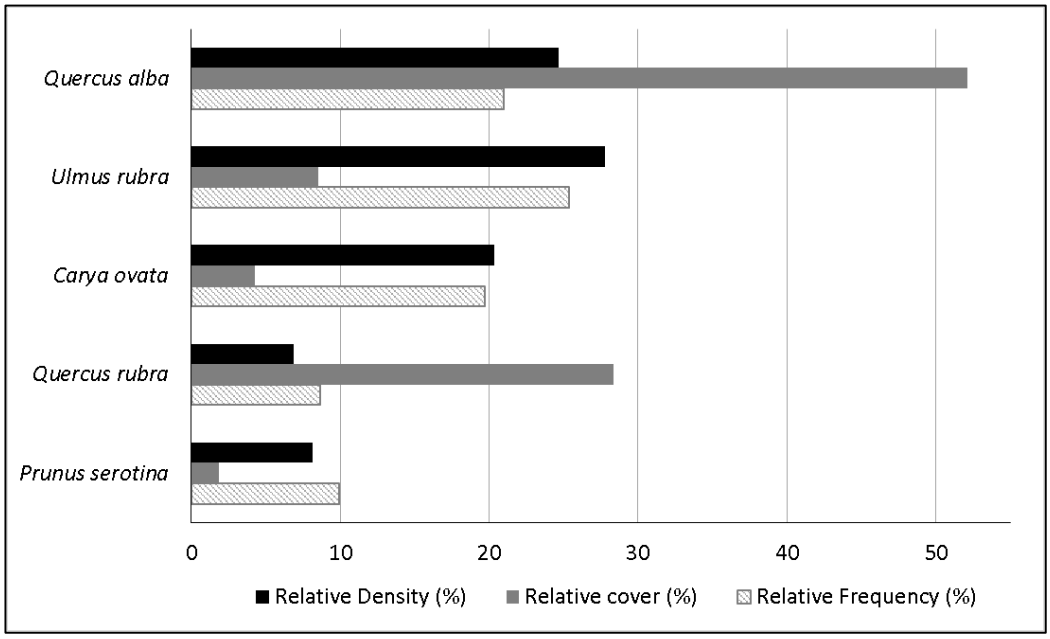

Figure 38. Relative species density (proportion of total stems/ha), cover (dominance; proportion of total basal area/ha), and frequency (distribution; proportion of PCQ points at which a given species is present) of the five tree species with the highest calculated importance value in the canopy layer of the eastern half of the oak savanna restoration study site at Nachusa Grasslands, IL, sorted based on importance value (top-high to bottom-low; calculation of importance value factors in all three relative stand structure variables).

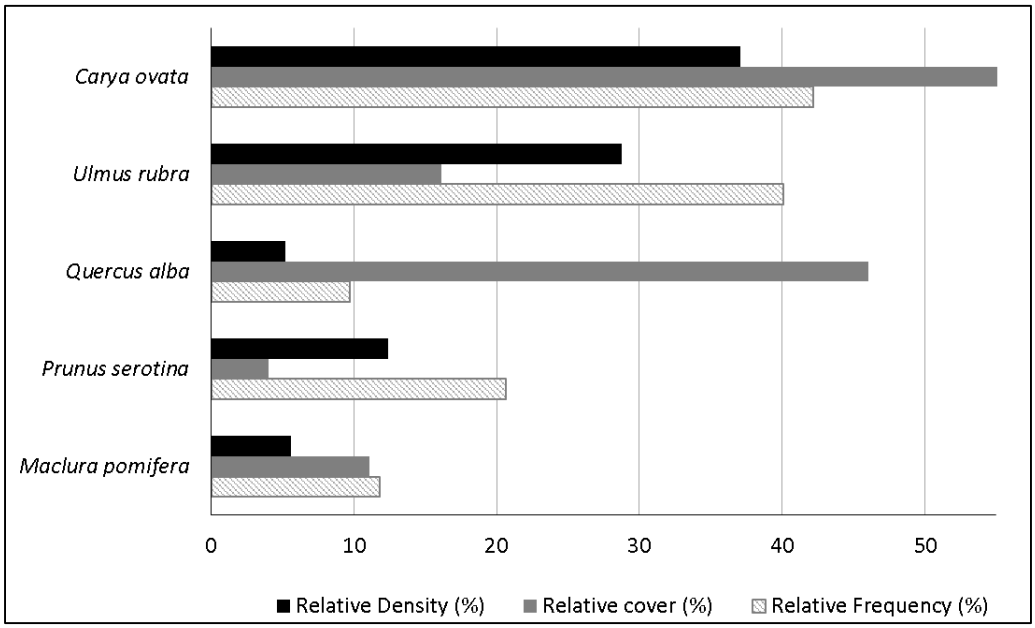

Figure 39. Relative species density (proportion of total stems/ha), cover (dominance; proportion of total basal area/ha), and frequency (distribution; proportion of PCQ points at which a given species is present) of the five tree species with the highest calculated importance value in the canopy layer of the western half of the oak savanna restoration study site at Nachusa Grasslands, IL, sorted based on importance value (top-high to bottom-low; calculation of importance value factors in all three relative stand structure variables).

5.3 UNDERSTORY STRUCTURE OF OAK SAVANNA RESTORATION STUDY SITE

Of the ten randomly selected plots (each 5 x 5 m; 25 m^2) used to survey the structure of the oak savanna restoration study site understory, none were empty. The total area sampled for this understory analysis was 0.025 ha. The density of Amur honeysuckle found in the oak savanna regeneration study site understory was 18,400 plants/ha, with an estimated average canopy cover of 51.8% ± 5.1% SE. Heights of the tallest branch (Figure 40) and the total number of branches (Figure 40) of each surveyed Amur honeysuckle shrub (n=1023) were recorded, in order to better understand the architecture of the Amur honeysuckle understory layer. Of the Amur honeysuckle surveyed, 54% of them were ≤1 m tall with an overall density of 10,000 stems/ha, while the other 46% of the Amur honeysuckle were >1 m tall with an overall density of 8,400 stems/ha. The mean height of Amur honeysuckle surveyed throughout the study site was 116.49 cm ± 1.59 cm SE (Figure 40), with an average of 5.97 stems/shrub ± 0.14 stems/shrub SE (Figure 41). The maximum Amur honeysuckle height recorded was 371 cm, while the minimum was 20 cm. Ultimately, the total number of Amur honeysuckle stems and the height of the tallest stem was not significantly correlated.

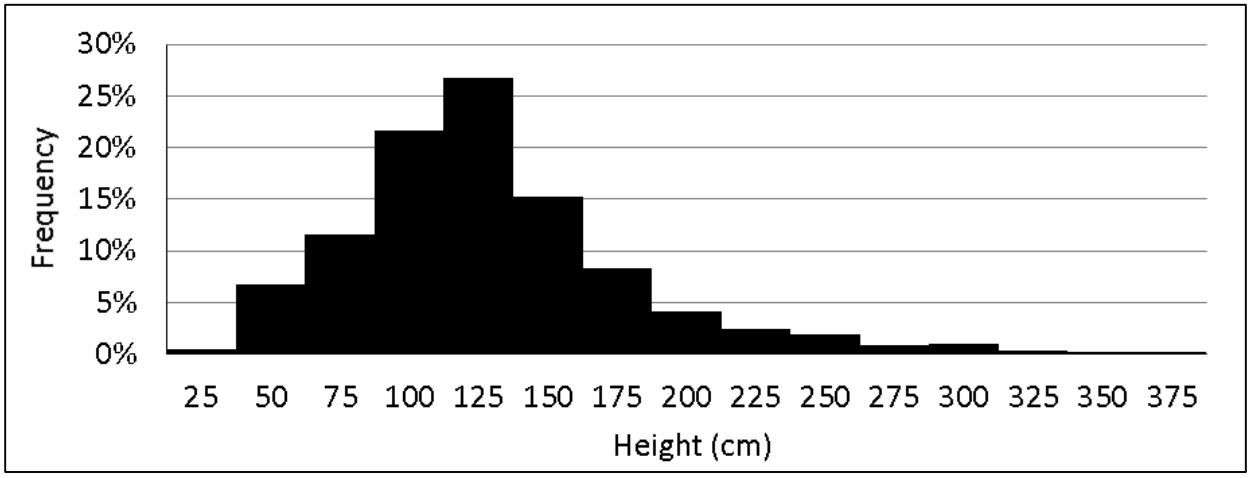

Figure 40. Histogram illustrating the distribution of Amur honeysuckle heights found throughout the oak savanna restoration study site at Nachusa Grasslands, IL Heights were taken on the tallest stem per individual surveyed.

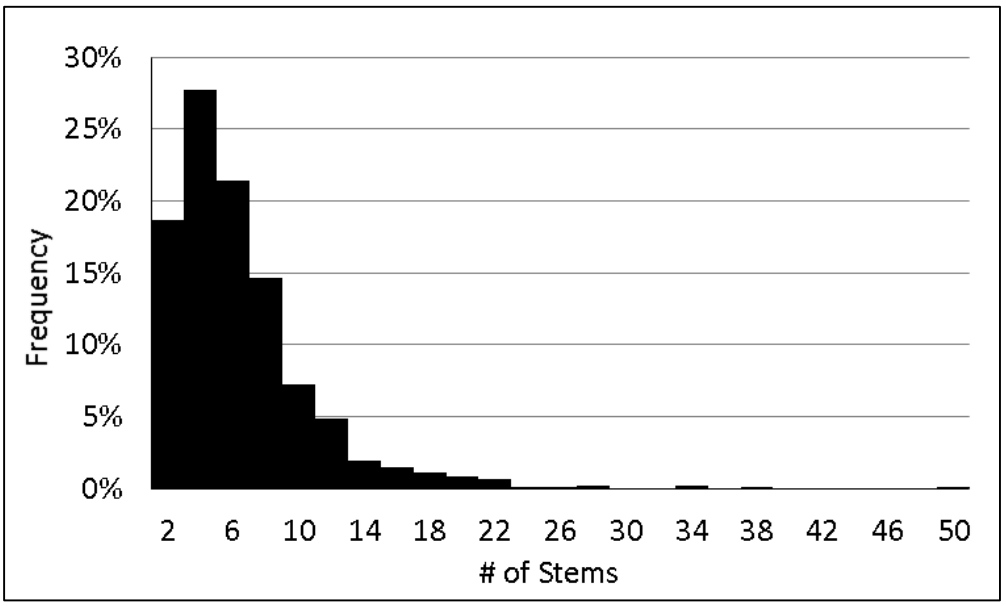

Figure 41. Histogram illustrating the distribution of the total number of Amur honeysuckle stems per shrub found throughout the oak savanna restoration study site at Nachusa Grasslands, IL.

The overall density of seedlings (≤30 cm) and saplings (>30 cm) within the study site was 21,680 stems/ha. Tree seedlings comprised 87% of the tree regeneration layer, with an overall density of 18,840 stems/ha, while saplings made up the remaining 13% of the tree regeneration layer, with an overall density of 2,840 stems/ha (Figure 42). *Ptelea trifoliata* (common hoptree or wafer ash) was the only tree species surveyed that had a higher density of saplings (320 stems/ ha; 57%) than seedlings (240 stems/ ha; 43%) (Figure 43). All other species found in the understory tree regeneration layer had more seedlings than saplings, including the three species that had only seedlings: *Tilia americana* (linden/basswood), *Quercus rubra* (red oak), and *Juniperus virginiana* (eastern redcedar) (Figure 43). Of all the tree seedlings and saplings, black cherry had the highest density (5920 stems/ ha, of which 95% were seedlings), followed by *Viburnum prunifolium* (blackhaw; 5400 stems/ ha, of which 94% were seedlings), and hickory species (4560 stems/ ha, of which 80% were seedlings) (Figure 42). Neither white oak seedlings nor saplings were found, although 35 were later located outside the plots, and used for recording leaf phenology and measuring photosynthetic efficiency for this study. The white oak seedlings used in this study ranged in height from 6.5 cm to 30 cm (i.e. the maximum height of seedlings defined in this study), with an average height of 14.1 ± 1.6 cm SE.

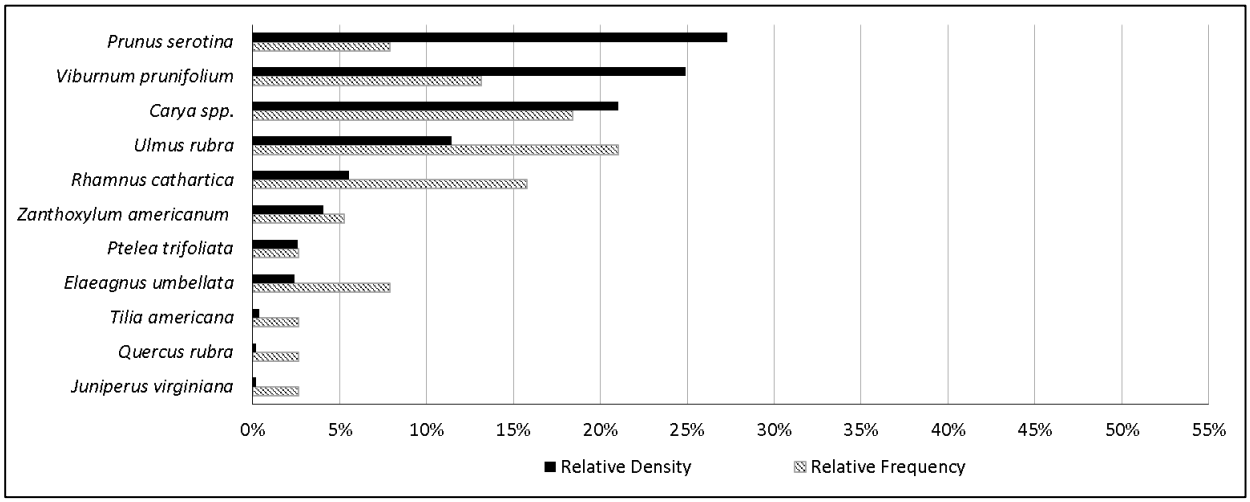

Figure 42. Relative species density (proportion of total stems/ha) and frequency (abundance; proportion of plots in which a given species is present) of the tree species observed in the understory layer (i.e. seedlings and saplings) of the oak savanna restoration study site at Nachusa Grasslands, IL, sorted based on density value (top-high to bottom-low).

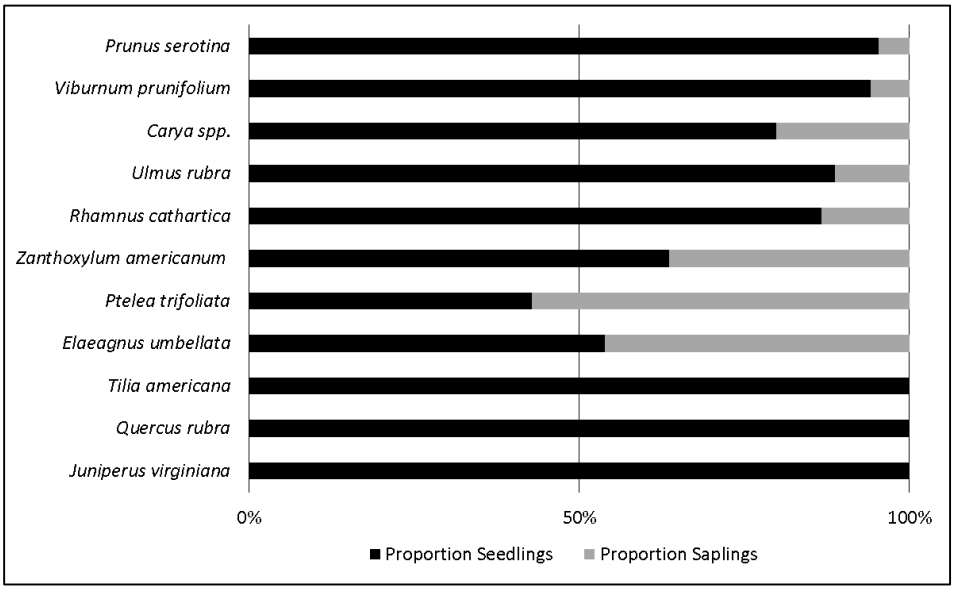

Figure 43. Proportion of seedlings and saplings comprising the overall density of each species surveyed in the understory regeneration layer in the oak savanna restoration study site at Nachusa Grasslands, IL. Black bars represent the proportion of seedlings, while the gray bars represent the proportion of saplings. Species sorted based on density (top-high to bottom-low).

5.4 CHARACTERIZATION OF LEAF PHENOLOGY IN THE STUDY SITE

As defined in the methods chapter, leaf phenology was recorded from 2011-2014 for spring leaf development and emergence (from dormancy to bud swell, bud break, leaves unfolding, until leaves fully opened), as well as for autumn leaf color transition and senescence for dominant trees (n=35), for white oak seedlings (n=10 to 20), and for Amur honeysuckle shrubs (n=13 to 30) growing in the oak savanna restoration study site (Appendix A). Dates associated with the recorded leaf phenology phases are reported in Day of Year, ranging from 1 to 365, with 1 representing January 1 and 365 representing December 31 (except in leap years when 366 represents December 31). The timeframe displayed on the leaf phenology figures in this section (i.e. 78 to 354 Day of Year) begins in mid-March (March 18 or 19, in a leap year and non-leap year, respectively) and ends in mid-December (December 19 or 20, in a leap year and non-leap year, respectively). The dominant trees species (n=7) for which both spring and autumn leaf phenology was recorded were representative of the tree species identified as having the seven highest importance values in the oak savanna restoration study site (i.e. *Quercus alba* (white oak; n=6), *Ulmus rubra* (slippery elm; n=2), *Carya ovata* (shagbark hickory; n=6), *Quercus rubra* (red oak; n=8), *Prunus serotina* (black cherry; n=5), *Celtis occidentalis* (hackberry; n=5), *Carya cordiformis* (bitternut hickory; n=3)). The active growth period was defined in this study as initiating with bud swell and ending when all leaves have fully senesced.

The time periods during which each leaf phenology stage occurred throughout the study varied from year to year and between species, as seen in the composite leaf

phenology timing diagram (Figure 44). Overall, the respective leaf phenology of *Prunus serotina* (black cherry) and *Ulmus rubra* (slippery elm) were the first to initiate each spring throughout all four years of the study (Figure 45). The initiation of bud swell, bud break, and the unfolding of leaves for black cherry often occurred within a few days of Amur honeysuckle, and once, one day before Amur honeysuckle in 2012, although statistically the bud swell, bud break, and leaves unfolding timing for all species surveyed in this study were not found to be significantly different than each other (Figure 45).

Black cherry and Amur honeysuckle had similar average leaf open periods (151 days ± 6 days SE and 164 days ± 6 days SE, respectively), which were found to be significantly longer than the average leaf open period for white oak seedlings surveyed in the oak savanna restoration study site (116 days ± 3 days SE), according to a nonparametric Kruskal-Wallis and nonparametric posthoc Tukey-like multiple comparisons test ($p<0.01$) (Figure 45). All other leaf open periods for the remaining species in this study were found to be statistically similar. Furthermore, the Amur honeysuckle color transition phenology phase, ending with leaf senescence (73 days ± 6 days SE), was found to be significantly longer than the same phenology phase for Slippery elm (35 ± 4 days SE), with all others being similar (Figure 45). In the end, when the leaf open to leaf senescence phenology periods were compared between all nine species across all four years of the study, Amur honeysuckle was found to have a significantly longer average leaf open to leaf senescence period (237± 6 days SE) than

shagbark hickory (159 ± 5 days SE), bitternut hickory (167 ± 3 days SE), and white oak trees (167 ± 5 days SE), respectively ($p<0.01$) (Figure 45).

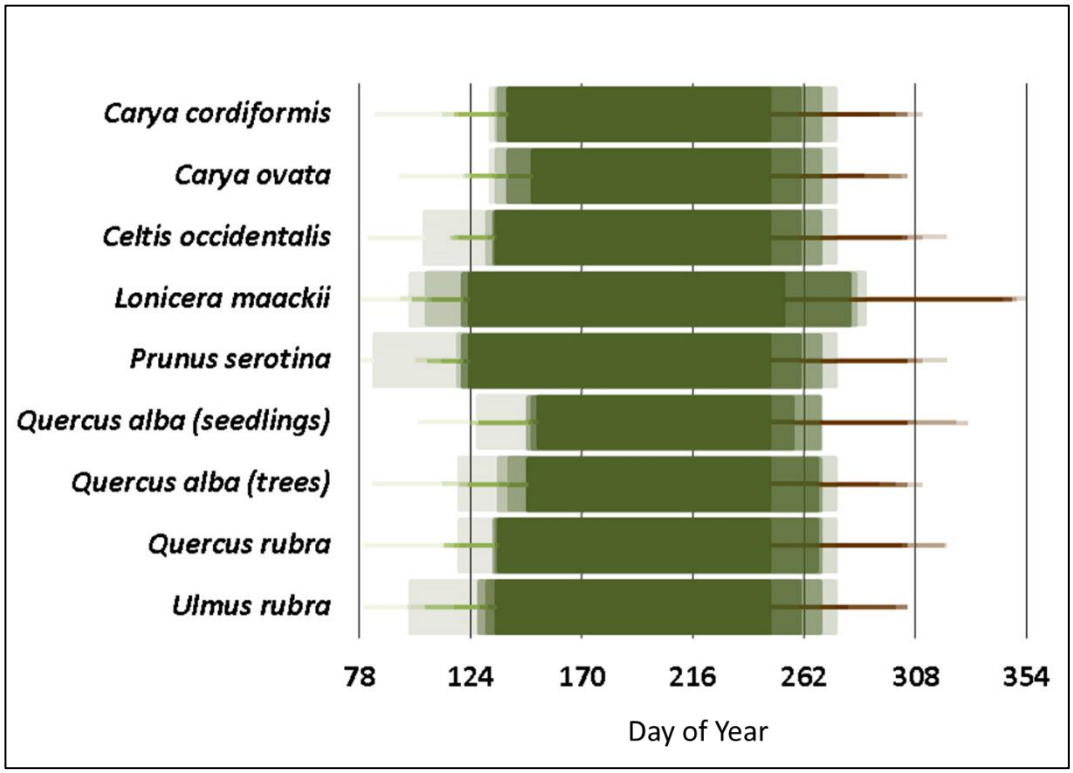

Figure 44. Composite figure depicting all leaf phenology timeframes for all four growing seasons. The first whisker (light green) represents the dates and timing associated with the leaf phenology stages: bud swell, bud break, and leaves unfolding. The box (dark green) represents the dates and timing associated with the fully open leaf phenology stage. The second whisker (brown) represents the dates and timing associated with the leaf phenology stages: leaves changing color and leaf senescence. *Species are listed in alphabetical order.*

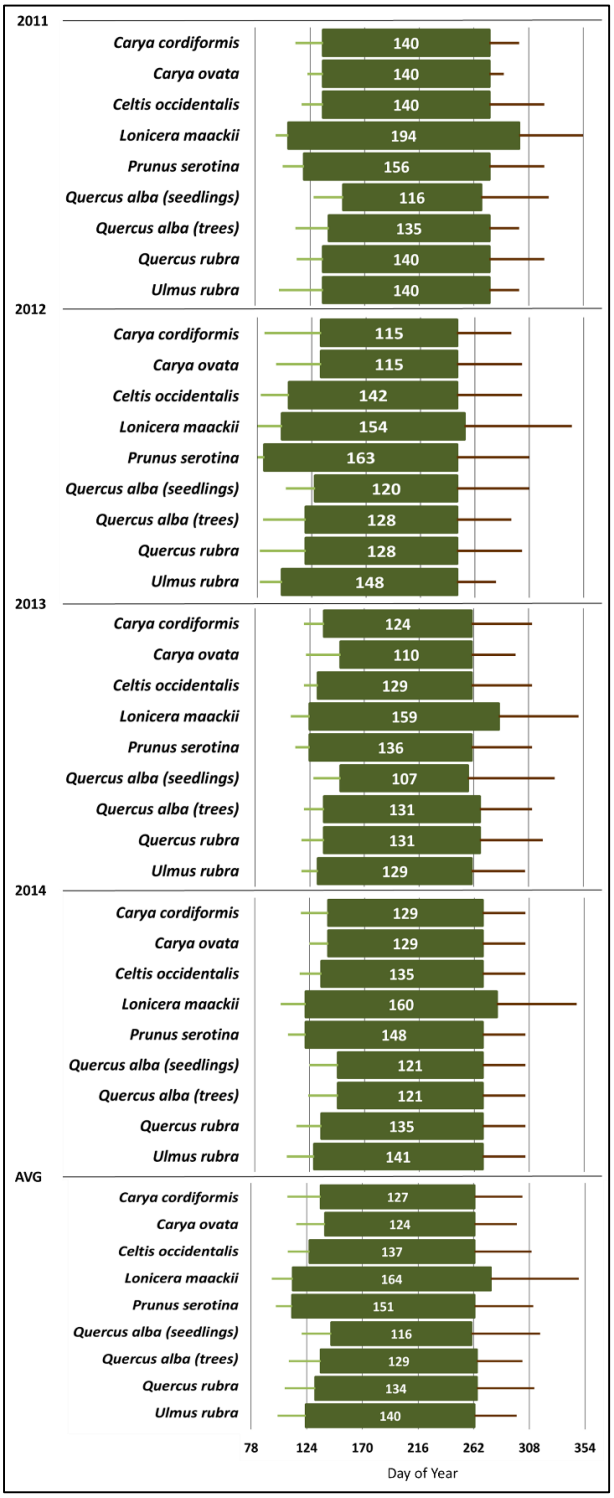

Figure 45. Leaf phenology of all species surveyed during the study period. The first whisker (light green) represents the dates and timing associated with the leaf phenology stages: bud swell, bud break, and leaves unfolding. The box (dark green) represents the dates and timing associated with the fully open leaf phenology stage. The numbers listed in the boxes indicate length of fully open phenology stage in days. The second whisker (brown) represents the dates and timing associated with the leaf phenology stages: leaves changing color and leaf senescence. Species are listed in alphabetical order.

For the purpose of this study, only the leaf phenology of the white oak trees, white oak seedlings, and Amur honeysuckle will be discussed in detail from here on, as these were the study species. Annual active photosynthetic periods were delineated for this study so as to capture the leaf open to leaf senescence phenology phases of only the white oak seedlings and Amur honeysuckle in the study site, as these were the only species for which carbon assimilation was calculated. The photosynthetically active period for this study began April 8 (Day of Year 98) and ended December 20 (Day of Year 354), so as to encompass only the timeframe during which the leaves of the white oak seedlings and Amur honeysuckle in the study site were fully open, and therefore the most photosynthetically active.

In general, the active growth period of Amur honeysuckle averaged 254 days ± 5 days SE, which was 57 days longer than the average white oak seedling active growth period (197 days ± 6 days SE) and 61 days longer than mature white oak trees average active growth period (193 days ± 6 days SE). Amur honeysuckle had the longest total active growth period in 2012 (266 days), along with white oak seedlings (206 days), and white oak trees (210 days). The shortest active growth period for Amur honeysuckle occurred in 2013 (242 days), while the shortest active growth period for both white oak seedlings (181 days) and white oak trees (182) occurred in 2014. The timeframe during which the leaves of Amur honeysuckle were fully open averaged 164 days ± 6 days SE, which was 48 more days than the average timeframe during which the leaves of white oak seedlings were fully open (116 days ± 3 days SE) and 35 more days than the average timeframe during which the leaves of mature white oak trees were fully open

(129 days ± 3 days SE). The longest span of time during which Amur honeysuckle leaves were fully open occurred in 2011 (181 days), while the longest timeframe during which white oak leaves were fully open occurred in 2014 (121 days) for seedlings and in 2011 (135 days) for mature trees. The shortest period of time during which leaves were fully open, on the other hand, occurred in 2012 (148 days) for Amur honeysuckle, in 2013 (107 days) for white oak seedlings, and in 2014 (121 days) for white oak trees.

Amur honeysuckle leaves were the first to unfold in all years, followed by white oak trees, and then white oak seedlings (Figure 46). Mature white oak leaves were the first to senesce in all years except 2014, when leaf senescence for white oak trees and white oak seedlings occurred on average at the same time (Figure 46). In all years, Amur honeysuckle leaves were the last to senesce, sometime in mid to late December (Figure 46). The active growth period (initiated by observation of the bud swell leaf phenology stage) for Amur honeysuckle within the oak savanna restoration study site began on average around Day of Year 95 ± 6 days SE, 14 days before the average initiation of bud swell among the white oak trees (Day of Year 109 ± 9 days SE) and 25 days before the average initiation of bud swell among the white oak seedlings (Day of Year 120 ± 6 days SE) (Figure 46). On average, Amur honeysuckle leaves were fully open by Day of Year 113 ± 6 days SE, which was 23 days before the leaves of the mature white oak trees were on average fully opened (Day of Year 136 ± 6 days SE) and 31 days before the leaves of white oak seedlings were on average fully opening (Day of Year 144 ± 6 days SE) (Figure 46). On average, white oak seedlings were the first to change color on Day of Year 260 ± 5 days SE, followed closely by the leaves of

mature white oak trees on Day of Year 265 ± 6 days SE (Figure 46). The mature white oak trees were on average fully senesced by Day of Year 302 ± 4 days SE, while the white oak seedlings on average were fully senesced by Day of Year 317 ± 6 days SE (Figure 46). Amur honeysuckle leaves began to color change color on average around Day of Year 279 ± 10 days SE and didn't fully senesce on average until Day of Year 349 ± 2 days SE (Figure 46).

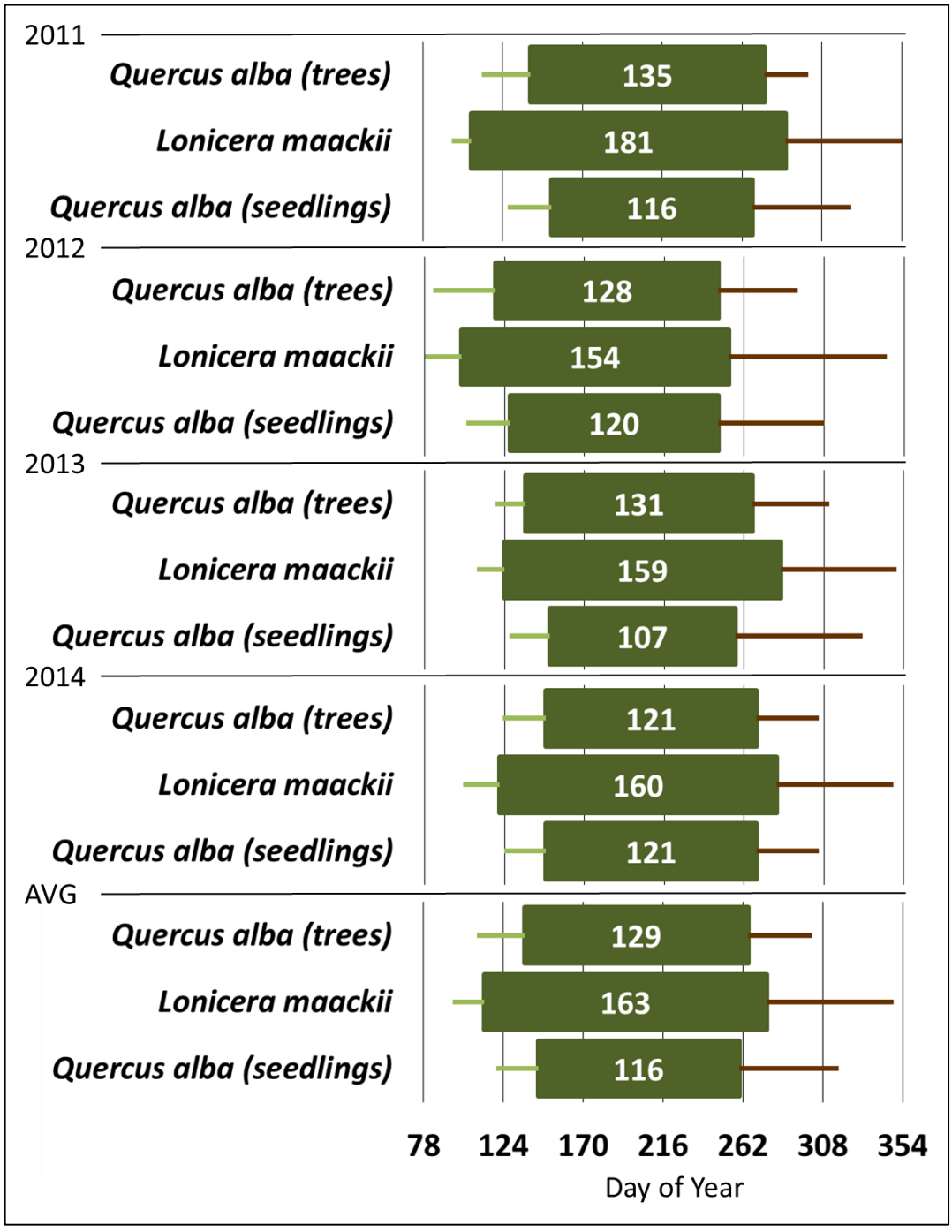

Figure 46. Annual and overall average leaf phenology of white oak trees, Amur honeysuckle, and white oak seedlings surveyed during the study period. *The first whisker (light green) represents the dates and timing associated with the leaf phenology stages: bud swell, bud break, and leaves unfolding. The box (dark green) represents the dates and timing associated with the fully open leaf phenology stage. The numbers listed in the boxes indicate length of fully open phenology stage in days. The second whisker (brown) represents the dates and timing associated with the leaf phenology stages: leaves changing color and leaf senescence. Species are listed in order of presence within the study site canopy structure, with mature white oak trees occurring in the upper tree canopy, Amur honeysuckle occurring in the understory mid-canopy, and white oak seedlings occurring in the understory canopy below both.*

5.5 CHARACTERIZATION OF UNDERSTORY LIGHT IN THE STUDY SITE

The time of day at which light was detected in the morning and ended in the evening remained relatively consistent between each light scenario, defined in the methods chapter as: 1) Full Sun - an open, full-sun light environment with no overstory tree canopy; 2) Amur honeysuckle (HS) light - the Amur honeysuckle understory light environment in the study site at one meter; 3) no HS encroachment - the white oak seedlings understory light environment in the study site at 30 cm without Amur honeysuckle encroachment (i.e. no Amur honeysuckle shrub within three meters of the light sensor); and 4) HS encroachment - the white oak seedlings understory light environment in the study site at 30 cm with Amur honeysuckle encroachment (Figure 15). In the full sun light scenario, the timeframe in which first light (PPFD >0) was detected ranged between 5:30 am to 8:30 am, with an ending timeframe ranging between 5:30 pm to 9 pm, with total daylight hours peaking in June (15.37 hours) (Figure 47a). At one meter above ground level (representative of the light received by Amur honeysuckle) in the oak regeneration study site, first light was detected between 5 am to 8 am, with an ending timeframe ranging between 5 pm to 8:30 pm, with total daylight hours peaking in May (14.73 hours) (Figure 47b). At 30 cm above ground level (representative of the light received by white oak seedlings) in the oak regeneration study site without Amur honeysuckle encroachment, first light was detected between 5:30 am to 8 am, with an ending timeframe ranging between 5 pm to 8:30 pm, with total daylight hours peaking in May (14.02 hours) (Figure 47c). Lastly, at 30 cm above ground level in the oak regeneration study site with Amur honeysuckle encroachment,

first light was detected between 5 am to 9:30 am, with an ending timeframe ranging between 5:30 pm to 8:30 pm, with total daylight hours peaking once again in May (13.37 hours) (Figure 47d). Overall, the full sun light scenario received a total of 129.84 daylight hours, while the one meter light scenario received 126.80 hours, the 30 cm without Amur honeysuckle encroachment scenario received 123.73 hours, and the 30 cm with Amur honeysuckle encroachment light scenario received the fewest daylight hours (119.43 hours). According to a nonparametric Kruskal-Wallis test, no statistical differences in monthly daylight hours were found between light scenarios.

As expected, the open, full sun scenario had the highest total seasonal light, or photosynthetically active radiation (PAR) (95651.2 mol/m^2/active growth period) (Table 6, Figure 48), with an average midday light level of 1138.3 ± 30.1 mol/m^2/leaf open to leaf senescence phenology phase. Of the three light scenarios measured *in situ* below the study site oak savanna restoration canopy, the next highest total seasonal light was recorded at one meter above the Amur honeysuckle canopy (17263.2 mol/m^2/active growth period; 18% of full sun scenario), followed by the total seasonal light measured at 30 cm with no Amur honeysuckle encroachment (13463.0 mol/m^2/active growth period; 14% of full sun scenario) and at 30 cm with Amur honeysuckle encroachment (10133.2 mol/m^2/active growth period; 11% of full sun scenario), respectively (Table 6, Figure 48). The average midday light level from leaf open to leaf senescence phenology phases for the one meter understory light scenario was 98.8 ± 3.2 mol/m^2/ phenology phase, while the midday average for the same phenology period in the understory light

scenario with and without Amur honeysuckle encroachment was 65.0 ± 2.8 mol/m^2/ phenology phase and 28.4 ± 2.1 mol/m^2/phenology phase, respectively.

In the full sun scenario, the total monthly light levels rose steadily, reached a peak in July (16053.4 mol/m^2), and then steadily decreased thereafter (Table 6, Figure 48). In all three oak savanna restoration understory light scenarios, April had the highest light levels (Table 6, Figure 48). Total seasonal light levels were found to be statistically different from one another according to a nonparametric Kruskal-Wallis test ($p<0.001$). According to a nonparametric Tukey-type multiple comparison post-hoc test, the full sun light level was determined to be different than the three other light levels (i.e. HS light, no HS encroachment, HS encroachment), which were in turn similar to one another (Figure 49).

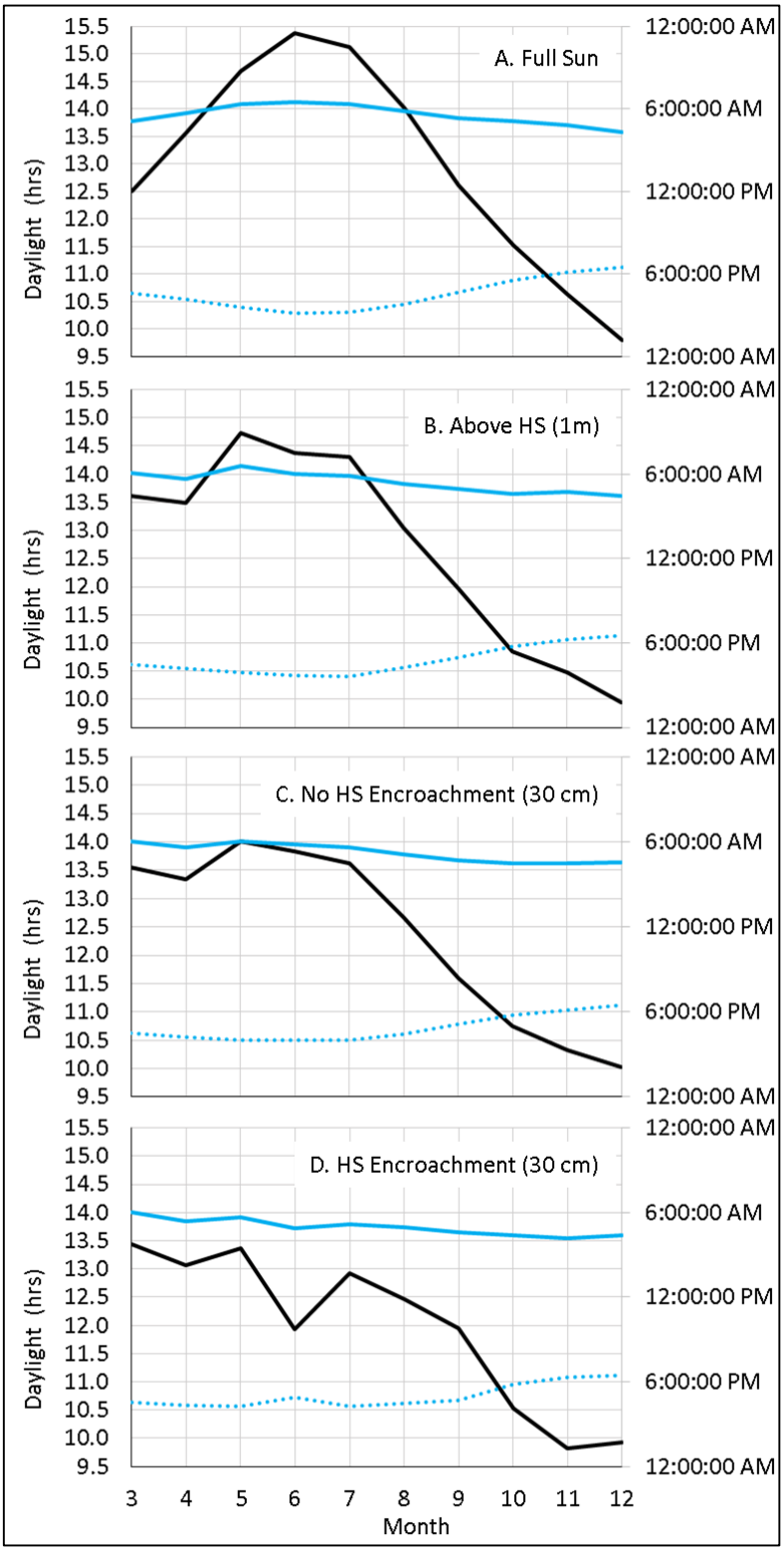

Figure 47. Total monthly hours of daylight received in each light scenario (black solid line), along with the average monthly beginning (blue solid line) and ending daylight (blue dotted line) timeframes in each light scenario measured at Nachusa Grasslands, IL

Table 6. Table listing total monthly and total seasonal light levels (mol/m²) for the four light scenarios in this study. All light scenarios, except full sun, were measured in situ within the understory of the oak savanna restoration study site. HS stands for Amur honeysuckle. The heights provided indicate the height above the ground at which the light was measured. Average light based on four years of collected light data. Standard error are reported for all overall averages.

Month	Full Sun	Above HS (1m)	No HS Encroachment (30 cm)	HS Encroachment (30 cm)
March	3130.6	1524.5	1265.7	1528.3
April	10810.5	5123.0	4437.3	4098.0
May	14225.0	3813.7	2564.8	1984.4
June	15052.9	1035.4	651.9	196.6
July	16053.4	1096.6	725.9	242.4
August	13662.9	1198.0	782.9	216.5
September	9681.9	761.7	543.2	224.3
October	6158.5	773.2	701.8	399.8
November	4728.0	1303.1	1183.3	763.0
December	2147.4	634.0	606.1	480.1
Total Seasonal Light	**95651.2 ± 1645.6**	**17263.2 ± 474.9**	**13463.0 ± 392.5**	**10133.2 ± 393.9**

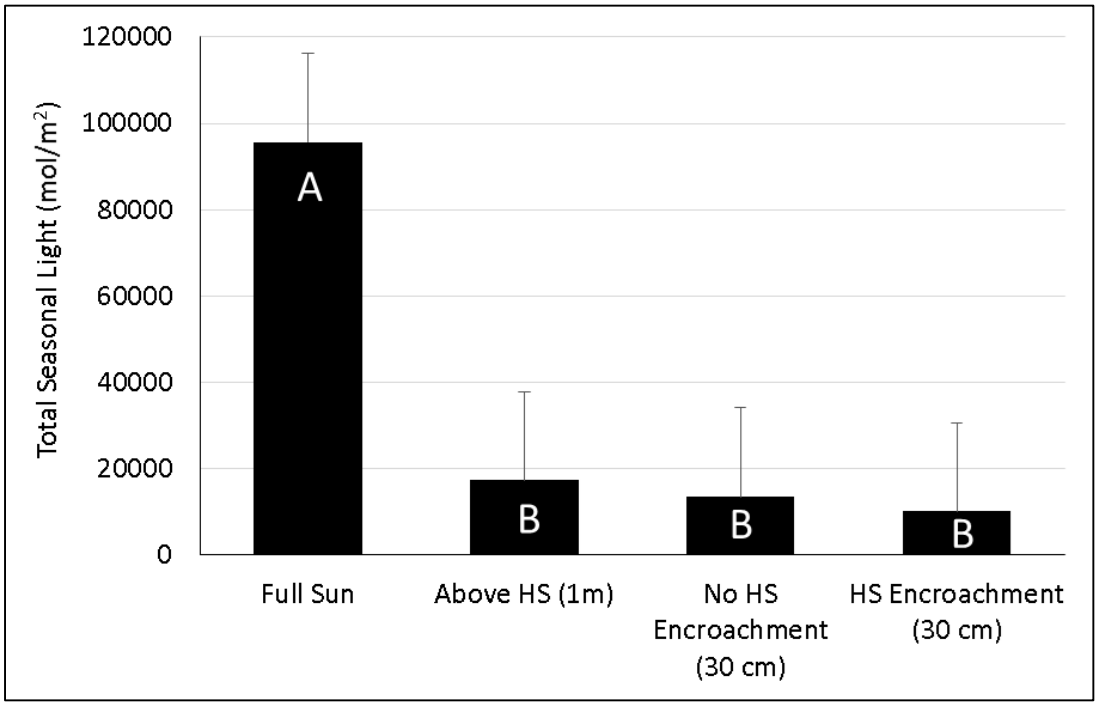

Figure 48. Total average seasonal light levels with standard error bars (95% confidence interval) for each light scenario measured at Nachusa Grasslands, IL. Light levels found to be statistically different according to a nonparametric Kruskal-Wallis test (P<0.001); letters denote statistical differences according to Tukey-type multiple comparisons post-hoc test. Average light levels based on four years of collected light data.

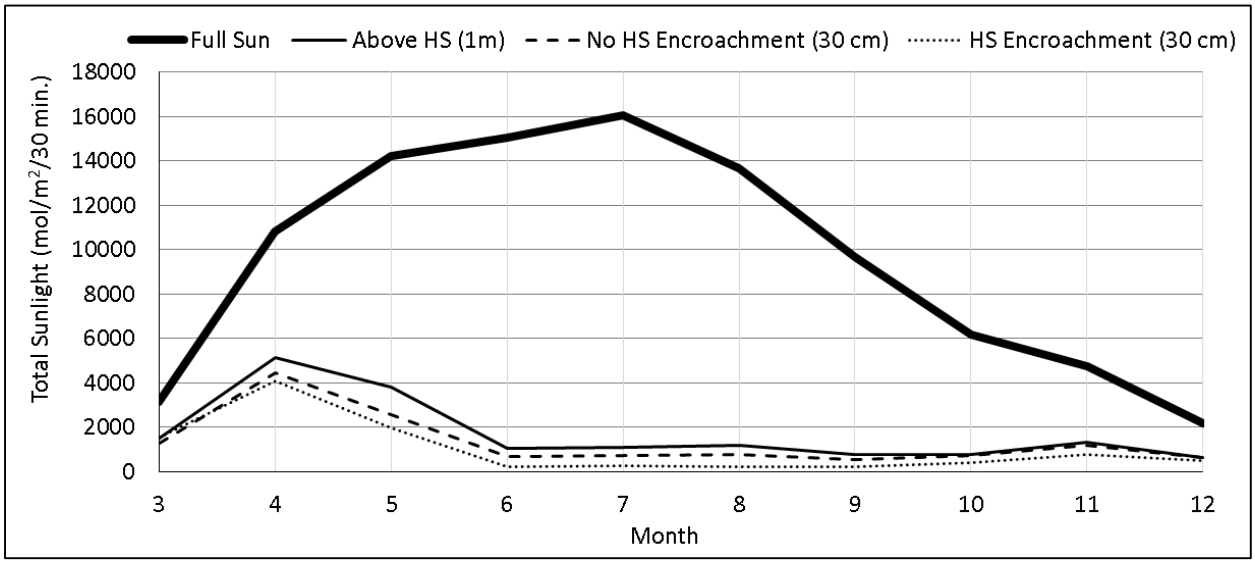

Figure 49. Total average monthly light levels measured in the full sun scenario near the Nachusa Grasslands headquarters, as well as for the three light scenarios measured in the oak savanna restoration study site beginning on March 23 and ending on December 20. Average light levels based on four years of collected light data.

5.6 PHOTOSYNTHETIC VARIABLES AND LIGHT CURVES

The overall average maximum assimilation rate (A_{max}) for Amur honeysuckle surveyed in the study site (n=39) was 5.981 ± 1.258 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, with the photosynthetically strongest (i.e. highest annual light curve) Amur honeysuckle shrubs (n=4) averaging 9.049 ± 0.994 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ and the photosynthetically weakest (i.e. lowest annual light curve) Amur honeysuckle shrubs (n=4) averaging 3.337 ± 1.122 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Table 7; Figure 50). The overall average light compensation point (LCP; light level at which photosynthesis = respiration) for Amur honeysuckle surveyed in the study site was 7.895 ± 1.928 SE µmol $\cdot m^{-2} \cdot s^{-1}$, while the overall average light saturation point (LSP; light level at which 90% of A_{max} is reached) was 218.844 ± 71.162 SE µmol $\cdot m^{-2} \cdot s^{-1}$ (Table 7; Figure 50). Furthermore, the overall average dark respiration rate (R_d; plant respiration at night) for Amur honeysuckle was -0.779 ± 0.301 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, and the average quantum yield efficiency (*Q*) of Amur honeysuckle

photosystems was 0.119 ± 0.054 SE µmol CO_2/PPFD (Table 7; Figure 50). When the annual average light curve variables (i.e. R_d, A_{max}, LCP, *Q*, and LSP) of Amur honeysuckle shrubs were compared across all years of the study (2011-2014) using the nonparametric Kruskal-Wallis test, significant differences were found for all variables (R_d: $p<0.01$, LCP: $p<0.01$, *Q*: $p<0.01$, and LSP: $p<0.001$, A_{max}: $p<0.001$) (Table 7). More specifically, according to the nonparametric Tukey-type multiple comparisons post-hoc test, R_d was found to be highest in 2011 and 2012 and lowest in 2013; LCP was found to be highest in 2011and lowest in 2013; *Q* was found to be highest in 2012 and lowest in 2011 and 2013; LSP was found to be highest in 2011 and 2014 and lowest in 2012; and A_{max} was found to be highest in 2011 and 2014 and lowest in 2012 (Table 7). Furthermore, when the light curve variables of photosynthetically weak and strong Amur honeysuckle shrubs were compared, only the LSP was found to be significantly higher ($p<0.05$) for photosynthetically strong Amur honeysuckle (Table 7).

The overall A_{max} for white oak seedlings surveyed in the study site (n=35) was 5.321 ± 0.600 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, with the photosynthetically strongest white oak seedlings (n=4) averaging 7.074 ± 0.775 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ and photosynthetically weak white oak seedlings (n=4) averaging 3.282 ± 0.754 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Table 8; Figure 51). The overall average LCP for white oak seedlings surveyed in the study site was 9.450 ± 1.184 SE µmol$\cdot m^{-2} \cdot s^{-1}$, while the overall average LSP for white oak seedlings surveyed in the study site was 206.974 ± 45.543 SE µmol$\cdot m^{-2} \cdot s^{-1}$ (Table 8; Figure 51). Furthermore, the overall average R_d for white oak seedlings was -0.724 ± 0.147 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, and the average *Q* of white oak seedlings photosystems

was 0.085 ± 0.022 SE µmol CO_2/PPFD (Table 8; Figure 51). When the annual average light curve variables (i.e. R_d, A_{max}, LCP, *Q*, and LSP) of white oak seedlings surveyed were compared across all years of the study (2011-2014) using the nonparametric Kruskal-Wallis test, a significant differences was only found for A_{max} ($p<0.01$), while all other variables (i.e. R_d, LCP, *Q*, and LSP) were found to be statistically similar (Table 8). More specifically, according to the nonparametric Tukey-type multiple comparisons post-hoc test, A_{max} was found to be highest in 2011 and 2014 and lowest in 2012 (Table 8). Furthermore, when the light curve variables of photosynthetically weak and strong white oak seedlings were compared, only the A_{max} was found to be significantly higher ($p<0.05$) for photosynthetically strong white oak seedlings (Table 8).

The overall A_{max} for white oak seedlings surveyed in the study site that survived until the end of the study period (n=19; referred to hereon as alive or surviving) was 5.662 ± 0.326 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, while the overall A_{max} for white oak seedlings surveyed in the study site that died before the end of the study period (n=7; referred to hereon as dead) was 3.963 ± 0.421 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Table 9; Figure 52). The overall average LCP for the surviving white oak seedlings surveyed in the study site was 9.350 ± 1.169 SE µmol$\cdot m^{-2} \cdot s^{-1}$, while the overall average LSP for the dead white oak seedlings surveyed in the study site was 24.050 ± 9.074 SE µmol$\cdot m^{-2} \cdot s^{-1}$ (Table 9; Figure 52). The overall average R_d for the surviving white oak seedlings was -0.724 ± 0.147 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, while the overall average R_d for the dead white oak seedlings was -1.111 ± 0.331 SE µmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ (Table 9; Figure 52). Furthermore, the overall average Q of the surviving white oak seedlings photosystems was 0.078 ±

0.017 SE µmol CO_2/PPFD, while the overall average Q of the dead white oak seedlings photosystems was 0.105 ± 0.056 SE µmol CO_2/PPFD (Table 9; Figure 52). When the annual average light curve variables (i.e. R_d, A_{max}, LCP, *Q*, and LSP) of white oak seedlings that survived until the end of the study period were compared to the light curve variables of white oak seedlings that died by the end of the study period using the nonparametric Mann-Whitney U test, a significant differences was only found for A_{max} ($p<0.01$), while all other variables (i.e. R_d, LCP, *Q*, and LSP) were found to be statistically similar (Table 9). More specifically, A_{max} was found to be highest in the white oak seedlings that survived until the end of the study period when compared to the white oak seedlings that died before the end of the study period (Figure 9).

Table 7. Table listing the average light curve variables for the photosynthetically (a) strong, (b) average, and (c) weak *Lonicera maackii* shrubs throughout all four growing seasons (2011-2014) of the study at Nachusa Grasslands, IL. Boxes denote statistical difference ($p<0.05$) between light curve variables of photosynthetically weak and strong Amur honeysuckle, while the asterisks denote average light curve variables that differ statistically from year to year. Standard errors are reported for overall averages.

(a) Variables	Years				
	2011 STG (n=1)	2012 STG (n=1)	2013 STG (n=1)	2014 STG (n=1)	AVG STG (n=4)
Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-0.518	-0.518	-0.185	-0.607	-0.457 ± 0.093
Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	8.498	6.224	3.543	9.074	6.835 ± 1.258
Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.062	0.086	0.053	0.069	0.068 ± 0.007
Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	427.150	206.448	347.212	386.547	341.839 ± 47.990
Max. Assimilation Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	10.833	6.986	7.709	10.667	9.049 ± 0.994

(b) Variables	Years				
	2011 AVG (n=11)	2012 AVG (n=8)	2013 AVG (n=9)	2014 AVG (n=14)	Overall AVG (n=39)
*Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-0.746 ± 0.096	-1.631 ± 0.418	-0.252 ± 0.078	-0.488 ± 0.060	-0.779 ± 0.301
*Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	14.310 ± 1.929	9.867 ± 1.462	4.777 ± 1.284	8.453 ± 1.463	9.352 ± 1.970
*Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.056 ± 0.003	0.263 ± 0.093	0.051 ± 0.004	0.063 ± 0.002	0.108± 0.052
*Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	396.121 ± 41.798	106.011 ± 29.247	211.983 ± 42.872	331.979 ± 22.986	261.523± 64.368
*Max. Assimilation Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	8.135 ± 0.673	3.264 ± 0.702	4.414 ± 1.063	8.109 ± 0.399	5.981 ± 1.258

(c) Variables	Years				
	2011 WK (n=1)	2012 WK (n=1)	2013 WK (n=1)	2014 WK (n=1)	AVG WK (n=4)
Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-0.510	-2.188	-0.182	-0.241	-0.780 ± 0.474
Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	11.133	9.843	3.506	3.544	7.006 ± 2.027
Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.048	0.351	0.055	0.069	0.131 ± 0.074
Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	258.723	32.551	78.265	203.769	143.327 ± 52.816
Max. Assimilation Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	4.674	1.277	1.599	5.796	3.337 ± 1.122

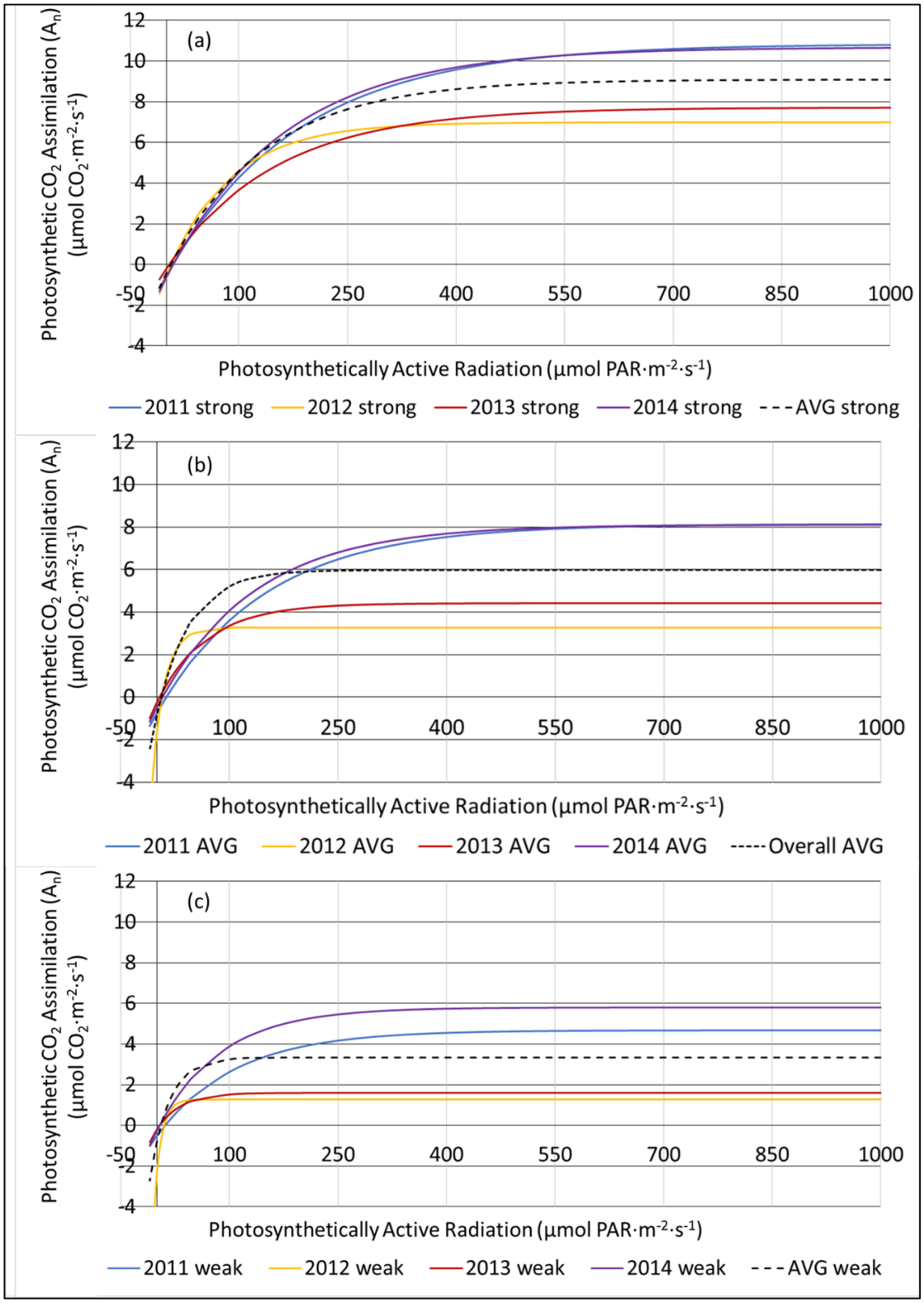

Figure 50. Average light curves for the photosynthetically (a) strong, (b) average, and (c) weak *Lonicera maackii* shrubs throughout all four growing seasons (2011-2014) of the study at Nachusa Grasslands, IL.

Table 8. Table listing the average light curve variables for the photosynthetically (a) strong, (b) average, and (c) weak *Quercus alba* seedlings throughout all four growing seasons (2011-2014) of the study at Nachusa Grasslands, IL. Boxes denote statistical difference ($p<0.05$) between light curve variables of photosynthetically weak and strong Amur honeysuckle, while the asterisks denote average light curve variables that differ statistically from year to year. Standard errors are reported for all overall averages.

(a) Variables	Years				
	2011 STG (n=1)	2012 STG (n=1)	2013 STG (n=1)	2014 STG (n=1)	AVG STG (n=4)
Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-0.185	-1.993	-0.940	-0.405	-0.881 ± 0.403
Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	4.148	5.367	16.198	6.724	8.110 ± 2.747
Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.045	0.439	0.062	0.062	0.152 ± 0.096
Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	438.598	41.345	319.170	317.885	279.250 ± 84.201
Max. Assimilation Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	8.327	4.862	7.175	7.932	7.074 ± 0.775

(b) Variables	Years				
	2011 AVG (n=7)	2012 AVG (n=7)	2013 AVG (n=7)	2014 AVG (n=14)	Overall AVG (n=35)
Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-0.372 ± 0.142	-1.080 ± 0.345	-0.794 ± 0.230	-0.651 ± 0.097	-0.724 ± 0.147
Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	6.853 ± 1.927	23.287 ± 9.361	13.126 ± 2.555	10.389 ± 1.394	13.414 ± 3.533
Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.051 ± 0.005	0.150 ± 0.067	0.062 ± 0.009	0.065 ± 0.003	0.082 ± 0.023
Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	330.259 ± 40.604	237.188 ± 77.254	240.036 ± 32.315	259.028 ± 15.125	266.628 ± 21.757
*Max. Assimilation Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	6.352 ± 0.554	3.734 ± 0.344	5.058 ± 0.668	6.140 ± 0.270	5.321 ± 0.600

(c) Variables	Years				
	2011 WK (n=1)	2012 WK (n=1)	2013 WK (n=1)	2014 WK (n=1)	AVG WK (n=4)
Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-1.183	-0.378	-0.342	-1.063	-0.741 ± 0.222
Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	16.474	4.889	9.579	13.690	11.158 ± 2.524
Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.080	0.083	0.039	0.086	0.072 ± 0.011
Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	179.778	81.641	124.708	165.176	137.826 ± 22.054
Max. Assimilation Rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	4.524	2.391	1.621	4.594	3.282 ± 0.754

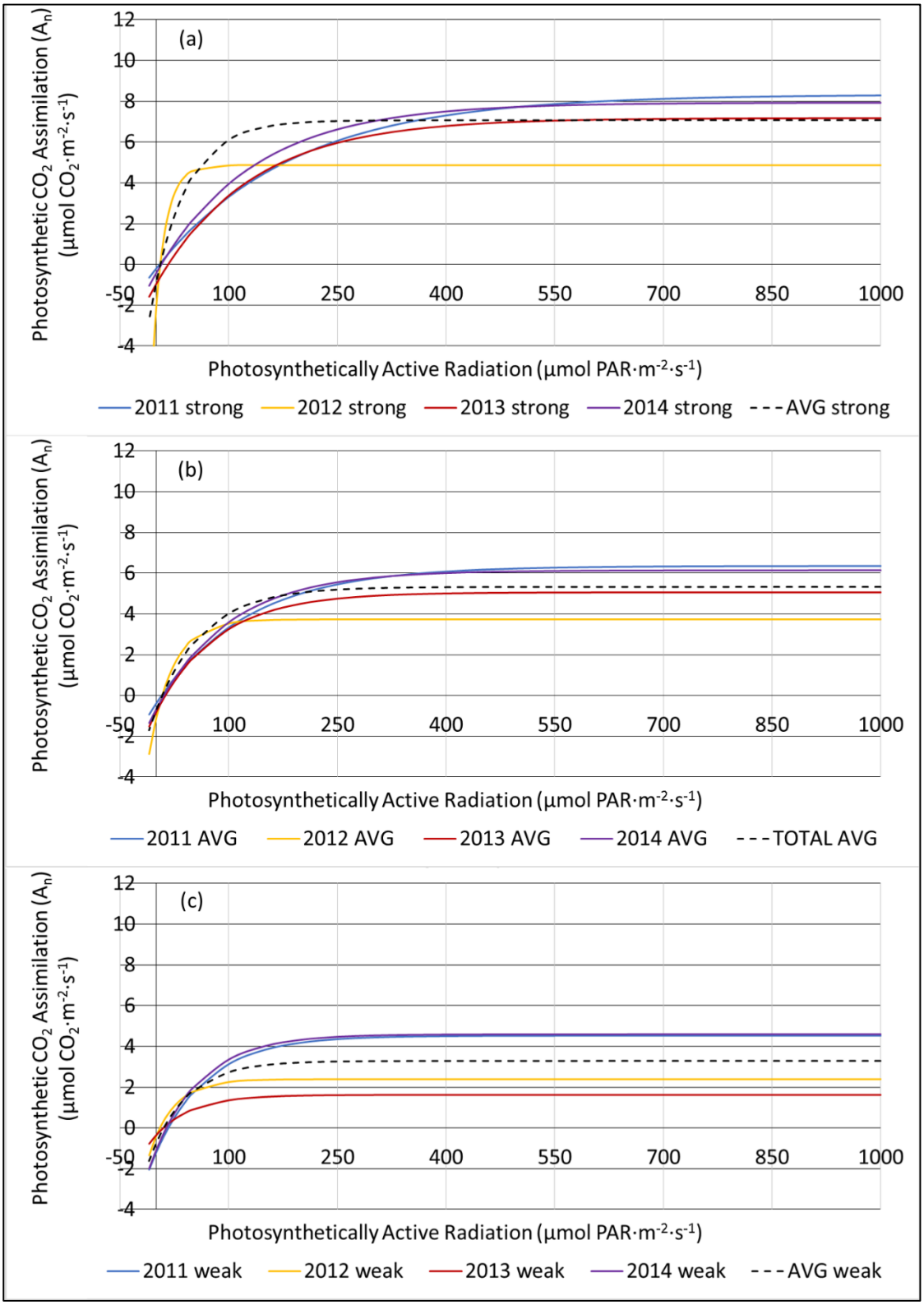

Figure 51. Average light curves for the photosynthetically (a) strong, (b) average, and (c) weak *Quercus alba* seedlings throughout all four growing seasons (2011-2014) of the study at Nachusa Grasslands, IL

Table 9. Table listing the average light curve variables for the *Quercus alba* seedlings that survived until the end of the study (AVG ALIVE) and the *Quercus alba* seedlings that died before the end of the study period (AVG DEAD) at Nachusa Grasslands, IL. Asterisks denote statistical differences ($p<0.05$).

Variables	Years	
	AVG ALIVE (n=19)	AVG DEAD (n=7)
Dark Respiration ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	-0.565 ± 0.080	-1.111 ± 0.331
Light Compensation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	9.350 ± 1.169	24.050 ± 9.074
Quantum Use Efficiency ($(\mu mol\ CO_2) \cdot (\mu mol\ PAR)^{-1}$)	0.078 ± 0.017	0.105 ± 0.056
Light Saturation Point ($\mu mol\ PAR \cdot m^{-2} \cdot s^{-1}$)	237.167 ± 17.672	270.679 ± 68.637
* **Max. Assimilation Rate** ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$)	5.662 ± 0.326	3.963 ± 0.421

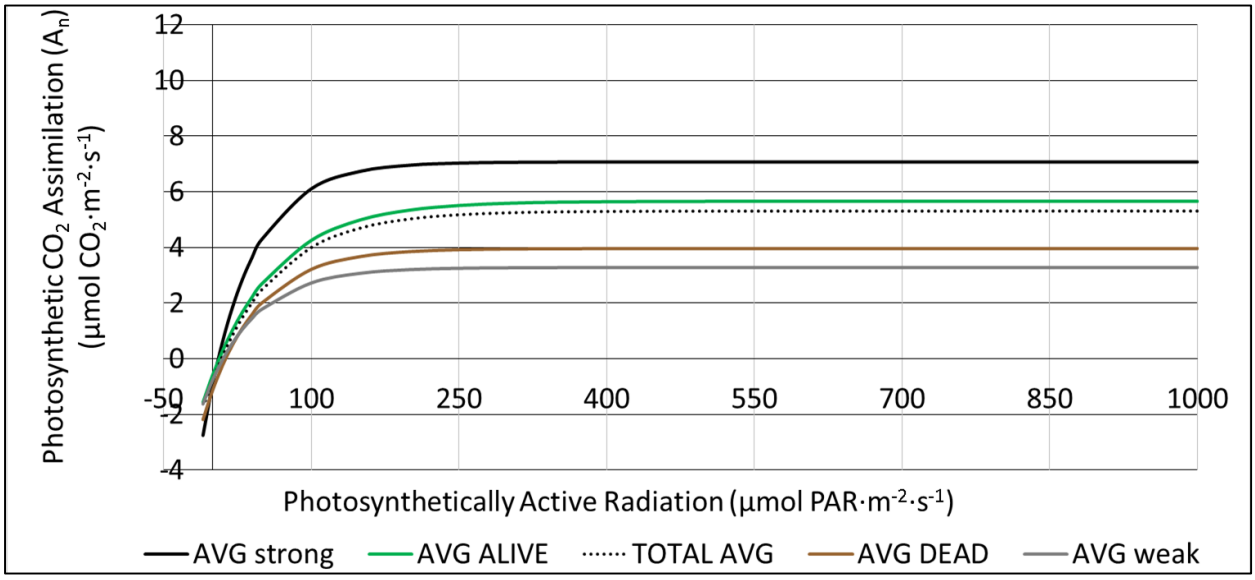

Figure 52. Summary chart illustrating the average light curves for *Quercus alba* seedlings that survived the entire study period (AVG ALIVE) and those that died before the conclusion of the study (AVG DEAD), as well as the overall average light curves for the photosynthetically strong, average, and weak *Quercus alba* seedlings found in the study site.

5.7 CARBON ASSIMILATION OF WHITE OAK SEEDLINGS AND AMUR HONEYSUCKLE

The average seasonal leaf-level carbon assimilation totals (initiating at leaf open and ending at leaf senescence) for white oak seedlings and Amur honeysuckle varied between light scenarios. The total average seasonal carbon gained by a photosynthetically average white oak seedlings modeled using the full sun light measured *in situ* near the Nachusa Grasslands headquarters was 9.320 ± 1.049 SE mols C/ m^2/season (Table 10; Figure 53). The total average seasonal carbon gained by a photosynthetically average Amur honeysuckle modeled using the understory light measured *in situ* one meter above the ground at the oak savanna restoration study site was 5.496 ± 0.658 SE mols C/ m^2/season (Table 10; Figure 53). Photosynthetically average white oak seedlings modeled using the understory light measured *in situ* 30 cm above the ground at the oak savanna restoration study site in areas without Amur honeysuckle encroachment, on the other hand, gained on average 1.778 ± 0.267 SE mols C/ m^2/season, while photosynthetically average white oak seedlings modeled using the understory light measured *in situ* 30 cm above the ground at the oak savanna restoration study site below Amur honeysuckle encroachment lost on average -0.484 ± 0.295 SE mols C/ m^2/season (Table 10; Figure 53).

When all four seasonal carbon totals (i.e. 2011-2014) for white oak and Amur honeysuckle were compared across light scenarios (i.e. full sun, HS light (1m), no HS encroachment, HS encroachment) by photosynthetic strength (i.e. weak, strong, average), Kruskal-Wallis nonparametric tests coupled with nonparametric posthoc

Tukey-like multiple comparisons tests found several significant differences. In general, the mean overall total carbon gained by white oak seedlings in the full sun light scenario were significantly higher than the mean overall total carbon lost by white oak seedlings in the Amur honeysuckle encroached light scenario, no matter the photosynthetic strength of the white oak seedlings (i.e. weak $p<0.05$, strong $p<0.01$, average $p<0.01$) (Table 10; Figure 53). On average, photosynthetically weak white oak seedlings in the full sun light scenario gained 5.378 ±0.989 SE mols C/ m^2/season, while the photosynthetically weak white oak seedlings in the Amur honeysuckle encroached light scenario lost 0.981 ± 0.698 SE mols C/ m^2/season (Table 10; Figure 53). Photosynthetically strong white oak seedlings in the full sun light scenario gained an average of 12.133 ± 1.496 SE mols C/ m^2/season, while the photosynthetically strong white oak seedlings in the Amur honeysuckle encroached light scenario lost 0.242 ± 0.549 SE mols C/ m^2/season (Table 10; Figure 53). Finally, photosynthetically average white oak seedlings in the full sun light scenario gained an average of 9.320 ± 1.049 SE mols C/ m^2/season, while the photosynthetically average white oak seedlings in the Amur honeysuckle encroached light scenario lost 0.484 ± 0.295 SE mols C/ m^2/season (Table 10; Figure 53).

When all four seasonal carbon totals for white oak and Amur honeysuckle were compared across photosynthetic strengths by light scenario, Kruskal-Wallis nonparametric tests coupled with nonparametric posthoc Tukey-like multiple comparisons tests found significant differences (Table 10; Figure 53). More specifically, the mean overall total carbon gained by strong white oak seedlings in the full sun light

scenario (12.133 ± 1.496 SE mols C/ m^2/season) and strong Amur honeysuckle in the 1m oak savanna restoration understory light scenario (7.922 ± 0.528 SE mols C/ m^2/season) were found to be significantly higher than the mean overall total carbon gained by weak white oak seedlings in the full sun light scenario (5.378 ± 0.989 SE mols C/ m^2/season) and weak Amur honeysuckle in the 1m oak savanna restoration understory light scenario (2.810 ± 2.046 SE mols C/ m^2/season), respectively ($p<0.05$) (Table 10; Figure 53). Additionally, the mean carbon totals gained during the leaf open (5) and leaf color change to leaf senescence (6-7) phenology phases for strong white oak seedlings in the full sun light scenario (9.168 ± 1.225 SE mols C/ m^2/season and 2.965 ± 0.456 SE mols C/ m^2/season, respectively) were found to be significantly higher than the mean carbon totals gained during the leaf open (5) and leaf color change to leaf senescence (6-7) phenology phases for weak white oak seedlings in the full sun light scenario (4.146 ± 0.886 SE mols C/ m^2/season and 1.232 ± 0.146 SE mols C/ m^2/season, respectively) ($p<0.05$) (Table 10; Figure 53). Similarly, the mean total carbon gained by photosynthetically strong Amur honeysuckle (6.004 ± 0.447 SE mols C/ m^2/season) was found to be significantly higher than the photosynthetically weak Amur honeysuckle (2.394 ± 1.328 SE mols C/ m^2/season) in the 1m oak savanna restoration understory light scenario during the leaves open phenology phase ($p<0.05$) (Table 10; Figure 53).

When all four carbon totals for the individual leaf open (5) and leaf color change to leaf senescence (6-7) phenology phases for white oak seedlings and Amur honeysuckle were compared to each other by light scenario and photosynthetic

strength, Mann-Whitney nonparametric tests found multiple significant differences. Specifically, the mean total carbon gained during the leaves open phenology phase was significantly higher than the mean total carbon gained during the leaves changing to senescence phenology phase by white oak seedlings in the full sun light scenario for all photosynthetic strengths (i.e. weak, strong, average; $p<0.05$) (Table 10; Figure 53). The photosynthetically weak white oak seedlings gained an average of 4.146 ± 0.886 SE mols C/ m^2/season during the leaf open phenology phase and an average of 1.232 ± 0.146 SE mols C/ m^2/season during leaf color change to leaf senescence phenology phase (Table 10; Figure 53). The photosynthetically strong white oak seedlings gained an average of 9.168 ± 1.225 SE mols C/ m^2/season during the leaf open phenology phase and an average of 2.965 ± 0.456 SE mols C/ m^2/season during leaf color change to leaf senescence phenology phase (Table 10; Figure 53). The photosynthetically average white oak seedlings gained an average of 7.010 ± 0.901 SE mols C/ m^2/season during the leaf open phenology phase and an average of 2.310 ± 0.311 SE mols C/ m^2/season during leaf color change to leaf senescence phenology phase (Table 10; Figure 53).

Additionally, the mean total carbon gained during the leaves open phenology phase was significantly higher than the mean total carbon gained during the leaves changing to senescence phenology phase for photosynthetically strong and average Amur honeysuckle in the 1m oak savanna restoration understory light scenario ($p<0.05$) (Table 10; Figure 53). The photosynthetically strong Amur honeysuckle gained an average of 6.004 ± 0.447 SE mols C/ m^2/season during the leaf open phenology phase

and an average of 1.918 ± 0.135 SE mols C/ m^2/season during leaf color change to leaf senescence phenology phase (Table 10; Figure 53). While the photosynthetically average Amur honeysuckle gained an average of 4.300 ± 0.425 SE mols C/ m^2/season during the leaf open phenology phase and an average of 1.196 ± 0.254 SE mols C/ m^2/season during leaf color change to leaf senescence phenology phase (Table 10; Figure 53).

The light curve variables for the surveyed white oak seedlings that survived until the end of the study period (2011-2014), as well as the light curve variables for the surveyed white oak seedlings that died by the end of the study were averaged and used to calculate seasonal carbon assimilation totals during leaf open to leaf senescence phenology phases, in order to characterize the physiological mechanisms of white oak based on actual in field morality scenarios. In the full sun light scenario at Nachusa Grasslands, the total seasonal carbon assimilation for the average surviving white oak seedling was 10.724 mols C/ m^2/season, while the total seasonal carbon assimilation for the average dead white oak seedling was 6.248 mols C/ m^2/season (Table 11; Figure 53). When modeled using the *in situ* oak savanna restoration study site understory light scenario without Amur honeysuckle encroachment, the total seasonal carbon assimilation for the average surviving white oak seedling was 3.005 mols C/ m^2/season, while the total seasonal carbon assimilation for the average dead white oak seedling was 0.456 mols C/ m^2/season in the same light scenario (Table 11; Figure 53). Using the final *in situ* oak savanna restoration study site understory light scenario - below Amur honeysuckle encroachment - the total seasonal carbon assimilation for the

average surviving white oak seedling was 0.367 mols C/ m^2/season, while the total seasonal carbon assimilation for the average dead white oak seedling was -1.931 mols C/ m^2/season in the same encroached light scenario (Table 11; Figure 53). No statistical differences were found between any of the seasonal carbon totals of surviving or dead white oak seedlings.

The overall seasonal accumulation patterns (i.e. cumulative totals) of the carbon assimilated by white oak seedlings and Amur honeysuckle also varied in the different light scenarios. More specifically, the average rate of carbon accumulation from leaf open to leaf senescence (linear slope of the cumulative carbon assimilation) was most rapid for white oak seedlings modeled in the full sun light scenario (slope: 0.582 mols C/ m^2/season), followed by the overall accumulation rate of carbon by Amur honeysuckle modeled in the one meter light scenario (slope: 0.036 mols C/ m^2/season), the white oak seedlings modeled in the light scenario without Amur honeysuckle encroachment (slope: 0.013 mols C/ m^2/season), and the white oak seedlings modeled in the light scenario with Amur honeysuckle (slope: -0.003 mols C/ m^2/season), respectively (Figure 54).

Table 10. Table listing seasonal carbon assimilation totals (mols/m²/phenology stage) for white oak seedlings and Amur honeysuckle shrubs (weak, strong, and average) modeled under the four different light scenarios (full sun, HS light, no HS encroachment, and HS encroachment) during each observed leaf phenology stage (5: leaves open, 6-7: color transition to senescence, 5-7: total carbon assimilation season). Superscript red letters denote statistical differences (p<0.05) between totals within photosynthetic strengths across light scenarios, red asterisks denote statistical differences (p<0.05) between totals within light scenarios and photosynthetic strength across phonological stage, and regular blue letters denote statistical differences (p<0.05) between totals across photosynthetic strengths. Standard errors are reported for all averages.

		Total Carbon Assimilation - Weakest (mol/m²/phenology stage)					Total Carbon Assimilation - Strongest (mol/m²/phenology stage)					Total Carbon Assimilation - Average (mol/m²/phenology stage)				
Light Scenario	Leaf Phenology Stage	2011	2012	2013	2014	AVG	2011	2012	2013	2014	AVG	2011	2012	2013	2014	AVG
Full Sun - WHITE OAK	5	5.297	3.512	1.942	5.832	4.146 ± 0.886*A	11.066	6.024	8.424	11.159	9.168 ± 1.225*B	8.584	4.927	6.086	8.445	7.010 ± 0.901*AB
	6-7	1.551	1.339	0.861	1.176	1.232 ± 0.146**A	3.736	1.928	3.724	2.471	2.965 ± 0.456**B	2.942	1.718	2.743	1.837	2.310 ± 0.311**AB
	TOTAL	6.848	4.851	2.803	7.009	5.378 ± 0.989^A A	14.802	7.952	12.148	13.630	12.133 ± 1.496^A B	11.526	6.645	8.828	10.282	9.320 ± 1.049^A AB
HS light (1 m)- AMUR HONEYSUCKLE	5	3.409	-1.077	2.029	5.214	2.394 ± 1.328A	6.857	6.628	4.960	5.572	6.004 ± 0.447*B	4.800	3.098	4.312	4.989	4.300 ± 0.425*AB
	6-7	0.865	-1.633	0.645	1.791	0.417 ± 0.727	1.796	2.322	1.763	1.789	1.918 ± 0.135**	1.157	0.496	1.495	1.635	1.196 ± 0.254**
	TOTAL	4.274	-2.710	2.674	7.004	2.810 ± 2.046^AB A	8.653	8.950	6.722	7.361	7.922 ± 0.528^AB B	5.957	3.594	5.808	6.624	5.496 ± 0.658^AB AB
No HS Encroachment - WHITE OAK	5	-0.162	1.552	0.356	0.286	0.508 ± 0.366	1.727	2.771	0.276	1.794	1.642 ± 0.514	-0.102	1.598	0.613	1.102	0.803 ± 0.363
	6-7	0.113	0.613	0.281	0.092	0.275 ± 0.121	1.109	0.826	0.427	0.566	0.732 ± 0.150	0.445	0.493	0.598	0.352	0.472 ± 0.051
	TOTAL	-0.049	2.165	0.638	0.378	0.783 ± 0.482^AB	2.836	3.597	0.704	1.211	2.374 ± 0.612^AB	2.355	2.091	1.211	1.454	1.778 ± 0.267^AB
HS Encroachment - WHITE OAK	5	-1.973	0.405	-0.334	-1.631	-0.883 ± 0.556	0.296	-0.271	-1.397	-0.038	-0.353 ± 0.367	-0.100	-0.420	-0.976	-0.694	-0.548 ± 0.187
	6-7	-0.403	0.232	0.035	-0.257	-0.098 ± 0.143	0.613	-0.083	-0.296	0.210	0.111 ± 0.197	0.456	-0.173	-0.040	0.010	0.063 ± 0.137
	TOTAL	-2.376	0.637	-0.299	-1.888	-0.981 ± 0.698^B	0.908	-0.355	-1.693	0.172	-0.242 ± 0.549^B	0.356	-0.593	-1.017	-0.684	-0.484 ± 0.295^B

Table 11. Table listing seasonal carbon assimilation totals (mols/m²/phenology stage) of both living and dead white oak seedlings modeled under three light scenarios (full sun, no HS encroachment, and HS encroachment) during each observed leaf phenology stage (5: leaves open, 6-7: color transition to senescence, 5-7: total growing season). No statistical differences were found. Standard errors are reported for all averages.

		Total Carbon Assimilation - Mortality (mol/m²/phenology stage)	
Light Scenario	Leaf Phenology Stage	ALIVE	DEAD
Full Sun - WHITE OAK	5	7.913	4.783
	6-7	2.811	1.464
	TOTAL	10.724	6.248
No HS Encroachment - WHITE OAK	5	1.968	0.291
	6-7	1.037	0.165
	TOTAL	3.005	0.456
HS Encroachment - WHITE OAK	5	-0.061	-1.564
	6-7	0.428	-0.367
	TOTAL	0.367	-1.931

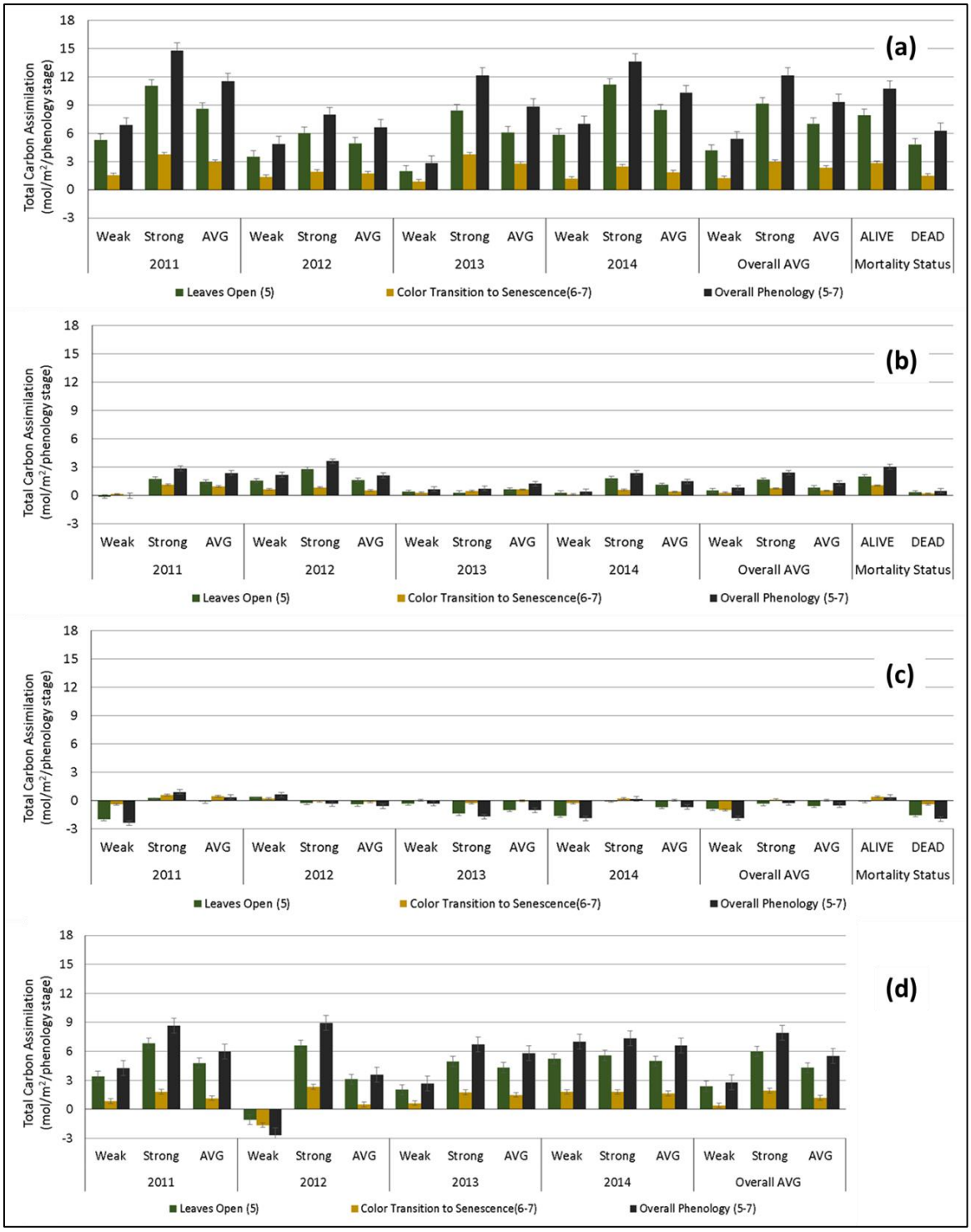

Figure 53. Seasonal carbon assimilation totals (mols/m²/phenology stage) for weak, strong, average, living, and dead white oak seedlings modeled under three different light scenarios: (a) full sun, (b) no HS encroachment at 30 cm above the ground, and (c) HS encroachment at 30 cm above the ground; along with weak, strong, and average Amur honeysuckle shrubs modeled under the (d) HS light scenario at one meter above the ground during each observed leaf phenology stage (i.e. 5: leaves open, 6-7: color transition to senescence, 5-7: total carbon assimilation season). Error bars represent 95% confidence interval.

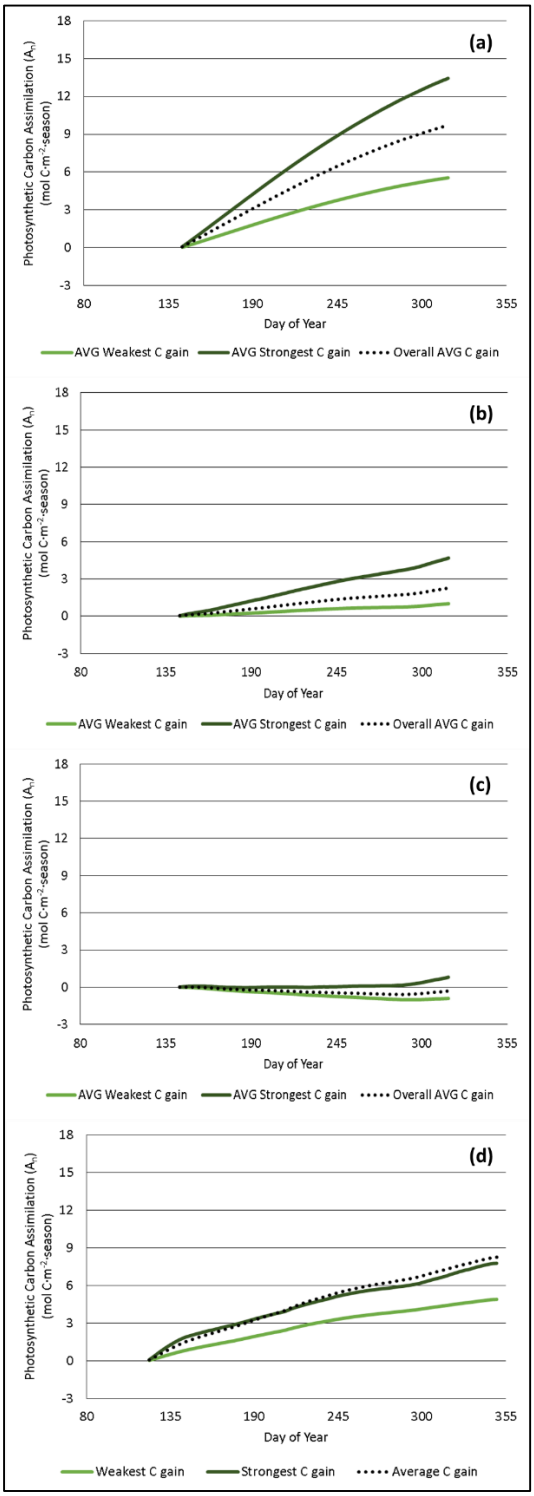

Figure 54. Overall average cumulative carbon gain under the (a) full sun, (b) no encroachment, and (c) encroachment light scenario for white oak seedlings, as well as for the (d) one meter light scenario for Amur honeysuckle at Nachusa Grasslands, IL. The dark green line (top) represents photosynthetically strong white oak seedling carbon assimilation. The dotted black line (middle) represents the average white oak seedling carbon assimilation. The light green line (bottom) represents photosynthetically weak white oak seedling carbon assimilation.

In addition to the variations found in the seasonal carbon assimilation totals, the daily carbon assimilation (A_n) of white oak seedlings and Amur honeysuckle during the leaves open phenology stage also varied from year to year, as well as between light scenarios and photosynthetic strengths. In general, across all light scenarios for both white oak seedlings and Amur honeysuckle, the photosynthetically strong plants had the highest daily average carbon assimilation rates, followed by the photosynthetically average plants and photosynthetically weak plants, respectively ($p<0.001$) (Table 12).

In the full sun light scenario at Nachusa Grasslands, average daily carbon assimilation of white oak seedlings ranged from 0.015 ± 0.0003 SE mols C/m^2/day (photosynthetically weak white oak seedlings in 2013) to 0.086 ± 0.001 SE mols C/m^2/day (photosynthetically strong white oak seedlings in 2014) (Table 12; Figure 55). The overall average daily carbon assimilation of photosynthetically average white oak seedlings in the full sun light scenario was 0.054 ± 0.007 SE mols C/m^2/day (Table 12; Figure 55). According to nonparametric Kruskal-Wallis tests, combined with nonparametric posthoc Tukey-like multiple comparison tests, significant differences ($p<0.001$) were found between the annual average daily carbon assimilation rates of white oak seedlings in the full sun light scenario (Table 12). More specifically, for both photosynthetically strong and average white oak seedlings, all years were found to have significantly different daily carbon assimilation rates, except 2011 and 2014 (Table 12). For photosynthetically weak white oak seedlings, all years were significantly different (Table 12).

The average daily carbon assimilation of Amur honeysuckles at the one meter light scenario in the oak restoration study site at Nachusa Grasslands ranged from -0.011 ± 0.0004 SE mols C/m^2/day (photosynthetically weak Amur honeysuckle in 2012) to 0.036 ± 0.001 SE mols C/m^2/day (photosynthetically strong Amur honeysuckle in 2012) (Table 12; Figure 56). The overall average daily carbon assimilation of photosynthetically average Amur honeysuckles in the one meter light scenario in the oak restoration study site was 0.023 ± 0.003 SE mols C/m^2/day (Table 12; Figure 56). Significant differences ($p<0.001$) were also found between the annual average daily carbon assimilation rates of Amur honeysuckle oak seedlings in the one meter light scenario based on nonparametric Kruskal-Wallis tests, combined with nonparametric posthoc Tukey-like multiple comparison tests (Table 12).More specifically, all years were found to be significantly different from one another for the photosynthetically weak Amur honeysuckle. For the photosynthetically strong Amur honeysuckle, 2011 and 2014 had statistically similar daily carbon assimilation, but were significantly different than 2012 and 2013, which also had statistically similar daily carbon assimilation (Table 12). All annual daily carbon assimilation averages for photosynthetically average Amur honeysuckle were found to be significantly different that one another, except 2013 and 2014, which were statistically similar (Table 12).

In the light scenario without Amur honeysuckle encroachment in the oak savanna restoration study site at Nachusa Grasslands, daily carbon assimilation of white oak seedlings ranged from -0.0003 ± 0.0004 SE mols C/m^2/day (photosynthetically weak white oak seedlings in 2011) to 0.019 ± 0.001 SE mols C/m^2/day (photosynthetically

strong white oak seedlings in 2012) (Table 12; Figure 57). The overall average daily carbon assimilation of photosynthetically average white oak seedlings in the understory light scenario without Amur honeysuckle encroachment was 0.007 ± 0.002 SE mols C/m^2/day (Table 12; Figure 57). According to nonparametric Kruskal-Wallis tests, combined with nonparametric posthoc Tukey-like multiple comparison tests, significant differences ($p<0.001$) were found between the annual average daily carbon assimilation rates of white oak seedlings in the understory light scenario without Amur honeysuckle encroachment (Table 12). For the photosynthetically weak white oak seedlings, 2013 and 2014 were similar, while 2011 and 2014 were similar for photosynthetically strong white oak seedlings and 2012 was similar to 2014 for the photosynthetically average white oak seedlings (Table 12). All other annual daily carbon assimilation averages were significantly different (Table 12).

Furthermore, in the light scenario with Amur honeysuckle encroachment, the daily carbon assimilation of white oak seedlings ranged from -0.014 ± 0.001 SE mols C/m^2/day (photosynthetically weak white oak seedlings in 2011) to 0.005 ± 0.0004 SE mols C/m^2/day (photosynthetically strong white oak seedlings in 2011) (Table 12; Figure 58). The overall average daily carbon assimilation of photosynthetically average white oak seedlings in the understory light scenario with Amur honeysuckle encroachment was -0.003 ± 0.002 SE mols C/m^2/day (Table 12; Figure 58). Significant differences ($p<0.001$) were also found between the annual average daily carbon assimilation rates of white oak seedlings in the understory light scenario with Amur honeysuckle encroachment based on nonparametric Kruskal-Wallis tests, combined with

nonparametric posthoc Tukey-like multiple comparison tests (Table 12). More specifically, photosynthetically weak white oak seedlings were found to have significantly different average daily carbon assimilation in all years but 2011 and 2014, which were similar (Table 12). Photosynthetically strong white oak seedlings, on the other hand, had significantly different average daily carbon assimilation for all years (Table 12). Annual daily carbon assimilation averages for photosynthetically average white oak seedlings were significantly different in all years, except 2012 and 2014, along with 2012 and 2013, which were statistically similar to one another (Table 12).

The average daily carbon assimilation for the surviving white oak seedlings in the full sun light environment was 0.062 ± 0.001 SE mols C/m^2/day, which was significantly higher than the average daily carbon assimilation for the white oak seedlings that died before the end of the study period was 0.036 ± 0.001 SE mols C/m^2/day ($p<0.001$) (Table 13; Figure 59). The average daily carbon assimilation for the surviving white oak seedlings in the light environment without Amur honeysuckle encroachment was 0.017 ± 0.0004 SE mols C/m^2/day, which was significantly higher than the average daily carbon assimilation for the white oak seedlings that died before the end of the study period was 0.003 ± 0.0003 SE mols C/m^2/day ($p<0.001$) (Table 13; Figure 59). The average daily carbon assimilation for the surviving white oak seedlings in the light environment with Amur honeysuckle encroachment was 0.002 ± 0.0005 SE mols C/m^2/day, which was significantly higher than the average daily carbon assimilation for the white oak seedlings that died before the end of the study period was -0.011 ± 0.0004 SE mols C/m^2/day ($p<0.001$) (Table 13; Figure 59). All average daily carbon

assimilation within each mortality category (i.e. alive and dead) were found to be significantly different among light scenarios, with full sun light scenarios having the highest average daily carbon assimilation and HS encroachment light scenario having the lowest average daily carbon assimilation (Table 13).

Table 12. Table listing daily carbon assimilation averages (mols/m²/day) for white oak seedlings and Amur honeysuckle shrubs (weak, strong, and average) modeled under the four different light scenarios (full sun, HS light, no HS encroachment, and HS encroachment). Red letters next to each daily carbon assimilation average denotes significant differences (p<0.05) among years within light scenarios. Red superscript letters by photosynthetic strengths denote overall significant differences (p<0.05) in daily carbon assimilation averages for all years among strengths. Standard errors are reported for all averages.

	Total Carbon Assimilation – Weakest[A] (mol/m²/day)					Total Carbon Assimilation - Strongest[B] (mol/m²/day)					Total Carbon Assimilation – Average[C] (mol/m²/day)				
Light Scenario	**2011**	**2012**	**2013**	**2014**	**AVG**	**2011**	**2012**	**2013**	**2014**	**AVG**	**2011**	**2012**	**2013**	**2014**	**AVG**
Full Sun – WHITE OAK	0.039 ± 0.001A	0.027 ± 0.0003B	0.015 ± 0.0003C	0.044 ± .001D	**0.034 ± 0.007**	0.085 ± 0.001A	0.044 ± 0.001B	0.067 ± 0.001C	0.086 ± 0.001A	**0.070 ± 0.010**	0.066 ± 0.001A	0.036 ± 0.001B	0.049 ± 0.001C	0.065 ± 0.001A	**0.054 ± 0.007**
HS light (1 m)-AMUR HONEYSUCKLE	0.017 ± 0.001A	-0.011 ± 0.0004B	0.012 ± 0.0002C	0.031 ± 0.001D	**0.012 ± 0.009**	0.035 ± 0.001A	0.036 ± 0.001B	0.034 ± 0.001B	0.032 ± 0.001A	**0.034 ± 0.001**	0.024 ± 0.001A	0.015 ± 0.001B	0.026 ± 0.001C	0.029 ± 0.001C	**0.023 ± 0.003**
No HS Encroachment - WHITE OAK	-0.0003 ± 0.0004A	0.012 ± 0.0003B	0.004 ± 0.0001C	0.002 ± 0.0003C	**0.004 ± 0.003**	0.016 ± 0.0004A	0.019 ± 0.001B	0.004 ± 0.0005C	0.015 ± 0.0004A	**0.014 ± 0.003**	0.002 ± 0.0004A	0.011 ± 0.0005B	0.007 ± 0.0004C	0.009 ± 0.0003B	**0.007 ± 0.002**
HS Encroachment - WHITE OAK	-0.014 ± 0.001A	0.003 ± 0.0004B	-0.002 ± 0.0002C	-0.012 ± 0.0004A	**-0.006 ± 0.004**	0.005 ± 0.0004A	-0.002 ± 0.001B	-0.009 ± 0.001C	0.001 ± 0.0003D	**-0.001 ± 0.003**	0.002 ± 0.0004A	-0.004 ± 0.001BC	-0.006 ± 0.0005C	-0.004 ± 0.0003B	**-0.003 ± 0.002**

Table 13. Table listing average daily carbon assimilation (mols/m²/day) of both living and dead white oak seedlings modeled under three light scenarios (full sun, no HS encroachment, and HS encroachment). No statistical differences were found. Red letters next to each daily carbon assimilation average denotes significant differences (p<0.05) among light scenarios within each mortality category. Asterisks denote overall significant differences (p<0.05) in daily carbon assimilation averages for all light scenarios among mortality categories. Standard errors are reported for all averages.

	Total Carbon Assimilation - Mortality (mol/m²/day)	
Light Scenario	**ALIVE***	**DEAD***
Full Sun - WHITE OAK	0.062 ± 0.001 A	0.036 ± 0.001 A
No HS Encroachment - WHITE OAK	0.017 ± 0.0004 B	0.003 ± 0.0003 B
HS Encroachment - WHITE OAK	0.002 ± 0.0005 C	-0.011 ± 0.0004 C

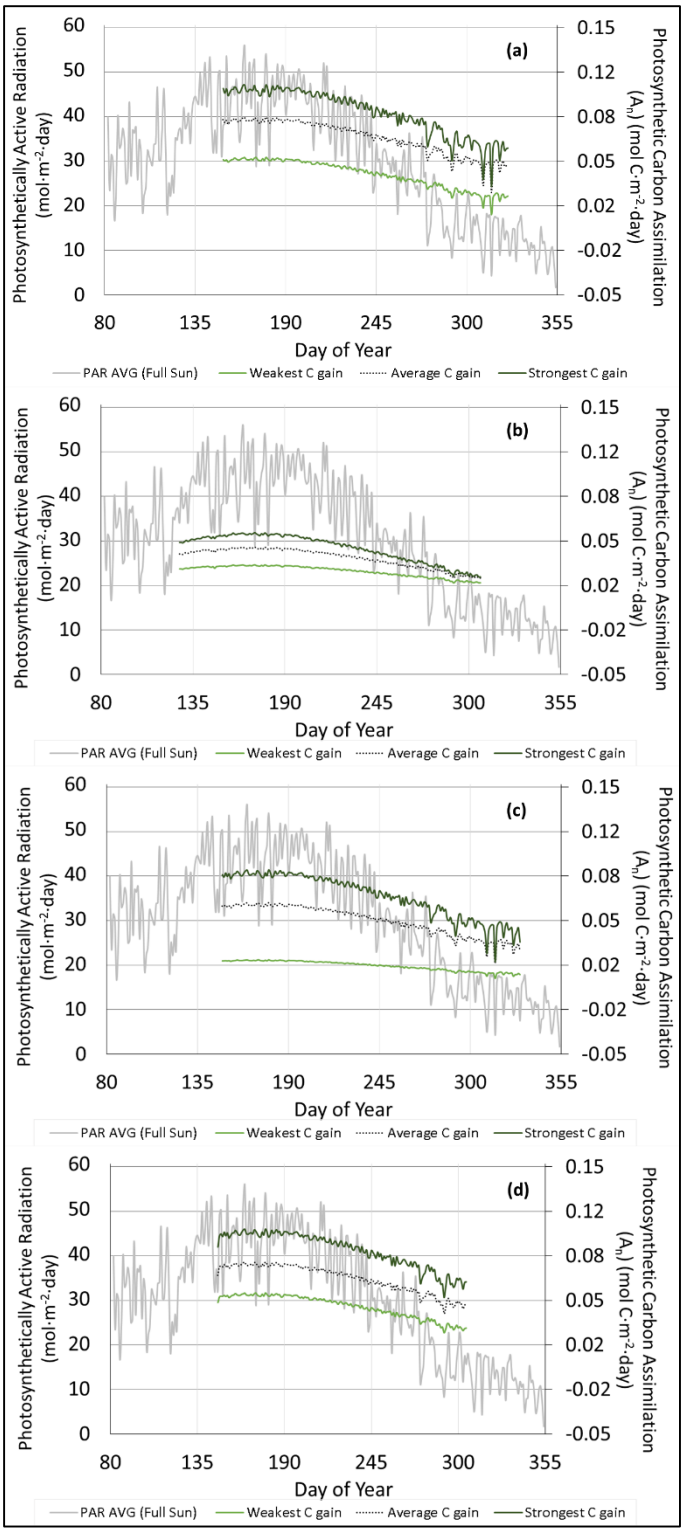

Figure 55. Daily carbon assimilation rates and daily light levels (grey line) of white oak seedlings in the full sun light scenario for (a) 2011, (b) 2012, (c) 2013, and (d) 2014 at Nachusa Grasslands, IL. The dark green line (top) represents photosynthetically strong white oak seedling carbon assimilation. The dotted black line (middle) represents the average white oak seedling carbon assimilation. The light green line (bottom) represents photosynthetically weak white oak seedling carbon assimilation.

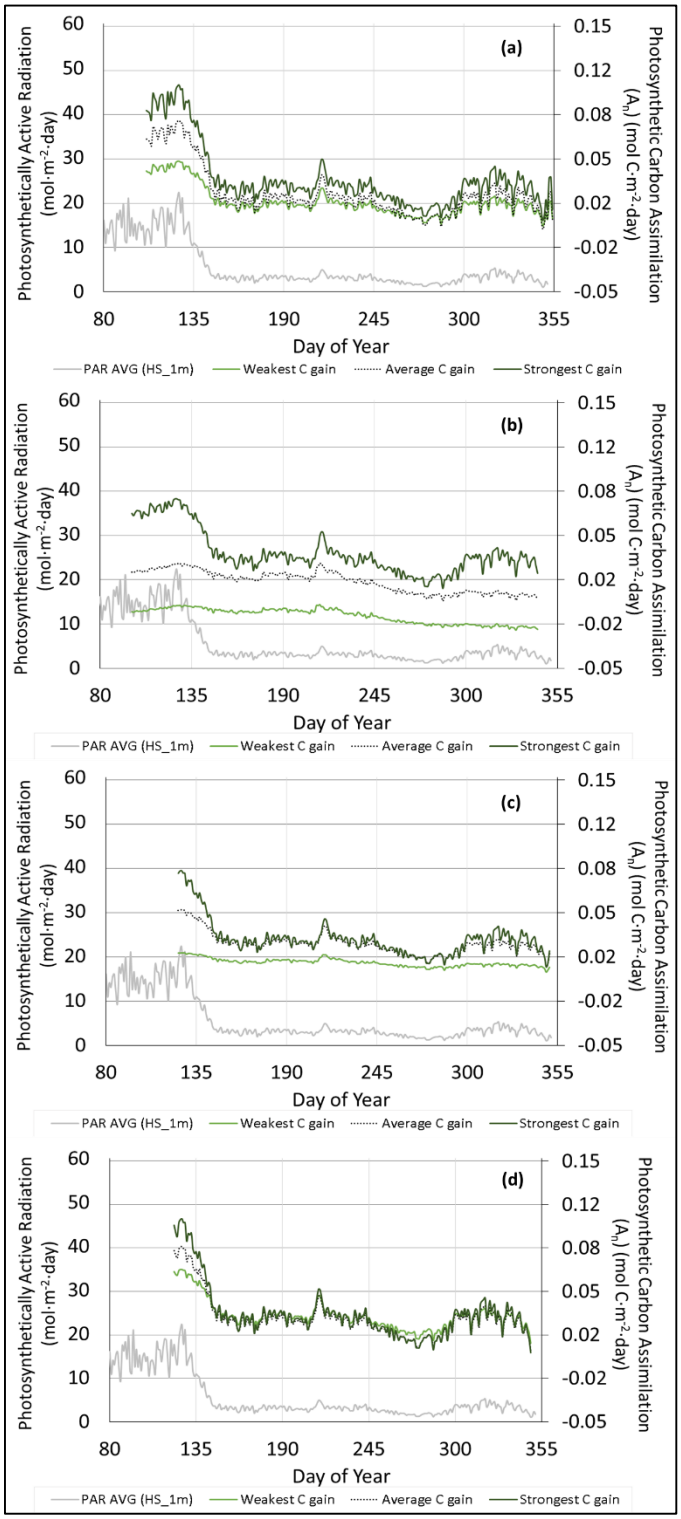

Figure 56. Daily carbon assimilation rates and daily light levels (grey line) of Amur honeysuckle in the one meter light scenario for (a) 2011, (b) 2012, (c) 2013, and (d) 2014 at Nachusa Grasslands, IL. The dark green line (top) represents photosynthetically strong Amur honeysuckle carbon assimilation. The dotted black line (middle) represents the average Amur honeysuckle carbon assimilation. The light green line (bottom) represents photosynthetically weak Amur honeysuckle carbon assimilation.

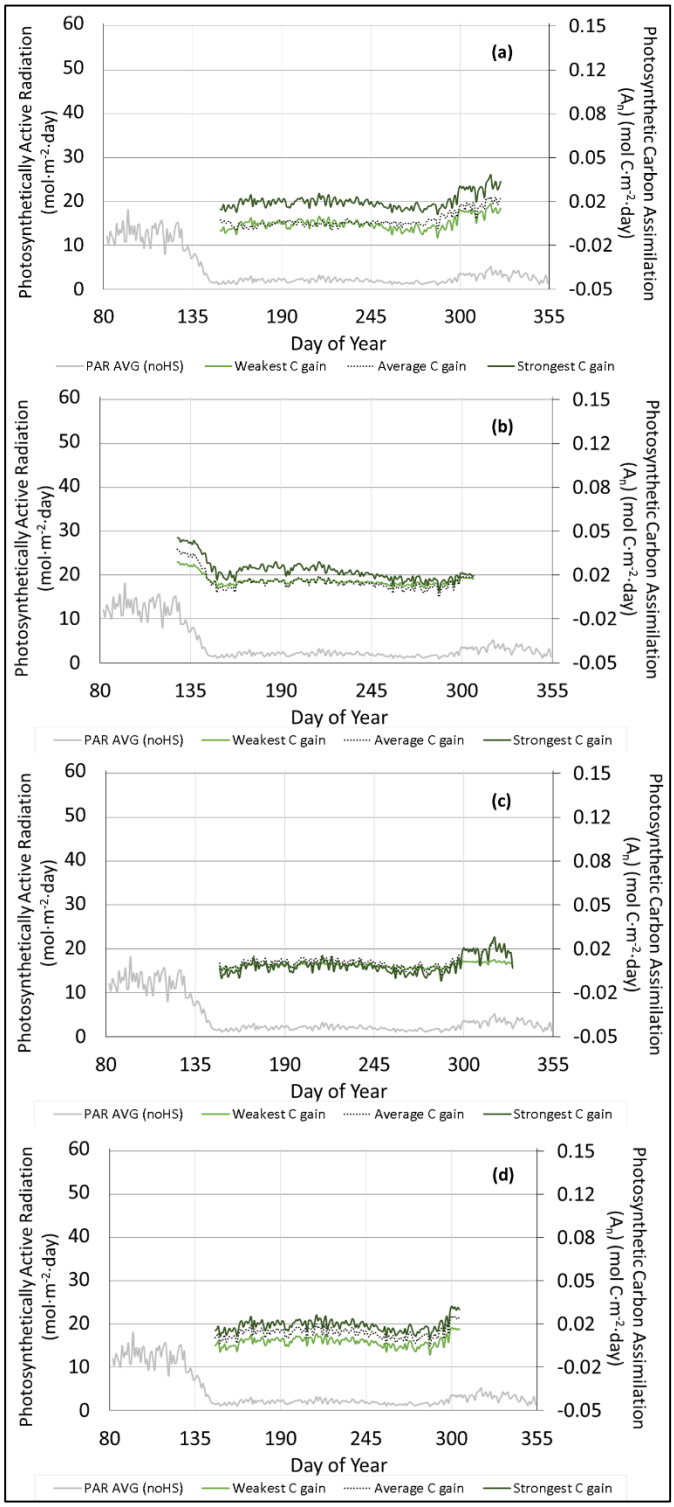

Figure 57. Daily carbon assimilation rates and daily light levels (grey line) of white oak seedlings in the light scenario without Amur honeysuckle encroachment for (a) 2011, (b) 2012, (c) 2013, and (d) 2014 at Nachusa Grasslands, IL. The dark green line (top) represents photosynthetically strong white oak seedling carbon assimilation. The dotted black line (middle) represents the average white oak seedling carbon assimilation. The light green line (bottom) represents photosynthetically weak white oak seedling carbon assimilation.

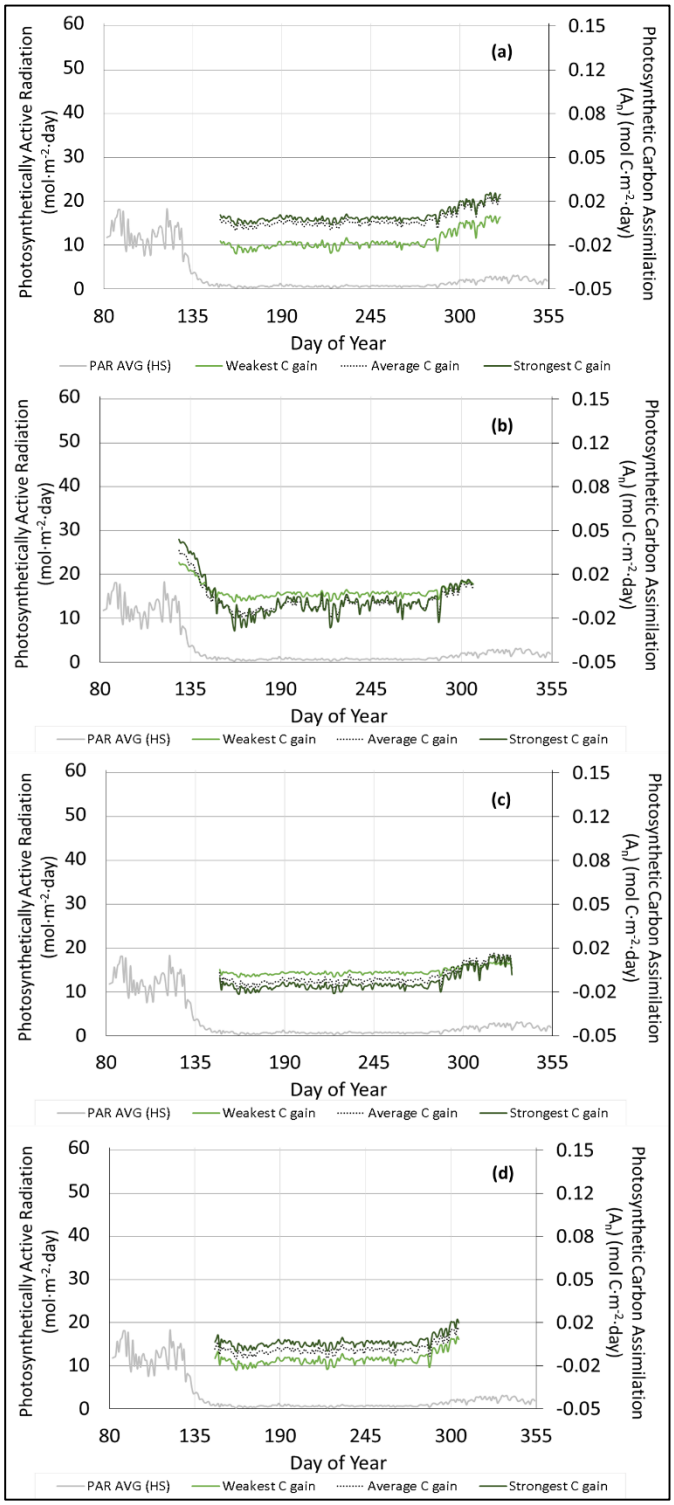

Figure 58. Daily carbon assimilation rates and daily light levels (grey line) of white oak seedlings in the light scenario with Amur honeysuckle encroachment for (a) 2011, (b) 2012, (c) 2013, and (d) 2014 at Nachusa Grasslands, IL. The dark green line (top) represents photosynthetically strong white oak seedling carbon assimilation. The dotted black line (middle) represents the average white oak seedling carbon assimilation. The light green line (bottom) represents photosynthetically weak white oak seedling carbon assimilation.

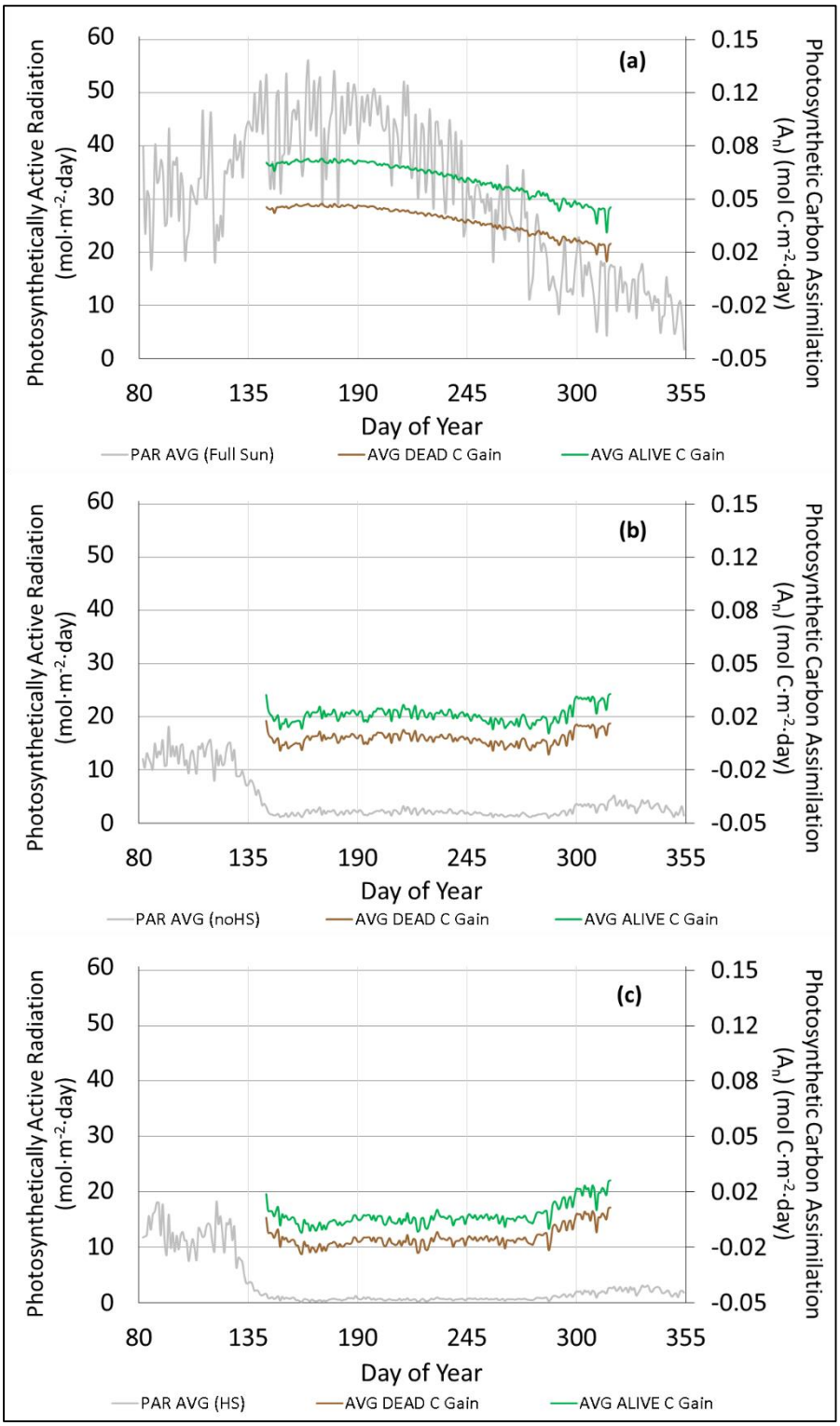

Figure 59. Average daily carbon assimilation rates and daily light levels (grey line) of white oak seedlings in the (a) full sun, (b) no encroachment, (c) encroachment light scenario at Nachusa Grasslands, IL. The green line (top) represents the daily carbon assimilation of surviving white oak seedlings, while the brown line (bottom) represents the daily carbon assimilation of the white oak seedlings that died before the end of the study period.

5.8 DISCUSSION

Ultimately the goals of this chapter were to characterize the current stand structure of the oak savanna restoration study site at Nachusa Grasslands, IL, in addition to assessing the ecological impact of the invasive encroachment and extended leaf phenology of Amur honeysuckle on understory light environments and seasonal carbon assimilation totals of both Amur honeysuckle and white oak seedlings. Specifically, findings from this research were meant to answer the following questions: What role does the extended leaf phenology of Amur honeysuckle play in its leaf-level seasonal carbon gain? What are the existing *in situ* light levels above and below Amur honeysuckle canopies and do those light levels inhibit the ability of *in situ* white oak seedlings to maintain a positive net leaf-level seasonal carbon balance?

Overall, the oak savanna restoration study site at Nachusa Grasslands had a density of 589 trees/ha, which was, as expected, much denser than the 2.5 trees/ha that Nuzzo (1986) defined as an extremely open oak savanna community. Furthermore, while the management strategies for the study site include regular light fires, the site has not experienced catastrophic disturbance events every 35-100 years, identified by Nuzzo (1986) and Apfelbaum and Haney (1991) as being important for reducing mesophication and encouraging the regeneration and recruitment of oak. The tree density of the oak savanna restoration study site at Nachusa Grasslands closely resembled the tree density reported for no burn upland oak savanna and woodland stands in east-central Minnesota, USA, which ranged from 168 to 552 stems/ha (Peterson and Reich 2001). The total basal area for the oak savanna restoration study

site, on the other hand, was higher than the basal area reported for no burn oak savanna sites in other parts of Midwestern North America, which ranged from 13.7 to 28.2 m^2/ha (Peterson and Reich 2001), and instead more closely matched the range of basal area surveyed in upland forests in southwestern Ohio, which ranged from 10.8 to 46.4 m^2/ha (Hutchinson and Vankat 1997).

Most of the basal area in the oak savanna restoration study site at Nachusa Grasslands was comprised of white oak trees ranging in size between 35 and 60 cm in diameter at breast height. Slippery elm, shagbark hickory, and white oak had the highest relative densities and relative frequencies, respectively, meaning that these species were relatively common and evenly distributed throughout the study site. The slippery elm and shagbark, however, had low relative covers, which suggests that they are relatively young and newly established in the oak savanna restoration study. The fact that white oak had the highest importance value (a value that factors in relative density, relative cover, and relative frequency) throughout the study site bodes well for the future success of the oak savanna restoration at Nachusa Grasslands, since the composition, structure, and function of Midwest oak savanna ecosystems are reliant on maintaining white oak as a dominant species (Rogers 1990; Abrams 1992; Brudvig and Evans 2006; Wang and Bauerle 2006).

Beyond the overstory canopy, it is essential that there is a healthy, viable regeneration layer of white oak seedlings in the understory of the study site, in order to maintain long term sustainability of white oak dominance (Apfelbaum and Haney 1991; Gazol and Ibanez 2010; Rebbeck et al. 2012). However, minimal evidence of oak

regeneration and recruitment was found in the understory of the oak savanna restoration study site at Nachusa Grasslands, which was heavily dominated by the invasive shrub, Amur honeysuckle and a fairly dense mesophytic tree regeneration layer. More specifically, the seedling and sapling densities found in the study site were dominated by black cherry, *Viburnum*, hickory, and slippery elm. This provides evidence that if left unmanaged, the study site would transition further to a closed canopy, mesophytic forest, which is similar to findings from Midwestern upland oak savanna, where black cherry in particular has experienced an increase in basal area and density in no burn units since 1984 (Peterson and Reich 2001). The transformations that have occurred in the oak savanna restoration study site at Nachusa Grasslands are similar to commonly reported transformations that have occurred in many Midwestern oak savanna sites, including: an increase in tree density, basal area and cover of mesophytic, shade-tolerant, fire-sensitive species and an increased decline in white oak regeneration and recruitment during the 20th century (Abrams 1992; Henderson 1995; Bowles and McBride 1998; Peterson and Reich 2001; Albrecht and McCarthy 2006; Wang and Bauerle 2006; Cowell et al. 2010; Brudvig et al. 2011; McEwan et al. 2011).

The density and canopy cover of Amur honeysuckle found in the oak savanna restoration study site at Nachusa Grasslands were comparable to other studies exploring heavily invaded site in the Midwest. More specifically, a study conducted in a variety of habitats in Ohio, including previously mowed meadows, old fields, and mature and regenerating forests found a similar Amur honeysuckle density as this study, with 21,380 plants/ha (Hartman and McCarthy 2004). Furthermore, the understory cover of

Amur honeysuckle in upland forests in southwestern Ohio were reported as commonly exceeding 50 percent, especially in forest stands having a tree basal area of less than 30 m^2/ha (Hutchinson and Vankat 1997), a basal area similar to the overall basal area estimated for the study site at Nachusa Grasslands. Furthermore, Hutchinson and Vankat (1997) found that Amur honeysuckle cover was positively related to estimated invasion times, with cover of greater than 50 percent only occurring in sites that had been invaded for at least 12 years. Preliminary research on the timing of Amur honeysuckle invasion in the oak savanna restoration study site at Nachusa Grasslands (Goldblum et al. unpublished), along with the average Amur honeysuckle cover found in this study, suggests that the invasion of Amur honeysuckle at the oak savanna restoration study site initiated more than a decade ago. Increased density of shade-tolerant and invasive species within previously open oak savanna communities suppresses the oaks and prevents them from ultimately recruiting to the canopy layer (Albrecht and McCarthy 2006).

In part, Amur honeysuckle encroachment suppresses oak regeneration and recruitment by creating shaded microsites within habitats they invade, which have been shown to decrease light availability, mainly as a result of their dense growth patterns and extended phenology (Luken et al. 1997a; Collier et al. 2002; Cipollini and Dorning 2008; McEwan et al. 2009, 2012). On average, the leaf out spring leaf phenology phase of Amur honeysuckle observed in the oak savanna restoration study site at Nachusa Grassland occurred about 30 days after Amur honeysuckle observed in four central Kentucky forests (McEwan et al. 2009). The difference in climate between locations

may account for the different spring phenology timing, but for both locations, Amur honeysuckle leaf open phase was reported as occurring significantly earlier than the native plants being studied. More specifically, this research found that by the time bud swell initiated for white oak seedlings in the understory of the oak savanna restoration study site at Nachusa Grasslands, the leaves of Amur honeysuckle shrubs were already fully open, creating a dense midstory canopy.

Many of the dominant overstory tree species in the oak savanna restoration study site at Nachusa Grasslands reached leaf open phase before white oak seedlings, thereby further reducing the amount of light reaching the white oak seedlings in the understory. Results from this research found that the total seasonal light measured at one meter above the ground in the oak savanna restoration study site understory at Nachusa Grasslands did not significantly differ from the total seasonal light measured at 30 cm above the ground, both with and without the presence of Amur honeysuckle, which indicates that the current dense overstory tree canopy in the oak savanna restoration study site at Nachusa Grasslands played a large role in the amount of seasonal light received by the understory. This is similar to findings in temperate deciduous forest, where 55 percent of full sun was reported as reaching the forest floor before the leaf-out of the overstory tree canopy, which was then reduced to one to three percent of full sun after the overstory tree canopy had fully developed leaves (Gill et al. 1998). Ultimately the understory mean midday light levels of the oak savanna restoration study site at Nachusa Grasslands were similar to both unmanaged, fire-suppressed (63.3 µmol/m^2) and moderately burned (100.1 µmol/m^2) oak savanna

remnant patches in Michigan, USA (Lettow et al. 2014). Therefore when designing management plans for the oak savanna restoration study site at Nachusa Grasslands, the overstory tree canopy density and basal area are just as important to thin as Amur honeysuckle when attempting to increase the amount of light received by the understory. This is further supported by Brudvig and Asbjornsen (2008) and Craig (2012) who found that white oak seedlings' overall survival rates, in addition to basal diameter, number of leaves, and seedling growth were higher in sites undergoing restoration treatments that included both the removal of large shrubs as well as mesophytic trees.

While the removal of overstory canopy trees is recommended as an important management strategy for increasing light levels within oak savanna restorations to promote the regeneration and recruitment of white oak seedlings, it may at the same time have counteractive results that should be addressed. Recent findings from an invasion model built to encapsulate characteristics found in four non-native invasive shrub species, including *Lonicera maackii*, suggest that invasive species growing in canopy gaps reached reproductive maturity at a younger age, which resulted in higher levels of offspring and an increased rate of spread (Iannone et al. 2014). Increased light levels may also increase the physiological efficiency of Amur honeysuckle and promote higher carbon assimilation rates, especially among the photosynthetically strong Amur honeysuckle, which had the highest light saturation point values in the oak savanna restoration understory at Nachusa Grasslands. Therefore, precautions (i.e. focusing management resources on invasive shrubs growing in canopy gaps) should be built into

management strategies associated with increasing light levels to the understory, to minimize the counteractive consequences of canopy thinning with the aim to conserve white oak (Iannone et al. 2014).

According to Albrecht and McCarthy (2009), light levels of around 35 percent full sunlight are required by white oak to reproduce adequately from seed, maintain positive carbon assimilation rates once the initial seed reserves are exhausted, and produce a sufficient amount of carbohydrates for recruitment into their next stage of development (Rogers 1990; Dey 2002). Given the average midday full sun measured in this study, 35 percent of full sunlight would be about 398.4 µmol /m^2/s, which is higher than the light saturation point for photosynthetically average white oak seedlings surveyed in the oak savanna restoration study site at Nachusa Grasslands, but close to the light saturation point for photosynthetically strong Amur honeysuckle shrubs surveyed in the study site. The low light saturation point found for white oak seedlings at Nachusa Grasslands generally supports Rebbeck et al. (2012) restoration recommendation that there would be no added benefit to opening or increasing light environments any higher than 18% of full sun (equivalent to about 204.9 µmol /m^2/s using the full sun measured at Nachusa Grasslands). More specifically, the findings from this research suggest that about 24 percent of full sun would be optimal (equivalent to about 273.2 µmol /m^2/s using the full sun measured at Nachusa Grasslands), which is slightly above the average light saturation point of the white oak seedlings surveyed in the oak savanna restoration study site. Although it is important to note that these physiological characteristics may vary geographically, therefore, if possible *in situ* physiological surveys of white oak

should be conducted at each restoration site to customize management strategies on a site to site basis.

Sullivan et al. (1996), estimated a mean, light-saturated net assimilation rate for mature white oak trees in the southern Appalachian Mountains as being 7.6 μmol/m^2/s. This study found that, on average, strong white oak seedlings surveyed in the oak savanna restoration study site at Nachusa Grasslands had a maximum assimilation rate of 7.1 μmol/m^2/s, which was significantly different than the weak white oak seedlings that had a maximum assimilation rate of 3.3 μmol/m^2/s. Furthermore, Rebbeck et al. (2012) found that white oak light compensation point was representative of deep shade (7.2 μmol/m^2/s), and may therefore be more shade tolerant than previously thought. The overall average light compensation point of white oak seedlings surveyed in this study was 13.4 μmol/m^2/s, which indicates that light compensation points may also vary geographically and supports the notion that white oak seedlings may be more moderately shade tolerant than previously thought.

Amur honeysuckle has also been classified as being moderately shade tolerant, with plastic physiological and morphological responses to changing light environments (e.g. branch architecture, germination viability, etc.) (Luken et al. 1995, Luken and Thieret 1996; Luken et al. 1997b; Bartuszevige et al. 2006). This study found that the light compensation point of strong Amur honeysuckle did not significantly differ from the light compensation point of weak Amur honeysuckle, and on average was 9.4 μmol/m^2/s. The light saturation point, however, was found to be significantly higher (about 17 percent of full sunlight) for strong Amur honeysuckle when compared to the

light saturation point of weak Amur honeysuckle (about seven percent of full sunlight). Both the light compensation point and light saturation points support the moderately shade tolerant classification of Amur honeysuckle identified in the literature. Even with this moderate shade tolerance, light was identified as still being an important variable in the success of Amur honeysuckle. For example, according to Hutchinson and Vankat (1997) light was the most important factor influencing Amur honeysuckle cover in a particular site, along with distance from seed source. Light availability was also found to be a limitation to the growth of Amur honeysuckle at the seedlings stage, with increased growth rates occurring under higher light conditions (Luken and Thieret 1996).

Previous studies have concluded that the net primary productivity of dense open grown thickets of honeysuckle (1350 g/m-2/yr-1) are nearly as productive as an entire woodland community (Whittaker 1975; Luken and Thieret 1996), potentially due to its extended leaf phenology, which allows a greater access to carbon (McEwan et al. 2006). Overall, the Amur honeysuckle shrubs in the oak savanna restoration study site at Nachusa Grasslands experienced about 48 more days with leaves open than white oak seedlings. On average, however, the extended leaf phenology of Amur honeysuckle that was observed in this study did not significantly increased the amount of total seasonal carbon gained by photosynthetically average Amur honeysuckle shrubs when compared to the total seasonal carbon gained by a photosynthetically average white oak seedlings, no matter the light scenario.

Furthermore, results from this research provide indirect evidence that environmental factors (i.e. temperature and precipitation) might be an important factor in

the overall carbon assimilation, particularly when it comes to the physiological variables involves with photosynthesis for Amur honeysuckle and white oak seedlings surveyed in the oak savanna restoration study site. Based on the annual differences found between the physiological variables involved with the carbon assimilation of both white oak seedlings and Amur honeysuckle, temperature was the differentiating factor between high and low dark respiration and light compensation point values, while precipitation was the differentiating factor between high and low quantum use efficiency, light saturation point, and maximum assimilation rates. More specifically, this study found that Amur honeysuckle had a significantly higher dark respiration and lower light compensation point during cooler years. Quantum use efficiency of Amur honeysuckle was found to be significantly higher in during the unusually dry year of the study, while light saturation point and maximum assimilation rates of Amur honeysuckle was highest during moist years. The maximum assimilation rates of white oak seedlings was also found to be significantly higher during moist years, and negatively impacted during the unusually dry year of the study.

Additionally, the oak savanna restoration study site at Nachusa Grasslands, white oak seedlings that survived until the end of this study (2011-2014) were found to have a significantly higher maximum assimilation rate than those white oak seedlings that died during the study. The higher A_{max} rate of the surviving white oak seedlings, however, did not produce significantly different average seasonal carbon assimilation totals among the surviving white oak seedlings and the white oak seedlings that died by the end of the study period, no matter then light scenario in which they were modeled.

As a result, other environmental or physiological factors unexplored directly in this research may have been involved in the mortality of the white oak seedlings.

5.9 CONCLUSION

Ultimately, this research helps clarify what impact invasive shrubs, like Amur honeysuckle, have on the light environment and carbon gain of white oak seedlings, and broadens the physiological understanding of white oak in its early and vulnerable life stages. The findings in this chapter speak to the role of Amur honeysuckle in altering resource competition dynamics and its impacts on native species, which will ultimately strengthen the interpretations concerning its invasive mechanisms and ecology. It also provides a case study by which average seasonal carbon assimilation totals and physiological attributes of white oak seedlings and Amur honeysuckle can be better understood, in order to assist with the conservation of white oak in the Midwest.

In the end, this research answered the following research questions: What role does the extended leaf phenology of Amur honeysuckle play in its leaf-level seasonal carbon gain? What are the existing *in situ* light levels above and below Amur honeysuckle canopies and do those light levels inhibit the ability of *in situ* white oak seedlings to maintain a positive net leaf-level seasonal carbon balance? More specifically, findings from this research provide no evidence that the extended leaf phenology of Amur honeysuckle produce significantly higher average carbon assimilation totals than the white oak seedlings in the oak savanna restoration study site at Nachusa Grasslands, no matter the photosynthetic strength of the plant. While, the mean midday light levels measured *in situ* above and below Amur honeysuckle

canopies in the understory of the oak savanna restoration study site at Nachusa Grasslands indicate that only around 8.7 percent of full sun is reaching plants one meter tall and around 2.5 percent of full sun is reaching plants growing under Amur honeysuckle encroachment. Furthermore, white oak seedlings did not maintain a positive net leaf-level seasonal carbon balance when modeled below the Amur honeysuckle encroachment light scenario. Given that total seasonal carbon assimilation for all three understory light scenarios were not found to be significantly different, management of both Amur honeysuckle encroachment and overstory tree canopies will play a crucial role in decreasing the regeneration and recruitment gap at Nachusa Grassland to sustain white oak as the dominant canopy species.

Based on the light saturation points of the white oak seedlings surveyed in the oak savanna restoration study site at Nachusa Grasslands, it is recommended that the light level be increased to about 24 percent of full sun (or 273.2 μmol /m^2/s). To achieve this, the light level within the understory needs to be increase by between 15 and 21.5 percent. Finally, when considering where to focusing attention and resources when reducing the basal area in the oak savanna restoration study site at Nachusa Grasslands to increase the understory light levels, overstory mesophytic trees should be removed, in addition to the management and reduction of Amur honeysuckle encroachment.

CHAPTER 6: RESULTS

ECOLOGICAL IMPACTS RELATED TO SOIL DYNAMIC PROPERTIES

6.1 INTRODUCTION

As mentioned previously, the main goal of this research was to further understand how the encroachment of Amur honeysuckle impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration study site located at Nachusa Grasslands in Lee County, Illinois, with particular focus on ecological mechanisms required for successful oak regeneration and recruitment. Results from the second research objective are reported in this chapter. The second research objective of this study was undertaken in order to assess general soil variability throughout the oak savanna restoration study site, and analyze soil quality, moisture/temperature, and nutrient characteristics in areas with and without Amur honeysuckle encroachment. More specifically, this results chapter addresses the following questions: Do aggregate stability, soil moisture/temperature, carbon/nitrogen ratios, and levels of other soil nutrients significantly differ in soil found under and away from Amur honeysuckle? Answers to this question will assess soil quality, moisture/temperature, and nutrient characteristics in areas with and without Amur honeysuckle encroachment, with implications for impact on white oak regeneration and recruitment. According to nonparametric Mann-Whitney U tests, no significant differences were found between the soil variables measured in the western and eastern

halves of the oak savanna restoration study site. Consequently, this chapter will only report soil results for the entire site as a whole, rather than separately for both the western and eastern half of the study site.

6.2 GENERAL SOIL VARIABILITY IN OAK REGENERATION STUDY SITE

6.2.1 General Site Soil Taxonomy

Collected primary for use in a separate study comparing uncultivated soil to restored soils (Osterloh et al. in preparation), 20 five meter soil cores were collected from the eastern side of the oak restoration study site at Nachusa Grasslands, as this was the only part of the site open enough to drive the hydraulic soil coring machine to each grid point. Official taxonomic subgroup soil profile classifications were assigned to each soil core based on the descriptions of each core (Appendix B). Soils in the oak savanna restoration study site at Nachusa Grasslands were dominated by Mollic Hapludalfs (50%) and Typic Argiudolls (30%), with smaller proportions of Typic Hapludalfs (10%), Lithic Hapludolls (5%), and Lithic Argiudolls (5%) (Table14). In

Table 14. Table lists each taxonomic subgroup soil classification present in the eastern half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA., along with the number of soil cores (n=20) assigned with each subgroup . Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

Soil Subgroup	Count
Mollic Hapludalf	10
Typic Argiudoll	6
Typic Hapludalf	2
Lithic Hapludoll	1
Lithic Argiudoll	1
TOTAL	20

general, all the soils found in the study site displayed similar dark A horizon colors, with depths that varied in thickness from one grid point to another (Appendix B).

6.2.2 General Site Soil Respiration and Temperature

The overall three year (2011-2013) average soil respiration (soil CO_2 efflux) for the oak savanna restoration study site was 2.250 µmol $m^{-2} \cdot s^{-1} \pm 0.025$ µmol $m^{-2} \cdot s^{-1}$ standard error (SE), with a peak mean soil respiration of 3.065 µmol $m^{-2} \cdot s^{-1} \pm 0.329$ µmol $m^{-2} \cdot s^{-1}$ in July (Table 15). When the soil respiration measurements taken throughout the entire oak savanna restoration study site were compared between years, a nonparametric Kruskal-Wallis test and nonparametric Tukey-like multiple comparison post hoc test found that all average annual soil respirations significantly differed from one another ($p<0.0001$), with 2011 having the highest average annual soil respiration (2.901 µmol $m^{-2} \cdot s^{-1} \pm 0.086$ µmol $m^{-2} \cdot s^{-1}$ SE), followed by 2013 (2.207 µmol $m^{-2} \cdot s^{-1} \pm 0.105$ µmol $m^{-2} \cdot s^{-1}$ SE), and 2012 (1.686 µmol $m^{-2} \cdot s^{-1} \pm 0.053$ µmol $m^{-2} \cdot s^{-1}$ SE), respectively (Figure 60).

Furthermore, the overall three year (2011-2013) average soil temperature at a depth of about 15 cm was 16.28 °C ± 0.05 °C SE. When the soil temperature (15 cm depth) measurements taken throughout the entire oak restoration study site were compared between years, a nonparametric Kruskal-Wallis test and nonparametric Tukey-like multiple comparison post hoc test found that the mean soil temperature in 2011 (16.979 °C ± 0.226 °C SE) was significantly warmer than the mean soil temperature in 2012 (16.374 °C ± 0.210 °C SE) ($p<0.01$) (Figure 61). All other differences were not significant. Ultimately, the average seasonal soil respiration measured throughout the oak savanna restoration study site had a high positive

correlation with the average soil temperature measured at a depth of about 15 cm (0.63; $R^2 = 0.39$) (Figure 62).

Table 15. Average monthly soil respiration values measured between 2011 and 2013 in the oak savanna restoration study site at Nachusa Grasslands, IL. Standard error are reported for all averages.

Month	Soil Respiration ($\mu mol\ m^{-2} \cdot s^{-1}$)
April	1.295 ± 0.230
May	2.065 ± 0.137
June	2.645 ± 0.332
July	3.065 ± 0.329
Aug	2.702 ± 1.146
Sep	1.363 ± 0.498
Oct	1.500 ± 0.235
Nov	0.584 ± 0.062
AVERAGE	**2.250 ± 0.025**

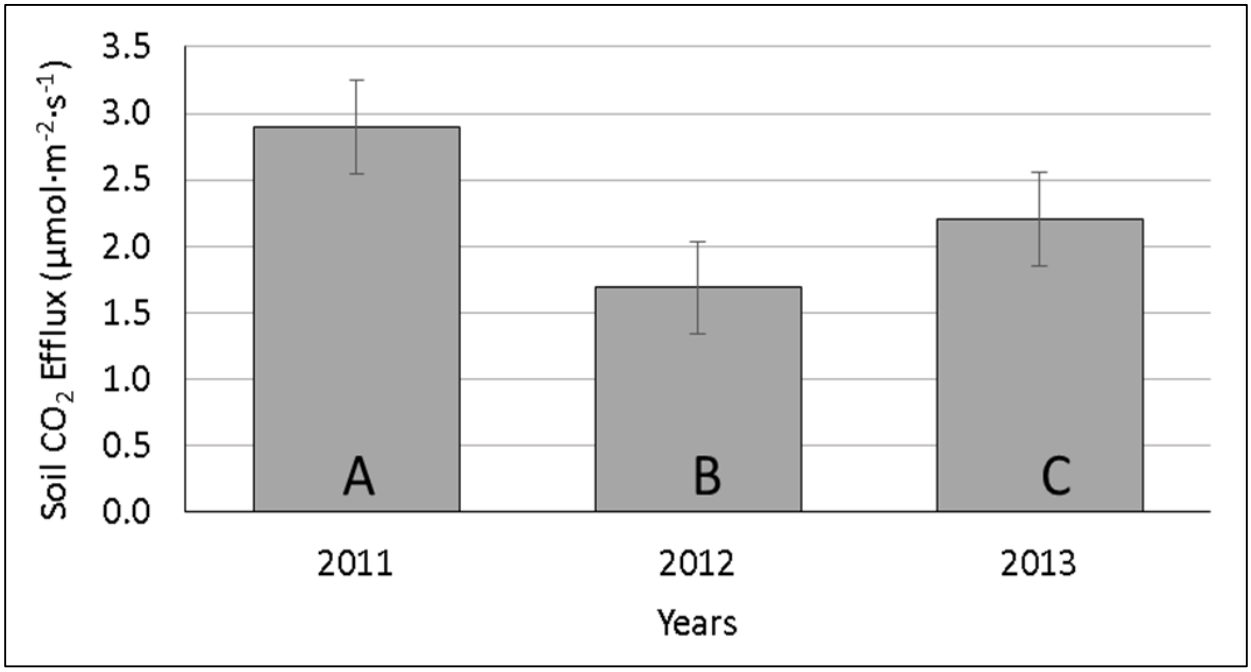

Figure 60. Average seasonal soil respiration (2011-2013) for the oak savanna restoration study site at Nachusa Grasslands, Illinois. Letters indicate statistical difference, while error bars represent 95% confidence interval.

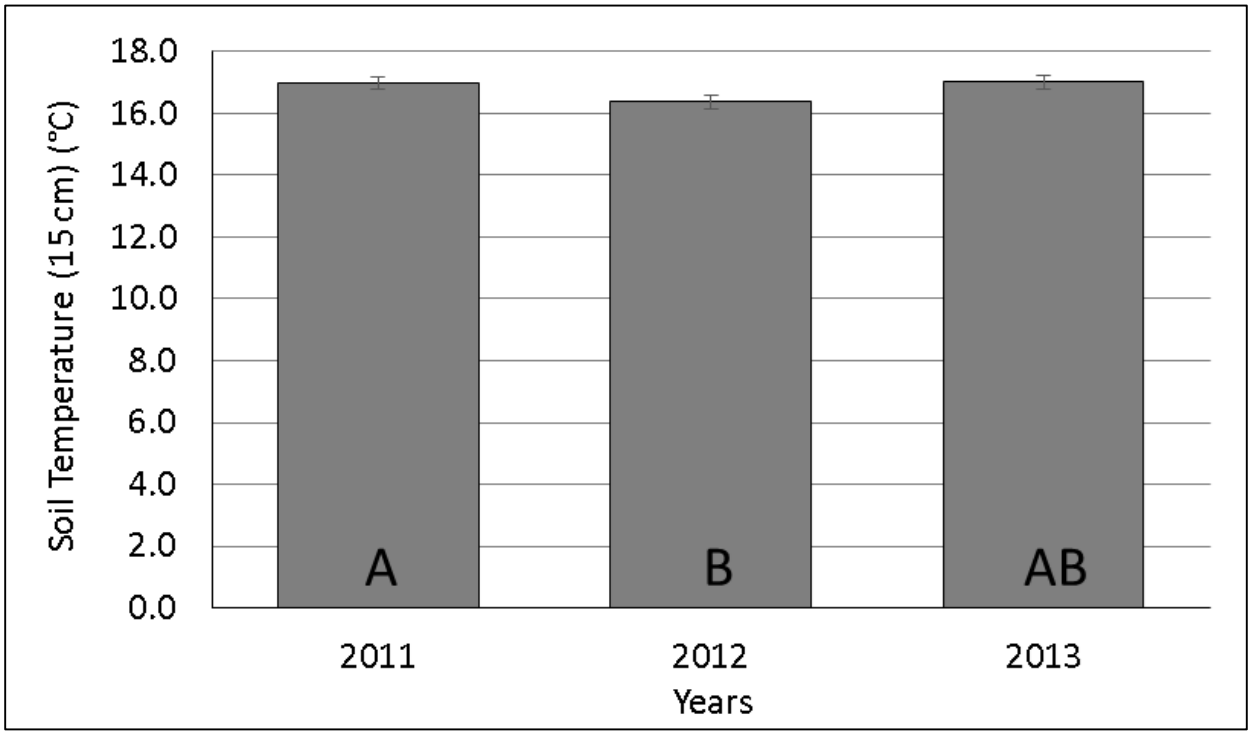

Figure 61. Average seasonal soil temperature measured at about 15 cm depth (2011-2013) for the oak savanna restoration study site at Nachusa Grasslands, Illinois. Letters indicate statistical difference, while error bars represent 95% confidence interval.

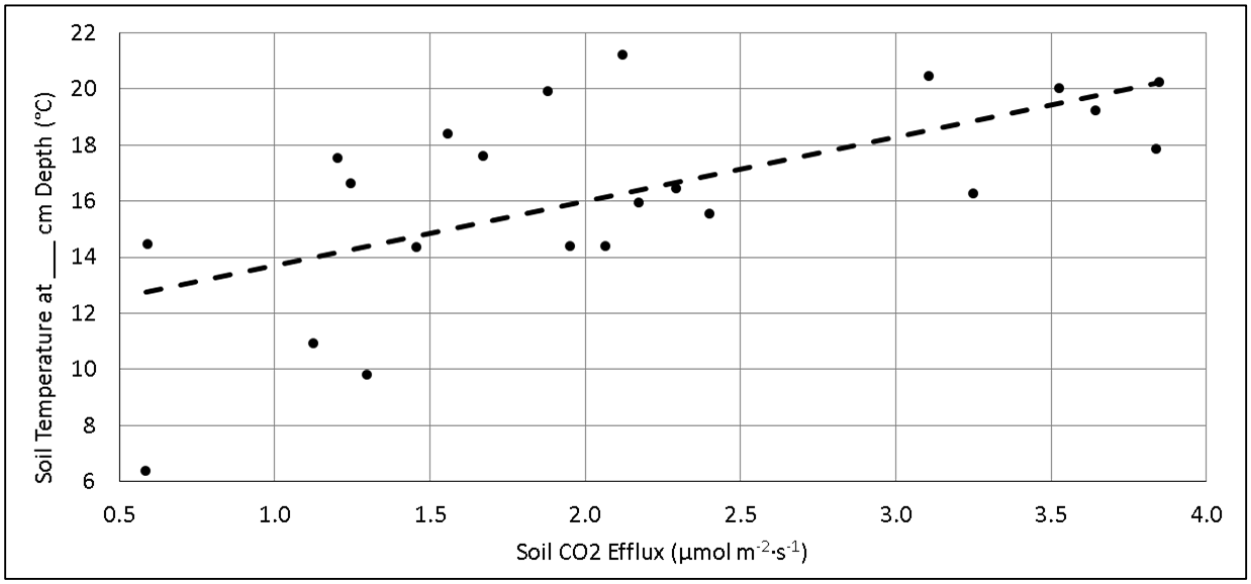

Figure 62. Relationship between average soil respiration and average soil temperature measured at about 15 cm depth in the oak savanna restoration study site at Nachusa Grasslands, Illinois ($y=2.2859x + 11.419$; $R^2 = 0.39$).

6.2.3 General Site Dynamic Soil Properties and Macronutrients

The average carbon nitrogen ratio for the entire study site was 13.9 ± 0.26 SE (ranging from12.3 to 19.2; n = 40) (Table 16). Overall, the A horizon soil texture throughout the oak savanna restoration study site varied between sandy loam, loam, and silt loam (n = 40) (Table 16). The overall average soil pH measured throughout the oak savanna restoration study site was 6.5 ± 0.2 SE, ranging from 5.2 to 7.3 (n=10) (Table 17). The mean Ca level for the oak savanna restoration study site was 2235 ppm ± 364 ppm SE, ranging from 843 ppm to 4168 ppm (n=10) (Table 17). The mean Mg level for the study site was 471 ppm ± 89 ppm SE, ranging from 158 ppm to 905 ppm (n=10) (Table 17). While the mean exchangeable K and forest P were 139 ppm ± 24 ppm SE (ranging from 67 ppm to 314 ppm) and 30 ppm ± 6 ppm SE (ranging from 16 ppm to 72 ppm), respectively (n=10) (Table 17).

Table 16. Soil moisture factor, percent nitrogen (N), percent carbon (C), carbon nitrogen ratio (C:N), particle size analysis results (percent sand, silt, and clay), and soil texture class for each A horizon soil samples from each grid point in the oak savanna restoration study site at Nachusa Grasslands, Illinois. Standard errors are reported for overall averages.

GRID #	MF	%N	%C	C:N	Particle Size Analysis			
					Sand	Silt	Clay	Texture Class
1	1.03	0.28	3.78	13.74	20.3	58.0	21.6	Silt loam
2	1.04	0.25	3.28	12.96	17.4	61.6	21.0	Silt loam
3	1.05	0.25	3.14	12.33	18.2	58.1	23.7	Silt loam
4	1.06	0.57	8.68	15.29	56.7	29.0	14.3	Sandy loam
5	1.03	0.27	3.65	13.39	33.1	55.5	11.4	Silt loam
6	1.03	0.23	2.90	12.54	29.4	57.7	12.9	Silt loam
7	1.03	0.23	2.97	12.68	17.0	69.7	13.3	Silt loam
8	1.03	0.26	3.49	13.18	41.3	45.2	13.4	Loam
9	1.10	0.61	10.82	17.79	67.7	28.3	3.9	Sandy loam
10	1.03	0.20	2.71	13.60	27.5	59.6	12.9	Silt loam
11	1.08	0.52	7.15	13.84	49.9	35.8	14.3	Loam
12	1.07	0.36	5.96	16.36	32.7	49.2	18.1	Silt loam
13	1.05	0.45	8.61	19.10	46.8	36.2	17.0	Loam
14	1.03	0.28	3.49	12.32	19.6	67.4	13.0	Silt loam
15	1.03	0.23	3.10	13.29	24.8	62.7	12.5	Silt loam
16	1.06	0.41	6.23	15.06	36.7	51.0	12.3	Silt loam
17	1.06	0.61	11.77	19.17	51.2	36.6	12.2	Loam
18	1.05	0.30	4.00	13.44	22.9	56.7	20.4	Silt loam
19	1.02	0.21	2.70	12.87	29.5	57.6	12.8	Silt loam
20	1.03	0.18	2.36	13.08	37.2	47.1	15.7	Loam
21	1.04	0.24	3.13	12.90	32.2	50.2	17.6	Silt loam
22	1.04	0.26	3.49	13.40	27.6	56.4	16.1	Silt loam
23	1.03	0.27	3.56	13.40	27.4	62.4	10.2	Silt loam
24	1.03	0.28	3.91	13.76	42.2	48.6	9.2	Loam
25	1.07	0.57	8.69	15.23	52.8	39.7	7.6	Loam
26	1.02	0.23	3.05	13.36	32.8	55.9	11.3	Silt loam
27	1.04	0.26	3.34	12.64	26.1	55.6	18.3	Silt loam
28	1.04	0.25	3.17	12.55	24.3	58.7	17.0	Silt loam
29	1.09	0.43	6.11	14.28	34.1	48.3	17.6	Loam
30	1.03	0.20	2.63	12.87	46.3	39.5	14.2	Loam
31	1.03	0.29	3.83	13.40	16.1	64.0	19.9	Silt loam
32	1.01	0.14	1.91	13.71	78.2	17.6	4.1	Sandy loam
33	1.02	0.19	2.57	13.24	68.6	22.5	8.9	Sandy loam
34	1.01	0.18	2.22	12.55	67.0	28.6	4.4	Sandy loam
35	1.02	0.16	2.17	13.19	63.0	30.8	6.2	Sandy loam
36	1.04	0.27	3.63	13.62	23.8	61.2	15.0	Silt loam
37	1.05	0.34	4.42	13.15	22.0	58.4	19.7	Silt loam
38	1.07	0.37	4.72	12.67	15.3	61.5	23.3	Silt loam
39	1.02	0.15	2.02	13.87	38.1	53.1	8.8	Silt loam
40	1.04	0.26	3.73	14.63	21.1	63.8	15.1	Silt loam
AVERAGE	**1.04** ± 0.003	**0.30** ± 0.02	**4.33** ± 0.38	**13.86** ± 0.26	**35.98** ± 2.63	**49.99** ± 2.09	**14.03** ± 0.80	**Loam**

*Table 17. Soil acidity (pH) and macro*nutrient levels (calcium (Ca), magnesium (Mg), exchangeable potassium (K), and forest phosphorous (P)) measured from soil samples collected from ten gird points throughout the oak savanna restoration study site at Nachusa Grassland, Illinois. Standard errors are reported for overall averages.

GRID #	pH	Ca (ppm)	Mg (ppm)	Exch K (ppm)	Forest P (ppm)
1	6.3	1658	372	117	17
4	7.3	3713	905	314	41
9	7.2	4168	807	205	72
15	6.5	1637	272	81	20
17	7.2	3551	861	186	38
20	6.3	1131	311	67	17
22	6.1	1860	284	102	16
30	6.4	2098	484	116	37
35	5.2	843	158	101	16
36	6.0	1695	256	102	26
AVERAGE	**6.5** ± 0.2	**2235** ± 364	**471** ± 89	**139** ±24	**30** ±6

6.2.4 General Site Soil Moisture and Temperature

Overall average daily and monthly volumetric soil water content (VWC; m^3/m^3) and soil temperatures (°C) at 5 cm depth were calculated using *in situ* measurements collected over three years (May 15, 2012 to December 15, 2014) from ECH_2O probes (Decagon Devices, Inc.; n = 9) placed in the environmental logging stations found throughout the oak savanna restoration study site. The three year mean daily soil moisture level for the study site was 0.197 m^3/m^3 VWC ± 0.017 m^3/m^3 VWC SE, ranging from 0.115 m^3/m^3 VWC in February to 0.302 m^3/m^3 VWC in April (Table 18). The three year mean total monthly soil moisture level for the study site was 279.457 m^3/m^3 VWC ± 24.534 m^3/m^3 VWC SE, ranging from 154.190 m^3/m^3 VWC in February to 434.452 m^3/m^3 VWC in April) (Table 18). The three year mean daily soil temperature at 5 cm depth for the entire oak savanna restoration study site was 10.62 °C ± 2.36 °C SE (ranging from 0.13 °C in January to 21.37 °C in July) (Table 18).

Table 18. Three year (2012-2014) mean daily soil moisture (m^3/m^3 VWC), mean daily total soil moisture (m^3/m^3 VWC), mean monthly total soil moisture (m^3/m^3 VWC), and mean daily soil temperature (°C) for each month in the oak savanna restoration study site at Nachusa Grassland, Illinois. Standard errors are reported for overall averages.

Month	Mean Daily Soil Moisture (m^3/m^3 VWC)	Mean Daily Total Soil Moisture (m^3/m^3 VWC)	Mean Monthly Total Soil Moisture (m^3/m^3 VWC)	Mean Daily Soil Temperature (°C)
January	0.139	6.690	210.740	0.14
February	0.115	5.507	154.190	0.13
March	0.219	10.491	276.271	3.86
April	0.302	14.482	434.452	9.67
May	0.254	12.212	378.576	15.81
June	0.255	12.230	366.895	19.20
July	0.194	9.312	288.679	21.37
August	0.148	7.109	220.378	20.65
September	0.134	6.433	192.981	17.36
October	0.153	7.333	227.311	11.42
November	0.235	11.295	338.857	5.01
December	0.216	10.292	264.151	2.14
AVERAGE	**0.197** ± 0.017	**9.449** ± 0.817	**279.457** ± 24.534	**10.62** ± 2.356

6.2.5 General Site Soil Quality – Aggregate Stability

Stable aggregates generally comprised an average of 91.5% ± 0.8% SE of the oak savanna restoration study site soil (4-0.25 mm), ranging from 71.7% to 99.3%, based on wet aggregate stability analyses conducted using A horizon soil samples taken throughout the study site near sampling grid points (n = 37) (Table 19; Figure 63). More specifically, 71.6% ± 2.3% SE of the overall average stable aggregates were 4-2 mm in size, while 10.3% ± 0.7% SE were 2-1 mm in size, 4.5% ± 0.5% SE were 1-0.5 mm in size, and the remaining 5.1% ± 0.7% SE of the average stable aggregates were 0.5-0.25 mm in size (Figure 64).

Table 19. Listed are the percent stable aggregates found in four size fractions, as well as the overall stable aggregate percentage (4-0.25 mm) for each available A horizon soil sample (blanks indicate inadequate sample volume) from throughout the oak savanna restoration study site at Nachusa Grasslands, Illinois. Standard errors are reported for overall averages.

GRID #	% Stable Aggregates				
	4-2 mm	2-1 mm	1-0.5 mm	0.5-0.25mm	4-0.25 mm
1					
2					
3					
4	87.2	2.5	0.8	1.9	92.4
5	76.0	10.7	3.5	3.3	93.5
6	86.7	4.7	1.4	2.4	95.3
7	85.7	6.0	1.6	1.5	94.7
8	79.8	5.6	2.9	4.2	92.4
9	81.8	6.6	2.2	2.1	92.6
10	70.0	15.3	2.8	3.4	91.4
11	62.3	14.7	6.6	6.0	89.6
12	67.6	13.4	4.7	5.6	91.4
13	75.2	10.5	3.1	2.9	91.7
14	60.7	15.9	8.1	6.0	90.7
15	58.2	17.6	8.6	6.5	90.9
16	73.7	10.7	4.1	3.2	91.7
17	91.6	1.0	0.4	0.8	93.8
18	68.1	13.4	4.9	4.6	91.0
19	73.7	13.8	2.5	2.5	92.5
20	73.1	13.1	3.8	4.2	94.1
21	82.9	7.4	1.6	2.3	94.2
22	78.1	9.8	3.0	3.4	94.4
23	52.6	17.0	9.4	8.4	87.4
24	54.1	11.8	9.1	10.5	85.6
25	78.6	7.0	3.2	3.1	92.0
26	62.5	13.6	6.6	7.9	90.5
27	77.1	8.9	3.3	3.7	93.1
28	85.6	5.8	1.6	1.7	94.7
29	85.2	4.6	1.2	1.5	92.5
30	68.2	13.4	5.0	5.9	92.5
31	75.1	11.3	4.2	3.5	94.0
32	35.2	9.0	12.5	15.0	71.7
33	32.5	12.3	13.0	20.9	78.6
34	58.6	12.3	6.9	8.7	86.5
35	77.3	9.1	2.4	4.3	93.1
36	69.2	15.8	5.6	4.1	94.8
37	84.6	6.4	2.1	2.6	95.8
38	59.3	13.5	7.7	10.4	90.9
39	91.3	4.2	1.5	2.3	99.3
40	71.0	12.1	6.4	5.9	95.5
AVERAGE	**71.6** ± 2.3	**10.3** ± 0.7	**4.5** ± 0.5	**5.1** ± 0.7	**91.5** ± 0.8

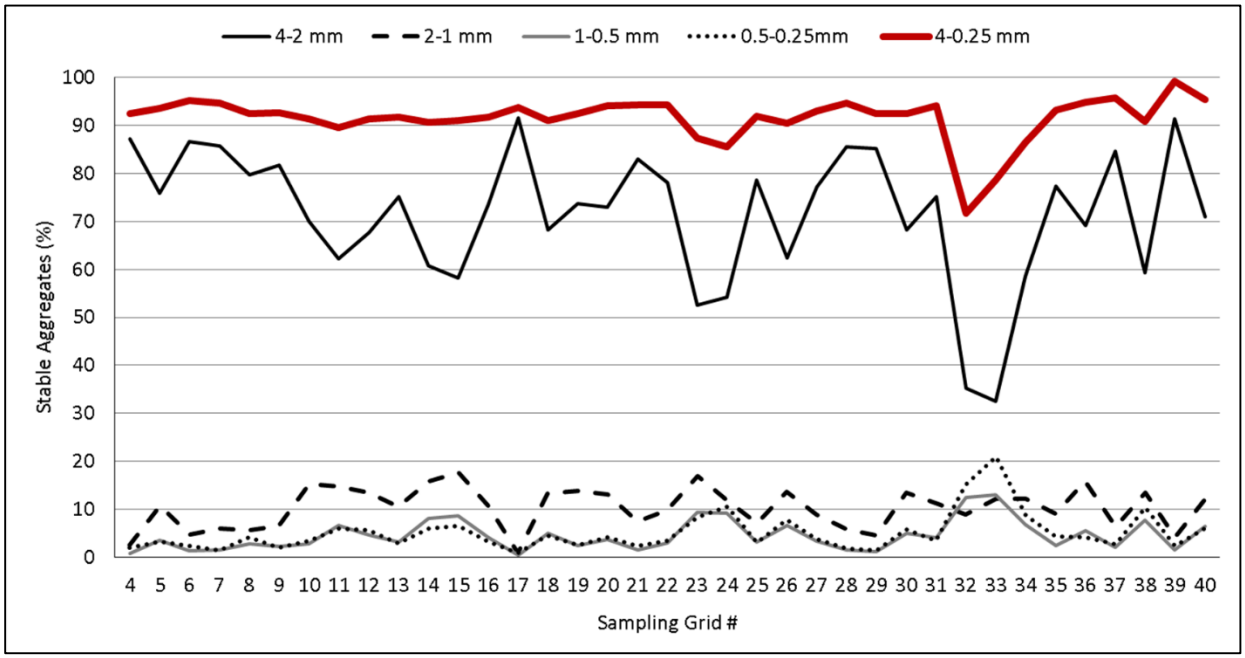

Figure 63. Percent of A horizon wet stable aggregates found in each size fraction (4-2, 2-1, 1-0.5, and 0.5-0.25 mm), as well as the overall mean percent wet stable aggregates for each grid point throughout the oak savanna restoration study site at Nachusa Grasslands, IL.. Sample volumes at grid point 1-3 were inadequate for sampling.

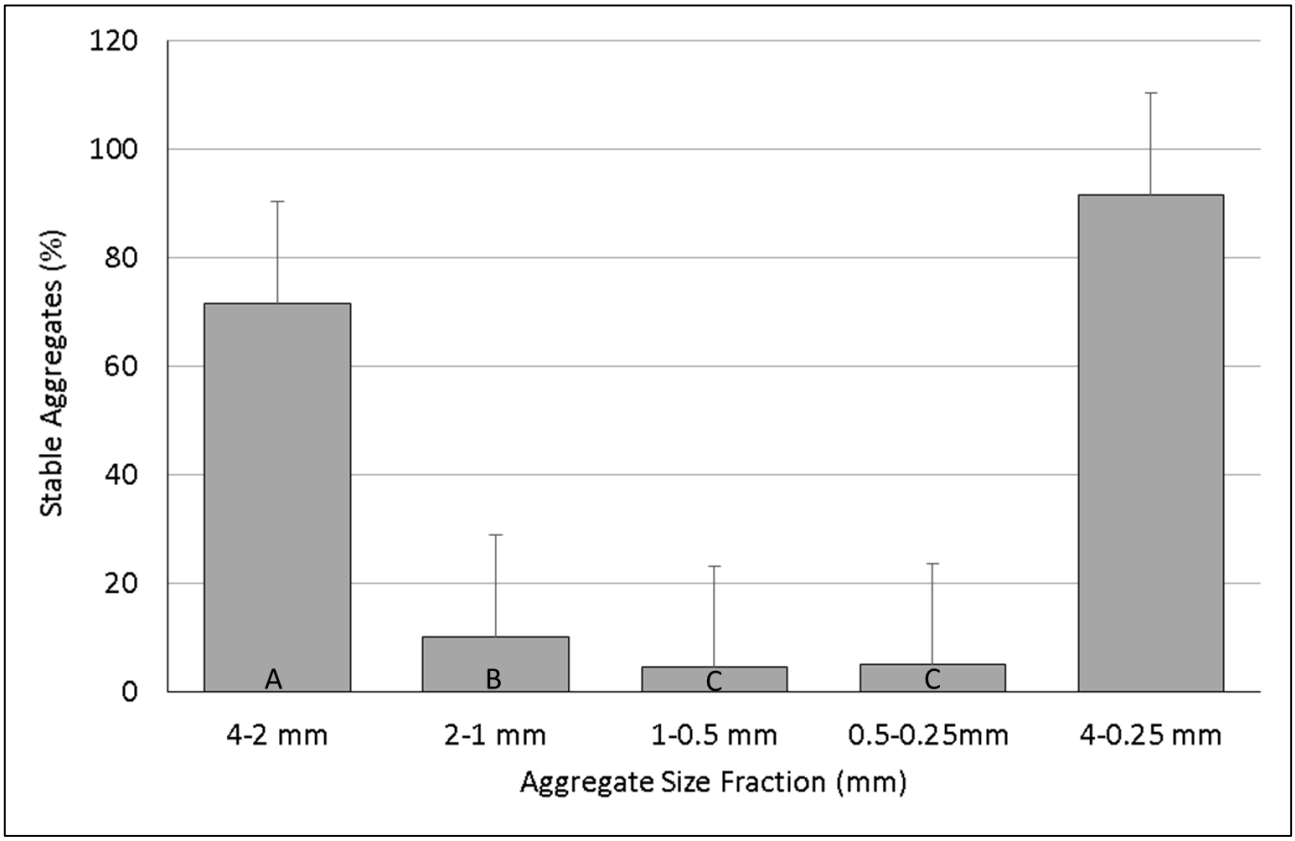

Figure 64. Overall mean percent of A horizon wet stable aggregates (4-0.25 mm) and breakdown of that proportion in each size fraction (4-2, 2-1, 1-0.5, and 0.5-0.25 mm) for soils collected throughout the oak savanna restoration study site at Nachusa Grasslands, IL. Error bars represent 95% confidence interval. Letters denote significance differences ($p<0.0001$).

6.3 SOIL VARIABILITY IN SITES WITH AND WITHOUT AMUR HONEYSUCKLE

6.3.1 Dynamic Soil Properties and Macronutrients

Particle size analyses were conducted on the top A horizon soil samples gathered under and away Amur honeysuckle within the oak savanna restoration study site, in order to explore whether there were differences in soil texture associated with the presence of Amur honeysuckle. The samples collected under Amur honeysuckle had on average 53.47% ± 3.52% SE sand particles (ranging from 36.64% to 68.67%), while the samples collected away from Amur honeysuckle had an average 52.29% ± 3.38% SE sand particles (ranging from 40.94% to 74.28%) (Table 20). As for the proportion of silt in each, the samples collected under Amur honeysuckle had on average 34.27% ± 2.28% SE silt particles (ranging from 25.06% to 47.41%), while the samples collected away from Amur honeysuckle had an average 37.85% ± 3.15% SE silt particles (ranging from 17.96% to 48.89%) (Table 20). Finally, clay particles composed, on average, 12.26% ± 1.59% SE of the samples collected under Amur honeysuckle, while the samples collected away from Amur honeysuckle had on average 9.86% ± 0.55% SE clay particles (ranging from 7.76% to 14.03%) (Table 20). A nonparametric Mann-Whitney U test found that there were no significant differences between the proportion of sand, silt, and clay found in soil samples collected under Amur honeysuckle (n=10) and the soil samples collected in adjacent areas without Amur honeysuckle (n=10). Ultimately, the A horizon soil texture of the soil found both under and away from Amur honeysuckle varied between sandy loam and loam (Table 20).

Based on a nonparametric Mann-Whitney U test, no significant differences were found between the average carbon nitrogen ratios of the soil samples collected under Amur honeysuckle (12.14 ± 0.09 SE; n=10) and the soil samples collected in adjacent areas without Amur honeysuckle (12.26 ± 0.20 SE; n=10) (Table 20). Additionally, no differences in soil pH, Ca, Mg, exchangeable K, forest P, cation exchange capacity (CEC; meg/100g), or hydrogen (H) levels were found between the soil samples collected under Amur honeysuckle (n=10) and the soil samples collected in adjacent areas without Amur honeysuckle (n=10) (Table 21). The overall average soil pH was 5.7 ± 0.1 SE, ranging from 5.2 to 6.5 (Table 21). The mean Ca level was 3714 ppm ± 253 ppm SE, ranging from 1890 ppm to 6516 ppm (Table 21). The mean Mg level was 527 ppm ± 40 ppm SE, ranging from 360 ppm to 1035 ppm (Table 21). The mean exchangeable K and forest P were 150 ppm ± 11 ppm SE (ranging from 80 ppm to 290 ppm) and 93 ppm ± 8 ppm SE (ranging from 64 ppm to 234 ppm), respectively (Table 21). While the mean CEC and H were 14.3 meg/100g ± 0.8 meg/100g (ranging from 9.7 meg/100g to 23.4 meg/100g) and 19.4% saturation ± 1.6% saturation (ranging from 10.5 to 34.0% saturation) (Table 21).

Table 20. Soil moisture factor, percent nitrogen (N), percent carbon (C), carbon nitrogen ratio (C:N), particle size analysis results (percent sand, silt, and clay), and soil texture class for each A horizon soil samples collected from under (n=10) and away (n=10) from Amur honeysuckle in the oak savanna restoration study site at Nachusa Grasslands, Illinois. Standard errors are reported for overall averages.

Sample Type	MF	%N	%C	C:N	Particle Size Analysis			
					Sand	Silt	Clay	Texture Class
HS	1.0047	0.14	1.75	12.14	65.9	25.1	9.0	Sandy loam
HS	1.0048	0.17	2.01	12.00	53.2	38.1	8.7	Sandy loam
HS	1.0044	0.16	1.92	12.01	55.7	35.6	8.7	Sandy loam
HS	1.0064	0.23	2.88	12.37	58.8	29.6	11.6	Sandy loam
HS	1.0037	0.16	1.96	12.17	68.7	25.1	6.3	Sandy loam
HS	1.0041	0.14	1.71	11.89	62.9	29.6	7.5	Sandy loam
HS	1.0078	0.16	1.86	11.84	46.4	34.6	19.0	Loam
HS	1.0077	0.29	3.74	12.82	36.6	47.4	15.9	Loam
HS	1.0071	0.27	3.19	11.92	49.0	35.3	15.8	Loam
HS	1.0078	0.24	2.89	12.19	37.5	42.4	20.1	Loam
no HS	1.0068	0.23	2.87	12.36	41.7	48.9	9.4	Loam
no HS	1.0064	0.22	2.45	11.14	40.9	45.0	14.0	Loam
no HS	1.0066	0.24	2.80	11.55	45.2	45.5	9.3	Loam
no HS	1.0047	0.15	1.80	11.81	48.1	41.7	10.3	Loam
no HS	1.0049	0.19	2.37	12.44	58.3	33.0	8.8	Sandy loam
no HS	1.0062	0.20	2.59	13.03	48.5	41.2	10.3	Loam
no HS	1.0058	0.21	2.72	13.13	48.5	43.3	8.3	Loam
no HS	1.0052	0.16	1.96	12.39	65.3	24.2	10.5	Sandy loam
no HS	1.0040	0.15	1.96	12.64	74.3	18.0	7.8	Sandy loam
no HS	1.0034	0.14	1.67	12.10	52.3	37.9	9.9	Sandy loam
Combined AVERAGE	**1.0056** ± 0.0003	**0.19** ± 0.01	**2.35** ± 0.13	**12.20** ± 0.11	**52.88** ± 2.63	**36.06** ± 1.94	**11.06** ± 0.86	**Sandy Loam**

Table 21. Soil acidity (pH) and macronutrient levels (calcium (Ca), magnesium (Mg), exchangeable potassium (K), and forest phosphorous (P), cation exchange capacity (CEC), and hydrogen (H)) measured in soil samples collected from under (n=10) and away (n=10) from Amur honeysuckle in the oak savanna restoration study site at Nachusa Grassland, Illinois. Standard errors are reported for overall averages.

Sample Type	pH	Ca (ppm)	Mg (ppm)	Exch K (ppm)	Forest P (ppm)	CEC (meg/100g)	H (% sat)
HS	5.9	3690	513	100	68	13.3	13.5
HS	5.2	2169	360	116	70	10.3	31.5
HS	5.5	3159	432	80	80	12.3	20.2
HS	6.1	5445	423	184	76	17.6	11.4
HS	5.6	3114	360	102	106	11.6	18.5
HS	5.5	2340	405	118	68	9.7	20.6
HS	6.5	4509	918	210	84	16.3	5.8
HS	5.6	6516	666	290	234	23.4	16.8
HS	5.7	4167	612	194	80	15.8	16.3
HS	6.0	4995	1035	152	70	19.3	12.0
no HS	5.3	3464	495	126	84	15.5	29.8
no HS	5.5	3636	540	156	100	14.9	22.7
no HS	5.4	3798	630	148	104	16.3	24.4
no HS	5.2	1890	414	174	88	10.1	34.0
no HS	5.5	3465	369	110	112	13.0	20.6
no HS	5.8	3195	369	188	90	11.5	15.2
no HS	5.8	4446	549	184	118	16.1	15.3
no HS	6.1	4455	558	144	68	15.2	10.5
no HS	5.4	2898	414	88	64	12.1	25.2
no HS	5.4	2925	468	140	96	12.4	23.9
Combined AVERAGE	**5.7** ± 0.1	**3714** ± 253	**527** ± 40	**150** ± 11	**93** ± 8	**14.3** ± 0.8	**19.4** ± 1.6

6.3.2 Soil Moisture and Temperature

Volumetric soil water content (VWC; m^3/m^3) and soil temperature (°C) at 5 cm depth were measured every 30 min. for two years (2013 and 2014) in the understory of the oak savanna restoration study site: near Amur honeysuckle stems (n=12), at Amur honeysuckle dripline (n=12), and at least one meter away from any Amur honeysuckle (n=6). Average daily volumetric soil water content levels (VWC; m^3/m^3) and daily soil temperatures were calculated for the active growth period of both white oak seedlings and Amur honeysuckle (May 16-December 14). According to a nonparametric Kruskal-Wallis test, no significant differences in either daily soil moisture (VWC; m^3/m^3) or daily soil temperature (°C) were found between in any of the measurements locations under or away from Amur honeysuckle (Table 22). The overall two year average daily soil moisture across all locations was 0.204 $m^3/m^3 \pm 0.003$ m^3/m^3 SE, while the overall two year average daily soil temperature across all locations was 14.5 °C ± 0.3 °C SE.

Table 22. Two year (2013-2014) seasonal mean daily soil moisture (m^3/m^3 VWC) and mean daily soil temperature (°C) for soil in the understory of the oak savanna restoration study site located: 1) at least one meter away from Amur honeysuckle (open; n=6), 2) near Amur honeysuckle stems (n=12), and 3) at Amur honeysuckle driplines (n=12) at Nachusa Grassland, Illinois. Standard errors are reported for overall averages.

	Soil Moisture (m^3/m^3 VWC)			Soil Temperature at 5 cm (°C)		
Month	**Open**	**Stem**	**Dripline**	**Open**	**Stem**	**Dripline**
May	0.306	0.244	0.289	17.29	16.75	17.08
June	0.317	0.275	0.305	19.19	18.73	18.89
July	0.231	0.221	0.223	20.14	19.70	19.83
August	0.152	0.152	0.150	20.65	20.31	20.49
September	0.146	0.153	0.152	17.02	16.83	16.93
October	0.149	0.158	0.154	11.46	11.30	11.42
November	0.217	0.231	0.232	4.14	4.06	4.25
December	0.142	0.196	0.156	0.89	0.87	0.94
AVERAGE	**0.207** ± 0.026	**0.204** ± 0.016	**0.208** ± 0.023	**13.85** ± 2.69	**13.57** ± 2.63	**13.73** ± 2.64

6.3.3 Soil Quality – Aggregate Stability

A Mann-Whitney U test found no significant differences within the proportion of stable soil aggregates measured in any of the size fractions (i.e. 4-2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm) from soil samples collected under (n=10) and away (n=10) from Amur honeysuckle in the understory of the oak savanna restoration study site (Table 23; Figure 65 and 66). Similarly, no significant differences were found within the overall proportion of stable soil aggregates for all size fractions combined (4-0.25 mm) from soil samples collected under (n=10) and away (n=10) from Amur honeysuckle in the understory of the oak savanna restoration study site (Table 23; Figure 65 and 66).

When combined, given there were no differences between presence and absence of Amur honeysuckle, the stable soil aggregates represented an average of 85.8% ± 0.8% SE of the combined soil collected under and away from Amur honeysuckle (4-0.25 mm), ranging from 78.2% to 90.9% based on the wet aggregate stability analyses (Table 23). More specifically, 53.1% ± 2.6% SE of the overall average stable aggregates were 4-2 mm in size, while 15.5% ± 0.7% SE were 2-1 mm in size, 8.2% ± 0.7% SE were 1-0.5 mm in size, and the remaining 9.0% ± 1.1% SE of the average stable aggregates were 0.5-0.25 mm in size (Table 23).

Table 23. Listed are the percent stable aggregates found in four size fractions (4-2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm), as well as the overall stable aggregate percentage (4-0.25 mm) for each available A horizon soil sample collected under (n=10) and away (n=10) from Amur honeysuckle in the oak savanna restoration study site at Nachusa Grasslands, Illinois. Standard errors

	% Stable Aggregates				
Sample Type	**4-2 mm**	**2-1 mm**	**1-0.5 mm**	**0.5-0.25mm**	**4-0.25 mm**
HS	32.9	13.9	10.0	23.6	80.4
HS	39.4	13.0	13.2	17.3	82.9
HS	65.7	14.0	3.9	3.9	87.4
HS	55.8	16.6	7.5	7.5	87.3
HS	67.6	12.7	4.3	4.3	88.9
HS	46.7	20.1	9.0	9.0	84.8
HS	37.8	16.7	11.9	11.9	78.2
HS	58.0	13.5	7.9	7.9	87.4
HS	68.5	11.6	4.6	4.6	89.3
HS	64.3	14.5	5.8	5.8	90.5
no HS	47.2	23.8	10.8	9.2	90.9
no HS	42.5	16.7	14.0	14.4	87.6
no HS	53.2	17.5	8.2	8.2	87.0
no HS	42.8	16.8	10.0	10.0	79.7
no HS	70.1	10.6	4.0	4.0	88.8
no HS	56.2	14.1	8.0	8.0	86.2
no HS	65.7	11.8	5.3	5.3	88.2
no HS	50.3	16.8	9.8	9.8	86.7
no HS	56.2	17.2	5.9	5.9	85.2
no HS	40.8	18.9	9.8	9.8	79.2
Combined AVERAGE	**53.1** ± 2.6	**15.5** ± 0.7	**8.2** ± 0.7	**9.0** ± 1.1	**85.8** ± 0.8

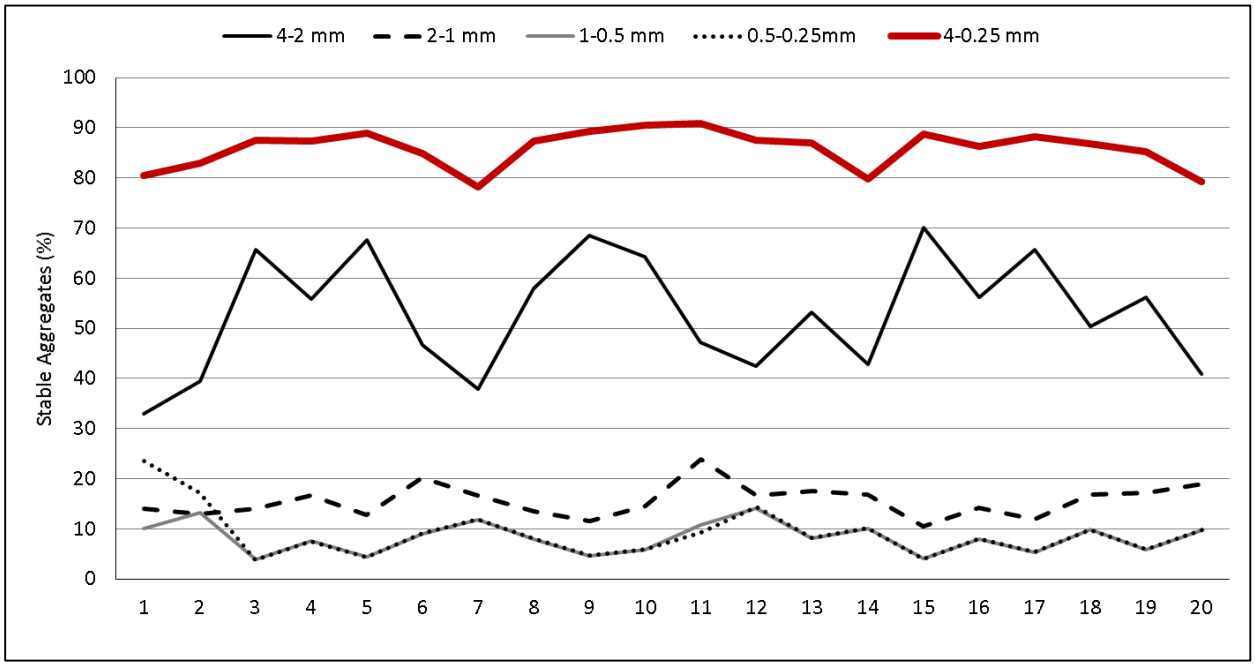

Figure 65. Percent of A horizon wet stable aggregates found in each size fraction (4-2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm), as well as the overall mean percent wet stable aggregates (4-0.25 mm) for each sample collected under (1-10) and away (11-20) from Amur honeysuckle in the oak savanna restoration study site at Nachusa Grasslands, IL.

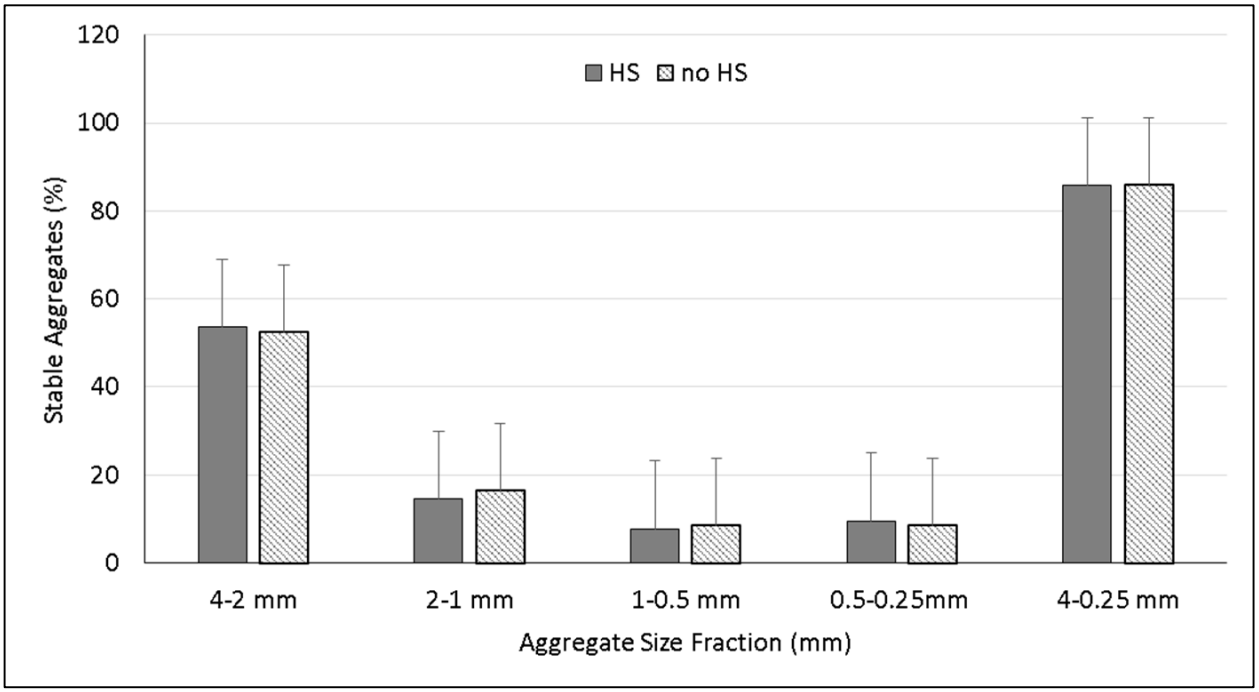

Figure 66. Overall mean percent of A horizon wet stable aggregates (4-0.25 mm) and breakdown of that proportion in each size fraction (4-2 mm, 2-1 mm, 1-0.5 mm, 0.5-0.25 mm) for soils collected under (HS) and away (no HS) from Amur honeysuckle in the oak savanna restoration study site at Nachusa Grasslands, IL. Error bars represent 95% confidence interval. No significant differences were found.

6.4 DISCUSSION

Ultimately, this chapter aimed to characterize the current soil variability of the oak savanna restoration study site at Nachusa Grasslands, IL, while also analyzing soil quality, moisture/temperature, and nutrient characteristics in areas with and without Amur honeysuckle encroachment, with overall implications for impact on white oak regeneration and recruitment.

White oak seedlings establish best on loose, deep, well-drained loamy soils with light to moderate litter cover and an adequate amount of soil moisture (Minckler 1965; Rogers 1990; Dey 2002). The soil texture classes found in the oak savanna restoration study site at Nachusa Grasslands fell within a range of loamy soils (i.e. sandy loam, loam, and silt loam). However, compared to many Midwest tall-grass oak savannas that developed on deep silty clay loam soils (Apfelbaum and Haney 1991), the soils found in the oak savanna restoration study site had less clay, given that no silty clay loam soils were identified in the site. Ultimately, white oak is adapted to all soil textures except fine textured soils (USDA 2015d), and all soils found in the study site were well within the range of ideal soil textures for white oaks, and therefore should not be considered as an inhibiting factor for the regeneration and recruitment of white oak in the oak savanna restoration study site. Additionally, Amur honeysuckle was found thriving across multiple soil textures within the oak savanna restoration study site, which suggests that soil texture was also not a limiting factor for Amur honeysuckle at Nachusa Grasslands.

Soil moisture has been reported as being essential for maintaining oak seed viability, supporting seedling survival until root maturity, regulating leaf-level plant

carbon dynamics, and influencing soil respiration rates; which itself is an environmental indicator of root respiration and microbial decomposition of soil organic matter (Hanson et al. 1993; Raich and Tufekciogul 2000; Dey 2002; Smith and Johnson 2004; Tang and Baldocchi 2005; Tang et al. 2005; Curiel Yuste et al. 2007; Kuzyakov and Gavrichkova 2010; Lewis 2011). The overall soil moisture found in the oak savanna restoration study site at Nachusa Grasslands was higher than soil moisture found in other oak savanna communities, by as much at 51% and as little as 16% (Tang et al. 2005). As a result, soil moisture was also determined to not be a limiting factor for the regeneration and recruitment of white oak in this study, especially given the medium drought tolerance and medium moisture usage of white oak (Larson and Whitmore 1970; USDA 2015d). In general, the soil moisture levels measured in the understory of the oak savanna restoration site indicated that the site was generally well drained (i.e. plants have access to available water throughout much of the growing season and soil is generally free of redoximorphic features related to excessive wetness; Soil Survey Division Staff 1993), and therefore ideal conditions for white oak (USDA 2015d). Ultimately, soil moisture and temperature are indispensable variables for understanding and evaluating vegetation patterns and dynamics, especially in relation to vegetation with dense canopy cover (e.g. invasive species encroachment, etc.) that might compete for water resources by altering transpiration rates, intercepting precipitation, creating shaded microsites, and lowering soil temperature (Breshears et al. 1998; Legates et al. 2010).

The fact that no significant differences in soil moisture or temperature were found in the oak savanna restoration study site across a gradient of Amur honeysuckle

encroachment was contradictory to previous research that found altered soil moisture levels in Amur honeysuckle invaded sites, in part as a result of the dense (almost monoculture) growth patterns, higher total foliar biomass, widespread shallow root systems, and extended phenology that allows less water to reach the forest floor (Trisel 1997; Collier et al. 2002; Cipollini and Dorning 2008; McEwan et al. 2012). These contradictory findings may be in part as a result of the dense overstory tree canopy found within the oak savanna restoration study site. Perhaps if this study was repeated in a more open canopy oak savanna restoration site at Nachusa Grasslands, the results may reflect the findings of previous research.

Plant-available mineral macronutrients (e.g. nitrogen, phosphorus, potassium, calcium, magnesium, etc.) are important to the initial establishment and growth of seedlings, as well as to the long-term survival of many plants, including white oak (Dey 2002). The overall average soil carbon nitrogen ratios found in the oak savanna restoration study site resembled soil carbon nitrogen ratios found in a Californian oak savanna community dominated by blue oak (12.5) (Curiel Yuste et al. 2007). This means that the oak savanna restoration study site has similar soil characteristics as other oak savanna communities. According to Bremner (1996), most cultivated soils contain between 0.06% and 0.5% nitrogen in the surface soil horizon. This study found that the never cultivated oak savanna restoration site contained an average of 0.19% nitrogen, which is 38% of the maximum nitrogen found in most cultivated soils.

Previous research has hypothesized that the shallow root system of Amur honeysuckle could potentially reduce availability of nutrients in the upper soil, thereby

decrease tree seedling survival as a result of root competition (Trisel 1997; Collier et al. 2002). Additionally, the extended leaf phenology of Amur honeysuckle has also been previously associated with altering rainwater chemistry, which results in a decreased depositions of ammonium nitrogen (NH4+-N) and higher cation concentrations (particularly magnesium (Mg2+) and potassium (K+)) (McEwan et al. 2012). The oak savanna restoration study site, on the other hand, had very high cation concentrations (i.e. Ca, Mg, Exchangeable K, Forest P) when compared to other Midwestern oak savanna sites in Ohio (Tenney 2007), which had a fraction of the nutrients (1% and 8%) found in this study at Nachusa Grasslands. The high nutrient availability found at Nachusa Grasslands indicates that nutrients are not a limiting factor for white oak in the oak savanna restoration site, especially given their adaptations to low fertility sites (USDA 2015d). Additionally, soil pH was identified as one of the most informative measurement in determining the characteristics of a soil, such as soil toxicity and essential nutrient availability (Thomas 1996). The ideal soil pH for white oak ranges from 6.8 to 4.5 (USDA 2015d), within which falls the overall average soil pH measured at the oak savanna restoration study site. Furthermore, no significant differences in any soil nutrient or acidity were found in the oak savanna restoration study site under or away from Amur honeysuckle, which suggests that the shallow root system and extended leaf phenology of Amur honeysuckle does not represent direct belowground competition for white oak regeneration and recruitment in this particular site.

Soil respiration is an important environmental indicator of root respiration and microbial decomposition of soil organic matter in a site (Kuzyakov and Gavrichkova

2010). The availability of nutrients and water for plant growth, as well as the activity of soil microbes are ultimately determined by soil biogeochemical processes and soil chemical properties which vary over space and through time (Bhandari and Ficklin 2009). Understanding these properties and processes are key to environmental monitoring, developing management strategies, and conducting soil quality assessments (Bhandari and Ficklin 2009). The overall average soil respiration (CO_2 efflux) measured in the oak savanna restoration study site closely resembled the mean soil respiration of a Californian oak savanna community dominated by *Quercus douglasii* (blue oak) (2.26 μmol $m^{-2} \cdot s^{-1}$) (Tang and Baldocchi 2005), in addition to a freshly burned or unburned Midwestern oak savanna site in Ohio (3.86 μmol $m^{-2} \cdot s^{-1}$) (Tenney 2007). The average soil respiration rate in a northeastern Kansas woodland (4.6 μmol $m^{-2} \cdot s^{-1}$) with a 39% higher mean tree density and 7% lower mean basal area, on the other hand was more than double that found in the oak savanna restoration study site at Nachusa Grasslands (Smith and Johnson 2004). The average peak monthly soil respiration in the Californian oak savanna community, however, was over 50% higher (6.25 μmol $m^{-2} \cdot s^{-1}$) than the peak monthly soil respiration measured in the Illinois oak savanna restoration study site, and occurred in June (Tang et al. 2005), while the peak soil respiration found in this study occurred in July. These findings suggest that soil respiration varies geographically.

Ultimately, the strong positive correlation found between average soil respiration and average soil temperature in the oak savanna restoration study site supported previous research findings that temperature and moisture availability influence soil

respiration rates (Hanson et al. 1993; Raich and Tufekciogul 2000). The R^2 value associated with the correlation between soil respiration and soil temperature found in this study, however, indicates that other variables, unexplored by this study, may also be an important component to this relationship (Tang et al. 2005; Curiel Yuste et al. 2007; Vargas et al. 2011).

Beyond soil moisture, temperature, and nutrients, the quality of a soil characterizes its ability to function within an ecosystem, in relation to supporting biological productivity (e.g. plant regeneration, growth, recruitment, etc.), improving plant and animal health, and preserving overall environmental quality; goals that are often also important for restoration projects (Doran and Parkin 1994; Doran et al. 1996; Karlen et al. 1997; Page-Dumroese et al. 2000, 2010). Among the dynamic soil properties that convey soil quality, soil aggregate stability is one of the most functionally important properties, since it can be used to assess the status of other critical ecosystem processes (i.e. soil infiltration rates, resistance to erosion, crop production, and soil sustainability) that are central components to developing and appropriately applying successful conservation land management strategies (Yoo et al. 1998; Amezketa 1999; Bird et al. 2002, 2007; Bronick and Lal 2005; Breetzke et al 2013; Nciizah and Wakindiki 2015).

According to the landmark hierarchical aggregate model developed by Tisdall and Oades (1982), particles (<0.020 mm) bind together via persistent binding agents to form stable micro-aggregates (0.020-0.250 mm) that are less impacted by management regimes than the macro-aggregates (>0.250 mm) formed of micro-aggregates bound

together by temporary binding agents. In general, all soils analyzed in the oak savanna restoration study site at Nachusa Grasslands (including those collected under Amur honeysuckle) had a high soil macro-aggregate (4-0.25 mm) stability, with the highest proportion of stable sand-free aggregates occurring in the 4-2 mm size fraction. When overall stable sand-free aggregate proportions (4-0.25 mm) found in the oak savanna restoration study site were compared to the mean proportion of sand-free aggregates (2-0.25 mm) found in vegetation communities located within the transition zone between grasslands and mesquite shrubland in New Mexico in areas with varying degrees of understory vegetation and disturbance (i.e. high grass and low disturbance, high grass and moderate disturbance, low grass and high disturbance) (Bird et al. 2002, 2007), the oak savanna restoration study site at Nachusa Grasslands had almost 50% more stable aggregates. This suggests that even given the high level of disturbance cause by Amur honeysuckle, the soil in the uncultivated oak savanna restoration study site at Nachusa Grasslands has a high quality, given the highly stable macro-aggregates.

Ultimately, Abrams (2003) reported that heavy competition for understory resources by shade-tolerant, mesophytic, and invasive species with oak seedlings usually occurs in all but the most dry (i.e. xeric) and nutrient-poor sites (Abrams 2003). The oak savanna restoration study at Nachusa Grasslands was neither xeric nor nutrient-poor, given the high soil moisture and nutrient findings of this research, suggesting that heavy composition for understory resources may exist within the site. Furthermore, previous research suggests that there are strong links between aboveground and belowground ecosystem properties (Kardol and Wardle 2010),

however, like McEwan et al (2012) and Wilson et al. (2013), this study found no significant differences between any of the soil characteristics (i.e. wet macro-aggregate soil stability, soil moisture, soil temperature, carbon nitrogen ratios, and nutrient levels) measured in adjacent soil samples collected under and away from Amur honeysuckle throughout the western half of the oak savanna restoration study site at Nachusa Grasslands. This suggests that competition by and/or presence of Amur honeysuckle had minimal impact on the soil dynamic properties in the oak savanna study site at Nachusa Grasslands.

In the end, the non-significant findings from this belowground assessment were found in areas with similar land-use histories, which has been identified as essential for detecting and confirming invader-induced ecological impacts, rather than ecological impacts that may result from one of the following: 1) historical land uses altering the site's soil nutrient characteristics in a way that would later facilitate the invasion; 2) pre-existing, unaltered soil nutrient characteristics that make the site more vulnerable to the invasion; or 3) a post-invasion modification to the site's ecosystem processes affecting its soil nutrient characteristics by the non-native invasive species, as a result of the invasion (Kourtev et al. 1998; Ehrenfeld 2003; Wilson et al. 2013; Iannone et al. 2015). As long as there are conflicting results concerning the impact of invasive species on belowground ecosystem properties, more research (including long term studies) is needed across a variety of geographic and temporal timescales.

6.5 CONCLUSION

Ultimately, understanding soil properties and processes and how they are altered (or unaltered in this case) by invasive species encroachment, are key to environmental monitoring, developing effective management strategies, and conducting soil quality assessments (Bhandari and Ficklin 2009). The nonsignificant findings of this chapter suggest that, when it comes to wet macro-aggregate soil stability, soil moisture, soil temperature, carbon nitrogen ratios, and nutrient levels in the oak savanna restoration study site at Nachusa Grasslands, there is no evidence that Amur honeysuckle alters these soil properties after invasion, or that these soil properties increase the invisibility or degree of invasion of the site.

The findings reported in this chapter expand our general understanding of dynamic soil and forest floor properties (e.g. soil moisture, carbon, nitrogen, and available plant nutrient levels) in relation to the environmental impacts of Amur honeysuckle encroachment, and provide further support that impact of soil characteristics may differ spatially from one site to another. Additionally, these findings facilitates a more accurate discussion about how the encroachment of Amur honeysuckle impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration study site located at Nachusa Grasslands in Lee County, Illinois, with particular focus on ecological mechanisms required for successful oak regeneration and recruitment. Ultimately, findings from this study provide no evidence that Amur honeysuckle alters or selects particular soil properties characteristics, meaning that the white oak regeneration and recruitment gap at this site

must be influenced by other environmental factors. Management efforts to increase white oak seedlings regeneration and recruitment in the oak savanna restoration study site at Nachusa Grasslands should therefore be focused on other understory resource competition dynamics beyond belowground properties.

CHAPTER 7: RESULTS

EVOLUTIONARY INVASION DYNAMICS OF AMUR HONEYSUCKLE

7.1 INTRODUCTION

Beyond assessing the ecological impacts of one of the most aggressive and abundant invasive species: Amur honeysuckle on white oak populations in Northern Illinois, this research also aimed to investigate the underlying evolutionary mechanisms associated with the spatial-temporal long distance dispersal patterns of Amur honeysuckle, as inferred by population genetics, to better understand the mechanisms and pathways by which this species is spreading throughout the Midwest United States. Specifically, this results chapter addresses the following questions: Did Amur honeysuckle spread into Illinois via natural and/or anthropogenically facilitated long-distance dispersal followed by outward expansion through local and/or regional dispersal and do the results from a genetic structure analysis support any of the following three proposed invasion pathways, identified based on historical records; specifically:

1) West via anthropogenically facilitated long-distance dispersal from the first recorded U.S. locations of entry for Amur honeysuckle: *New York Botanical Garden, NY and Arnold Arboretum of Harvard University, MA* (Luken and Thieret 1996);

2) West from the site that first recorded the invasive and escapable nature of Amur honeysuckle near Chicago: *Morton Arboretum, Lisle, IL* (Luken and Thieret 1996); and/or

3) North and south from regional sites in IL: *Hidden Springs State Forest, Strasburg, IL and Trail of Tears State Forest, Jonesboro, IL* (EDDMapS 2015).

Answers to this question will assess the general geographic and evolutionary patterns associated with the historic range expansion of the Amur honeysuckle shrub throughout the eastern and central United States, with implications for identifying past and future invasion pathways and potentially redefining our understanding of long distance dispersal with regards to invasive species.

7.2 DNA EXTRACTION VERIFICATION RESULTS

After extracting the genomic DNA from each Amur honeysuckle sample collected from the seven subpopulations (n=80; including the samples collected from the western and eastern half of the oak savanna restoration study site), a Thermo Scientific NanoDrop Spectrophotometer was used to measure the nucleic acid concentration of 1µl of each sample (Table 24). The NanoDrop values were used as an approximate verification for the success of the DNA extraction. All samples that had higher than 200 ng/µl were diluted, as per the Type-it Microsatellite PCR Kits (Qiagen Inc., Valencia, CA) protocol.

Table 24. Table of the seven populations from which Amur honeysuckle DNA was extracted, accompanied by the geographic coordinates of each site, the number of samples analyzed from each location, the assigned population ID, and NanoDrop results with standard error listed in parentheses.

Site	Geographic Coordinates		Sample Size	Population ID	NanoDrop (ng/ul)
Study Site at Nachusa Grasslands (West), IL	41°53'48.55"N	89°22'20.81"W	12	NGW.IL	160.6 (± 60.3)
Study Site at Nachusa Grasslands (East), IL	41°53'48.25"N	89°22'04.40"W	12	NGE.IL	501.2 (± 132.2)
Morton Arboretum, IL	41°48'43.57"N	88°05'00.16"W	12	MA.IL	86.1 (± 11.2)
Hidden Springs State Forest, IL	39°18'54.44"N	88°41'17.13"W	12	HS.IL	32.2 (± 8.2)
Trail of Tears State Forest, IL	37°29'06.04"N	89°21'53.76"W	8	TT.IL	12.5 (± 1.0)
New York Botanical Garden, NY	40°51'43.54"N	73°52'38.73"W	12	NYBG	75.2 (± 7.0)
Arnold Arboretum at Harvard University, MA	42°17'55.46"N	71°07'30.90"W	12	AA.MA	27.4 (± 11.0)
		TOTAL	80		

7.3 PCR VERIFICATION RESULTS

Polymerase chain reactions (PCR) (n=400) were conducted for each of the 80 individuals sampled across all five microsatellite marker loci using primer pairs specifically developed for Amur honeysuckle (Barriball 2012; Rocha et al. 2014; Sigma/Genosys, The Woodlands, TX, USA) (Table in Methods). Following the PCR step, the samples were separated using gel electrophoresis to verify the success of the PCR. Gel electrophoresis was also used as a quality control diagnostic tool to visualize the fragment sizes, to ensure that the alleles generally fell within the expected size range of between 100-300 base pairs (bp) depending on the locus (Figure 67; Table 25). Yields of the fragments on standard 1% agarose gels varied within and among subpopulations, but all allele size fragments generally fell within the expected allele size range (Figure 67). Ultimately, findings from the verification trials conducted in this study suggest that the yield strengths observed using agarose gel electrophoresis did not

provide a consistent standard by which to determine the viability of a sample for the final capillary fragment analysis at the DNA Analysis Facility on Science Hill at Yale University. More specifically, multiple samples that failed to be visualized on the agarose gel during the initial electrophoresis verification step, ended up producing measureable peaks during the capillary fragment analysis. As a result, all samples were sent to the DNA Analysis Facility on Science Hill at Yale University regardless of their initial screening on the gel.

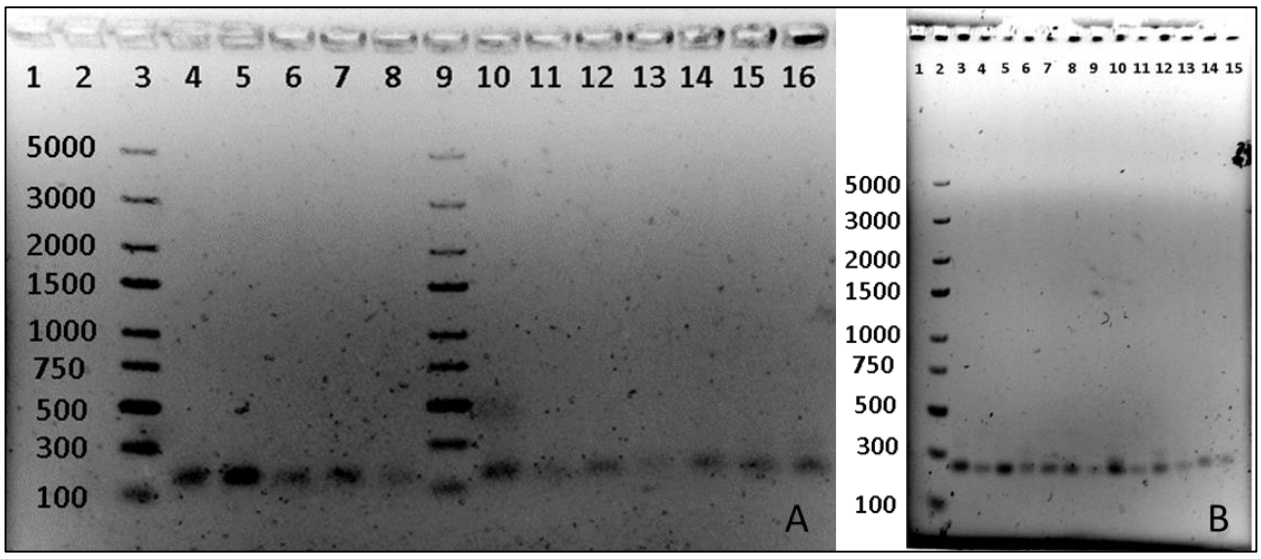

Figure 67. Example electrophoresis agarose gel images used for Amur honeysuckle PCR and allele size verification. Variation of yields within (on same gel) and between populations (across gels) are present in image. Gel A shows amplicons of samples from NYBG population for Tri8 locus, while gel B shows amplicons of samples from the eastern half of Nachusa Grasslands for Di19 locus. GeneRuler Express DNA ladder sizes are reported for reference.

7.4 FRAGMENT ANALYSIS – ALLELE SIZE CURVES

Following capillary fragment analyses conducted at the DNA Analysis Facility on Science Hill at Yale University, raw .fsa output files were used to score the codominant microsatellite markers (via peaks) for all Amur honeysuckle PCR samples (n=400; 80 individuals, 5 loci) using Peak Scanner Software (version 2.0, Applied Biosystems). All samples containing detectable peak(s) was/were identified as either homozygous (i.e. one peak) (Figure 68) or heterozygous (i.e. two peaks) (Figure 69), and corresponding genotype scores (i.e. allele sizes) were assigned and recorded for downstream population genetic analysis using GeneAlEx 6.501 software (Peakall and Smouse 2006, 2012). Samples were not used in the analysis if they had undetectable signals or had more than two peaks, as more samples would be required to differentiate artifacts from sample contamination. Overall, allele sizes were successfully scored for an average of 60 ± 8 samples out of the 80 samples analyzed across each of the five loci, with Di3 having the largest scored sample size (n=73) and Tri8 having the lowest number of scored samples (n=34) (Table 25). A total of 60 alleles was found across the five loci examined in this study, 51 of which were unique (Tables 25 and 26).

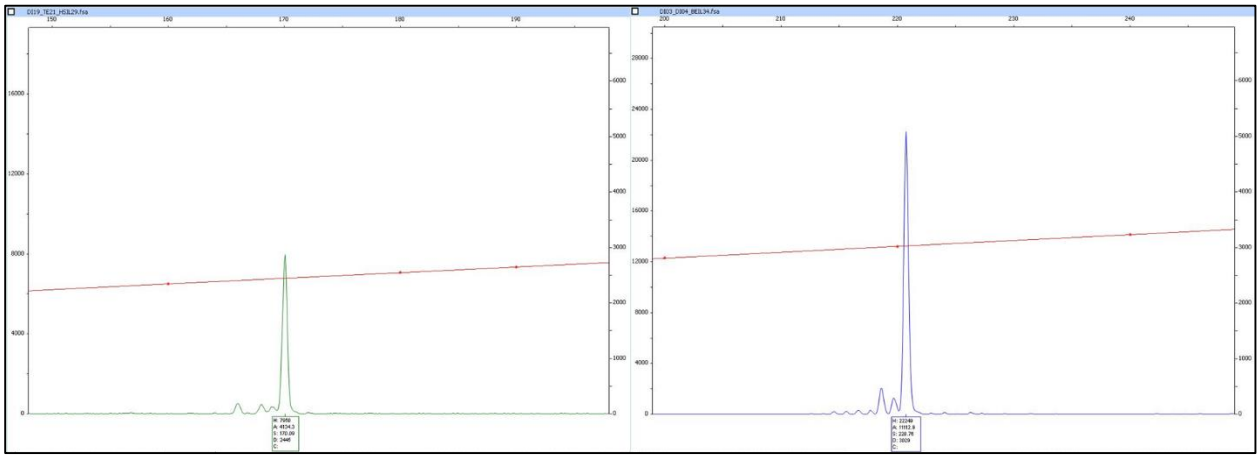

Figure 68. Example allele size peaks produced by the Peak Scanner Software for homozygous samples from HS.IL population for Tet21 locus (left) and NGE.IL population for Di3 locus.

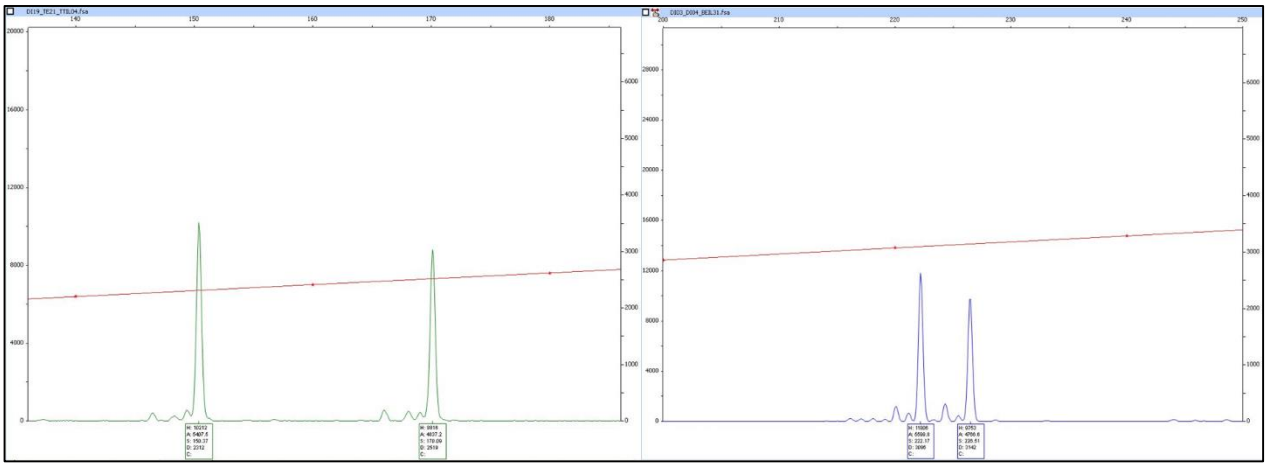

Figure 69. Example allele size peaks produced by the Peak Scanner Software for heterozygous samples from TT.IL population for Tet21 locus (left) and NGE.IL population for Di3 locus.

Table 25. Adjusted total sample size reports for the number of alleles that were successfully scored by locus of the 80 samples analyzed. Also reported are the number of unique alleles scored, the allele size range, mean total allele frequency, F-statistics including: F, FIS, FIT, and FST, along with number of alleles (Na), effective number of alleles per locus (Ne), observed heterozygosity (Ho), and Nei's expected heterozygosity (He) for each of the five codominant loci used in this study (i.e. Di3, Di4, Di19, Tet21, Tri8). Standard errors are reported in parentheses when relevant.

Locus	Adjusted Total Sample Size (original n=80)	Number of Alleles	Allele Size Range	Mean Total Allele Frequency	F	F_{IS}	F_{IT}	F_{ST}	Na	Ne	Ho	He
Maack-Di3	73	5	216-226	0.200 (0.093)	0.161 (0.153)	0.148	0.259	0.130	3.286 (0.286)	2.299 (0.176)	0.469 (0.090)	0.551 (0.032)
Maack-Di4	72	24	102-182	0.042 (0.008)	-0.037 (0.072)	-0.029	0.113	0.138	7.714 (1.169)	5.380 (0.802)	0.813 (0.051)	0.790 (0.029)
Maack-Di19	71	8	245-269	0.125 (0.046)	0.274 (0.107)	0.269	0.358	0.121	4.000 (0.309)	3.095 (0.282)	0.482 (0.081)	0.660 (0.032)
Maack-Tet21	52	12	134-202	0.083 (0.024)	0.516 (0.125)	0.535	0.648	0.244	4.286 (0.421)	2.869 (0.286)	0.293 (0.073)	0.630 (0.036)
Maack-Tri8	34	11	133-189	0.091 (0.022)	-0.121 (0.184)	-0.065	0.139	0.192	4.429 (0.719)	3.653 (0.531)	0.720 (0.096)	0.676 (0.060)
Total	**302**	**60**	**102-269**									
Grand Mean	**60 (8)**	**12 (3)**		**0.083 (0.013)**	**0.159 (0.068)**	**0.171 (0.109)**	**0.303 (0.097)**	**0.165 (0.023)**	**4.743 (0.385)**	**3.459 (0.269)**	**0.556 (0.046)**	**0.661 (0.021)**

Table 26. Allele frequencies for each allele by locus (i.e. Di3, Di4, Di19, Tet21, Tri8) for all seven subpopulations of Amur honeysuckle used in this study. Total allele frequencies are also reported. Table produced using GenAlEx 6.501.

Locus	Allele	NGW.IL	NGE.IL	MA.IL	HS.IL	TT.IL	NYBG	AA.MA	TOTAL
Di3	**216**	0.083	0.091	0.389	0.045	0.063	0.000	0.250	0.130
	220	0.083	0.182	0.222	0.000	0.000	0.000	0.167	0.096
	222	0.583	0.591	0.333	0.727	0.625	0.500	0.583	0.568
	224	0.000	0.000	0.056	0.000	0.000	0.500	0.000	0.075
	226	0.250	0.136	0.000	0.227	0.313	0.000	0.000	0.130
Di4	**102**	0.292	0.042	0.000	0.222	0.000	0.000	0.000	0.083
	104	0.000	0.000	0.000	0.000	0.000	0.000	0.136	0.021
	106	0.250	0.125	0.000	0.111	0.063	0.056	0.000	0.090
	110	0.000	0.000	0.000	0.000	0.000	0.111	0.000	0.014
	114	0.000	0.000	0.045	0.000	0.000	0.000	0.091	0.021
	120	0.000	0.000	0.091	0.000	0.000	0.000	0.000	0.014
	124	0.083	0.125	0.000	0.389	0.500	0.000	0.000	0.139
	128	0.000	0.000	0.045	0.000	0.000	0.000	0.045	0.014
	130	0.000	0.000	0.091	0.000	0.000	0.000	0.045	0.021
	134	0.125	0.042	0.045	0.000	0.250	0.000	0.000	0.063
	138	0.125	0.333	0.000	0.167	0.125	0.000	0.000	0.111
	140	0.000	0.000	0.227	0.000	0.000	0.000	0.000	0.035
	142	0.083	0.292	0.182	0.111	0.063	0.167	0.045	0.139
	144	0.000	0.042	0.000	0.000	0.000	0.167	0.045	0.035
	146	0.000	0.000	0.000	0.000	0.000	0.000	0.182	0.028
	150	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.007
	152	0.042	0.000	0.045	0.000	0.000	0.000	0.000	0.014
	156	0.000	0.000	0.000	0.000	0.000	0.000	0.182	0.028
	158	0.000	0.000	0.136	0.000	0.000	0.167	0.000	0.042
	160	0.000	0.000	0.045	0.000	0.000	0.333	0.000	0.049
	162	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.007
	172	0.000	0.000	0.045	0.000	0.000	0.000	0.045	0.014
	176	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.007
	182	0.000	0.000	0.000	0.000	0.000	0.000	0.045	0.007
Di19	**245**	0.150	0.167	0.182	0.056	0.357	0.091	0.545	0.218
	247	0.250	0.417	0.227	0.333	0.286	0.318	0.136	0.282
	249	0.550	0.208	0.318	0.611	0.357	0.227	0.091	0.324
	251	0.000	0.000	0.045	0.000	0.000	0.000	0.000	0.007
	253	0.000	0.000	0.000	0.000	0.000	0.318	0.000	0.049
	255	0.000	0.000	0.000	0.000	0.000	0.000	0.227	0.035
	261	0.050	0.208	0.227	0.000	0.000	0.000	0.000	0.077
	269	0.000	0.000	0.000	0.000	0.000	0.045	0.000	0.007
Tet21	**134**	0.000	0.000	0.071	0.083	0.000	0.000	0.000	0.019
	138	0.000	0.200	0.000	0.083	0.000	0.000	0.000	0.029
	144	0.222	0.000	0.000	0.000	0.000	0.000	0.000	0.038
	150	0.056	0.000	0.071	0.250	0.250	0.000	0.100	0.096
	156	0.056	0.400	0.286	0.000	0.000	0.000	0.600	0.202
	164	0.000	0.000	0.286	0.000	0.000	0.611	0.000	0.144
	170	0.500	0.400	0.000	0.417	0.667	0.111	0.000	0.269
	178	0.000	0.000	0.000	0.083	0.000	0.000	0.000	0.010
	182	0.167	0.000	0.000	0.083	0.083	0.111	0.000	0.067
	186	0.000	0.000	0.286	0.000	0.000	0.000	0.000	0.038
	190	0.000	0.000	0.000	0.000	0.000	0.167	0.250	0.077
	202	0.000	0.000	0.000	0.000	0.000	0.000	0.050	0.010
Tri8	**133**	0.200	0.000	0.000	0.000	0.167	0.000	0.056	0.059
	143	0.200	0.000	0.500	0.000	0.000	0.167	0.167	0.118
	149	0.100	0.000	0.000	0.125	0.000	0.000	0.056	0.044
	152	0.200	0.188	0.000	0.750	0.333	0.000	0.000	0.191
	158	0.000	0.188	0.000	0.000	0.167	0.333	0.000	0.088
	164	0.000	0.250	0.000	0.000	0.000	0.167	0.056	0.088
	167	0.300	0.375	0.500	0.125	0.333	0.167	0.111	0.250
	173	0.000	0.000	0.000	0.000	0.000	0.000	0.222	0.059
	180	0.000	0.000	0.000	0.000	0.000	0.000	0.056	0.015
	183	0.000	0.000	0.000	0.000	0.000	0.000	0.278	0.074
	189	0.000	0.000	0.000	0.000	0.000	0.167	0.000	0.015

7.5 GENETIC DIVERSITY

All five codominant loci used in this study were polymorphic for all seven subpopulations examined in this study, meaning that two or more alleles occurred in each locus in the same subpopulation (Peakall and Smouse 2012). The allele frequencies (i.e. the direct count of the proportion of different allele sizes; Peakall and Smouse 2012) varied within and among subpopulations and loci, with a grand mean allele frequency of 0.083 ± 0.013 across all loci (Table 26; Figure 70; Figure 71). The grand mean for the actual number of alleles (Na) (i.e. alleles with nonzero frequency; Yeh and Boyle 1997) was 4.74 ± 0.39, while the grand mean for the effective number of alleles (Ne) (i.e. the estimatated reciprocal of homozygosity; Hartl and Clark 2007) was 3.46 ± 0.27 (Table 27; Figure 72). The grand mean of the observed heterozygosity (i.e. proportion of samples that were heterozygous at a given locus; Peakall and Smouse 2012) was 0.556 ± 0.046, while the grand mean expected heterozygosity (i.e. proportion of heterozygosity expected under random mating based on the allele frequencies of each allele; Peakall and Smouse 2012) was 0.661 ± 0.021 (Table 27; Figure 72).

The following results report the Wright's F-statistics found in this study calculated using GeneAlEx 6.501. The grand mean of the Fixation Index (F), or Inbreeding Coefficient (IC), over all loci and subpopulations was 0.159 ± 0.068. The grand mean for the IC within individuals relative to the subpopulation (F_{IS}) (measuring the heterozygosity reduction of individuals due to non-random mating with its subpopulation; Peakall and Smouse 2012) was 0.171 ± 0.109 (Table 25). The grand mean for the IC within individuals relative to the toal (F_{IT}) (measuring the impact of non-

random mating within subpopulation and genetic differentiation between subpopulations; Peakall and Smouse 2012) was 0.303 ± 0.097 (Table 25). Finally, the grand mean of the IC within subpopulations relative to the total (F_{ST}) (measuring genetic differentiation between subpopulations, or in other words the proportion of the total heterozygosity distributed between subpopulations ; Peakall and Smouse 2012) was 0.165 ± 0.023 (Table 25). Nei's genetic distances were also calculated for each pair of subpopulations (Table 28).

Several significant genetic differentiations were found among certain subpopulations when analyzed by locus using Shannon Diversity Indicies for all pairwise subpopulation combinations with GeneAlEx 6.501 software (Figure 71). More specifically, the Amur honeysuckle subpopulations sampled from the western (NGW.IL) and eastern (NGE.IL) half of the oak savanna restoration study site at Nachusa Grasslands were found to have significant genetic differences in three of the five loci analyzed (Figure 71). Across all five loci, the western oak savanna restoration study site subpopulation from Nachusa Grasslands (NGW.IL) was found to be genetically similar to the subpopulation in Hidden Springs State Forest in central Illinois (HS.IL) (Figure 71). Across all but two loci (Di4 and Tri8), the western oak savanna restoration study site subpopulation from Nachusa Grasslands (NGW.IL) was also found to be genetically similar to the subpopulation in Trail of Tears State Forest in southern Illinois (TT.IL) (Figure 71). The New York Botanical Gardens (NYBG) subpopulation was found to have significant genetic differences from all other subpopulations across all but one locus (Tri8) (Figure 71). Additionally, the Arnold Arboretum subpopulation at Harvard

University (AA.MA) was found to have significant genetic differences from all other subpopulations across all but two loci (Di3 and Tri8) (Figure 71).

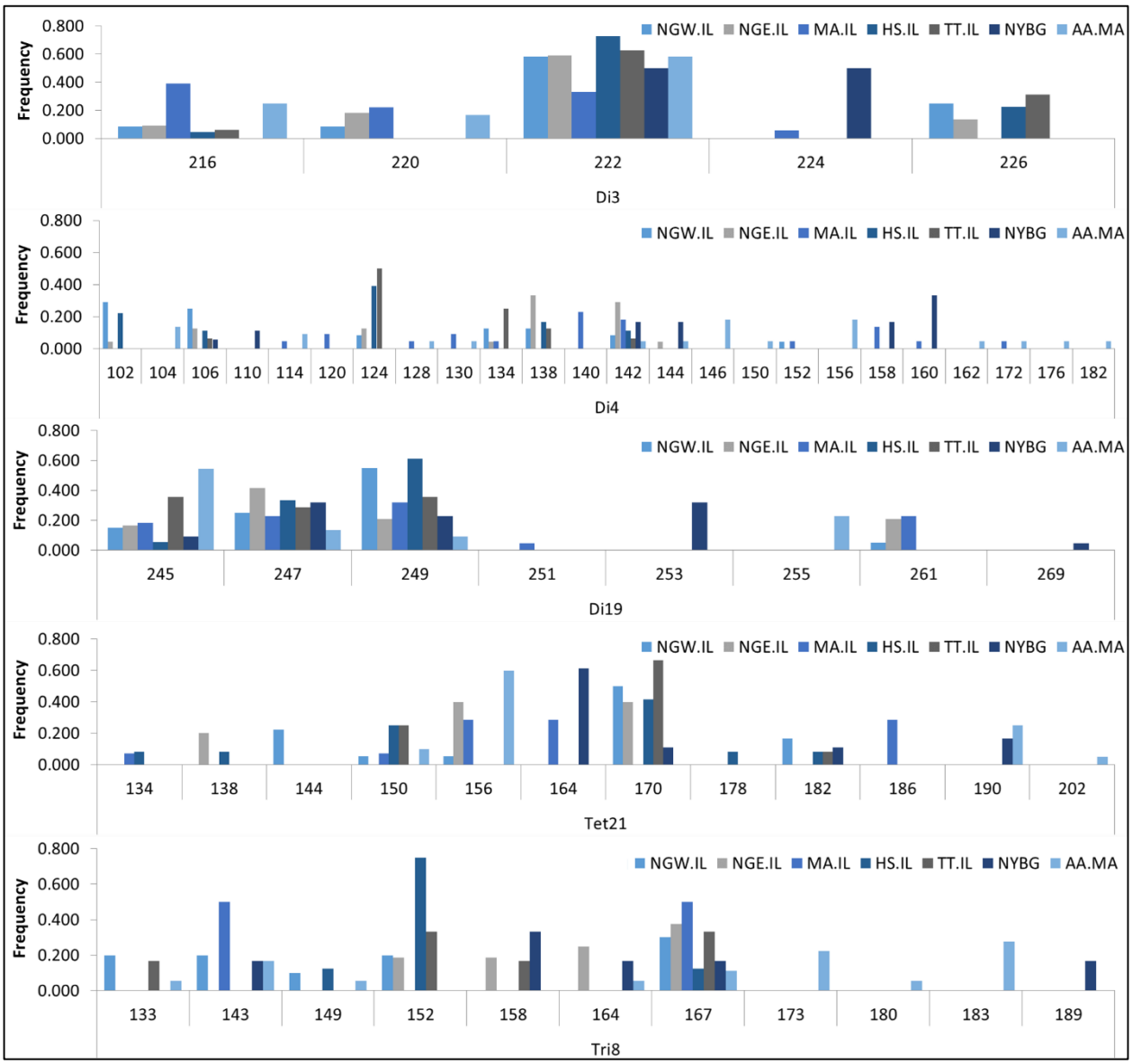

Figure 70. Allele frequencies graphed by locus (i.e. Di3, Di4, Di19, Tet21, Tri8; top to bottom) for all seven subpopulations of Amur honeysuckle used in this study (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL, NYBG, AA.MA; left to right). Graphs produced using GenAlEx 6.501.

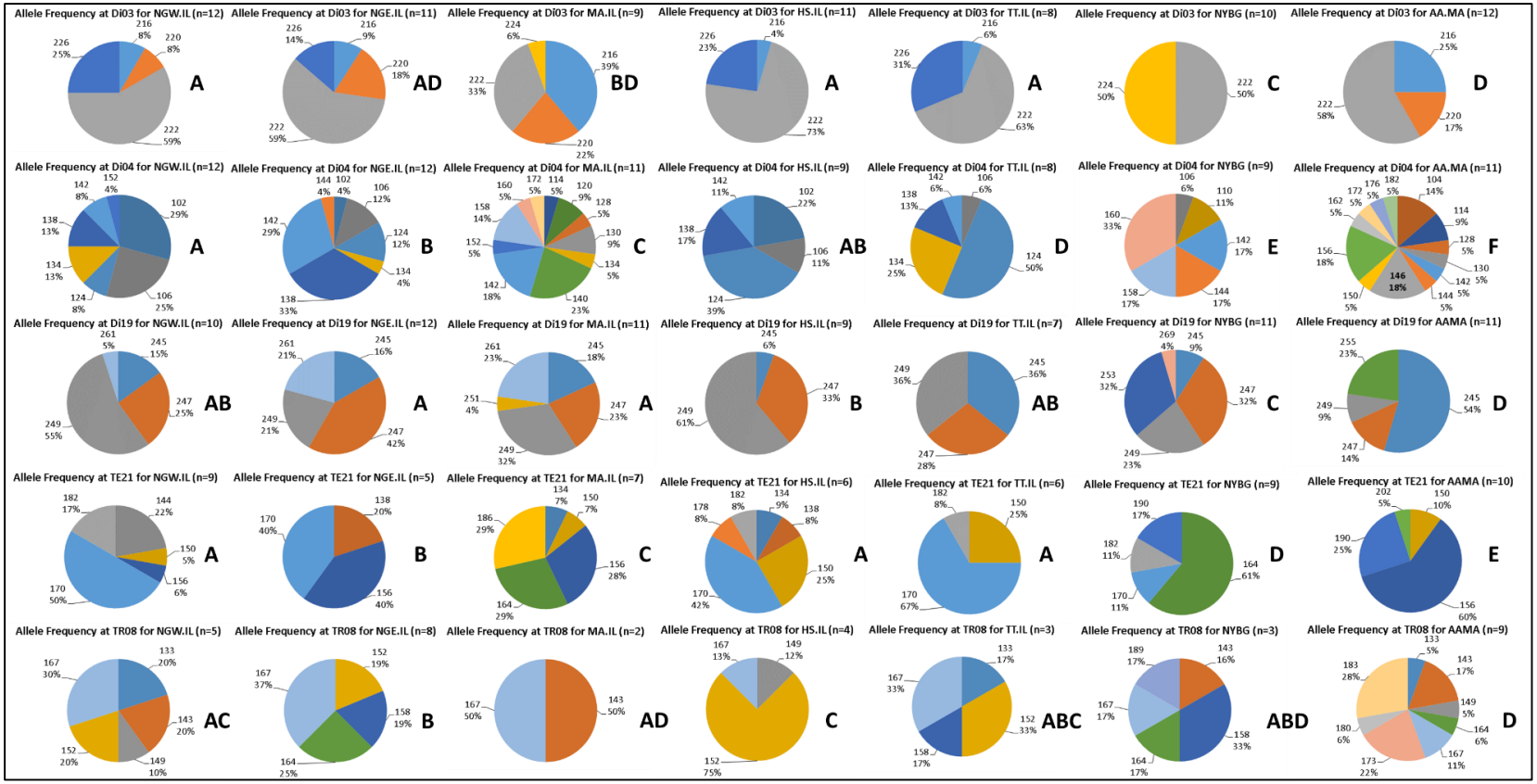

Figure 71. Graphical representation of allele frequencies at each locus (i.e. Di3, Di4, Di19, Tet21, Tri8; top to bottom) by subpopulation (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL, NYBG, AA.MA; left to right). Sample sizes (n) for each loci and subpopulation are reported. Letters represent significant differences among subpopulations within each loci based on Shannon Diversity Indices. Graphs produced using GenAlEx 6.501.

Table 27. Sample Size (N), number of alleles (Na), effective number of alleles per locus (Ne), observed heterozygosity (Ho), and Nei's expected heterozygosity (He) for each Amur honeysuckle subpopulation and loci in this study. Standard errors are reported in parentheses for all mean values. Table produced using GenAlEx 6.501.

Pop	Locus	N	Na	Ne	Ho	He
NGW.IL	Di3	12	4.00	2.40	0.67	0.58
	Di4	12	7.00	5.14	0.83	0.81
	Di19	10	4.00	2.56	0.40	0.61
	Tet21	9	5.00	3.00	0.22	0.67
	Tri8	5	5.00	4.55	1.00	0.78
	MEAN	9.600 (1.288)	5.000 (0.548)	3.530 (0.553)	0.624 (0.141)	0.689 (0.045)
NGE.IL	Di3	11	4.00	2.44	0.55	0.59
	Di4	12	7.00	4.30	0.83	0.77
	Di19	12	4.00	3.47	0.75	0.71
	Tet21	5	3.00	2.78	0.00	0.64
	Tri8	8	4.00	3.66	0.88	0.73
	MEAN	9.600 (1.364)	4.400 (0.678)	3.330 (0.328)	0.601 (0.161)	0.687 (0.032)
MA.IL	Di3	9	4.00	3.18	0.67	0.69
	Di4	11	11.00	7.56	1.00	0.87
	Di19	11	5.00	4.17	0.55	0.76
	Tet21	7	5.00	3.92	0.14	0.74
	Tri8	2	2.00	2.00	1.00	0.50
	MEAN	8.000 (1.673)	5.400 (1.503)	4.166 (0.929)	0.671 (0.160)	0.712 (0.061)
HS.IL	Di3	11	3.00	1.72	0.36	0.42
	Di4	9	5.00	3.95	0.78	0.75
	Di19	9	3.00	2.05	0.44	0.51
	Tet21	6	6.00	3.79	0.50	0.74
	Tri8	4	3.00	1.68	0.50	0.41
	MEAN	7.800 (1.241)	4.000 (0.632)	2.638 (0.508)	0.517 (0.070)	0.564 (0.075)
TT.IL	Di3	8	3.00	2.03	0.63	0.51
	Di4	8	5.00	2.98	0.88	0.66
	Di19	7	3.00	2.97	0.14	0.66
	Tet21	6	3.00	1.95	0.33	0.49
	Tri8	3	4.00	3.60	0.33	0.72
	MEAN	6.400 (0.927)	3.600 (0.400)	2.705 (0.314)	0.462 (0.129)	0.609 (0.047)
NYBG	Di3	10	2.00	2.00	0.00	0.50
	Di4	9	6.00	4.76	0.56	0.79
	Di19	11	5.00	3.78	0.73	0.74
	Tet21	9	4.00	2.35	0.56	0.57
	Tri8	3	5.00	4.50	0.67	0.78
	MEAN	8.400 (1.400)	4.400 (0.678)	3.479 (0.559)	0.501 (0.130)	0.676 (0.058)
AA.MA	Di3	12	3.00	2.32	0.42	0.57
	Di4	11	13.00	8.96	0.82	0.89
	Di19	11	4.00	2.66	0.36	0.62
	Tet21	10	4.00	2.30	0.30	0.57
	Tri8	9	8.00	5.59	0.67	0.82
	MEAN	10.600 (0.510)	6.400 (1.860)	4.366 (1.304)	0.513 (0.098)	0.694 (0.067)
GRAND	**MEAN**	**8.629 (0.483)**	**4.743 (0.385)**	**3.459 (0.269)**	**0.556 (0.046)**	**0.661 (0.021)**

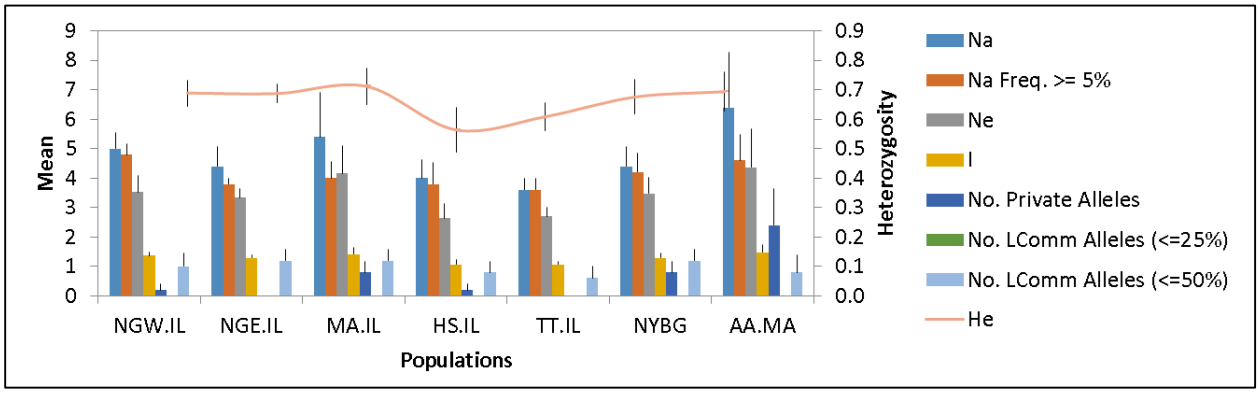

Figure 72. Mean allelic patterns across all seven subpopulations of Amur honeysuckle used in this study. Specifically, mean number of different alleles (Na), mean number of different alleles with a frequency greater than or equal to 5%, mean number of effective alleles (Ne), mean Shannon's Information Index, mean number of private alleles or alleles unique to a single subpopulation, mean number of locally common alleles found in 25% or fewer subpopulations, mean number of locally common alleles found in 50% or fewer subpopulations, and mean expected heterozygosity (He). Graph produced using GenAlEx 6.501.

Table 28. Nei's genetic distance between all pairs of sampled subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL, NYBG, AA.MA) reported as a tri distance matrix calculated using GenAlEx 6.501

NGW.IL	NGE.IL	MA.IL	HS.IL	TT.IL	NYBG	AA.MA	
0.000							**NGW.IL**
0.302	0.000						**NGE.IL**
0.616	0.548	0.000					**MA.IL**
0.202	0.374	1.008	0.000				**HS.IL**
0.192	0.299	0.899	0.177	0.000			**TT.IL**
0.826	0.734	0.693	0.968	0.899	0.000		**NYBG**
0.839	0.570	0.588	1.085	0.877	1.114	0.000	**AA.MA**

7.6 SPATIAL ANALYSIS OF GENETIC DIVERSITY

According to an analysis of molecular variance (AMOVA) using a codominant allelic distance matrix for the calculation of F_{ST} (with individual analysis suppressed), 87% of the genetic differentiation found in this study occurred within the Amur honeysuckle subpopulations, while the remaining 13% of the genetic differentiation occurred among the Amur honeysuckle subpopulations (F_{ST}=0.129; $p<0.05$). Patterns of

genetic differentiation (Nei's genetic distances, F_{ST}, and $^{S}H_{ua}$) among subpopulations were visualized using Principal Coordinate Analyses (PCoA) conducted by GeneAlEx 6.501 software. All three PCoAs revealed similar patterns and generally supported the significant findings of the Shannon Diversity Indices analysis (Figures 73-75). More specifically, the PCoAs suggested that the New York Botanical Gardens subpopulation was genetically isolated from all other subpopulations across all variables (Figures 73-75). According to the PCoAs visualizing Nei's genetic distance (Figure 73) and F_{ST} (Figure 74), both the Arnold Arboretum subpopulation at Harvard University in MA and the Morton Arboretum subpopulation in Lisle, Illinois were also dispersed and isolated from other subpopulations. The clumping of the Arnold Arboretum subpopulation at Harvard University in MA and the Morton Arboretum subpopulation in Lisle, Illinois in the PCoA visualizing the $^{S}H_{ua}$ genetic differentiation, on the other hand, suggest these subpopulations may share some genetic relationship (Figure 75). Finally, the other four Illinois subpopulations (i.e. NGE.IL, NGW.IL, TT.IL, and HS.IL) were somewhat linearly spaced along one axes within all PCoAs, with the Hidden Springs State Forest subpopulation located the furthest from the other isolated subpopulations (i.e. NYBG, MA.IL, AA.MA), meaning it was likely the most genetically distant subpopulation from the New York Botanical Gardens, Arnold Arboretum, and Morton Arboretum subpopulations (Figures 73-75).

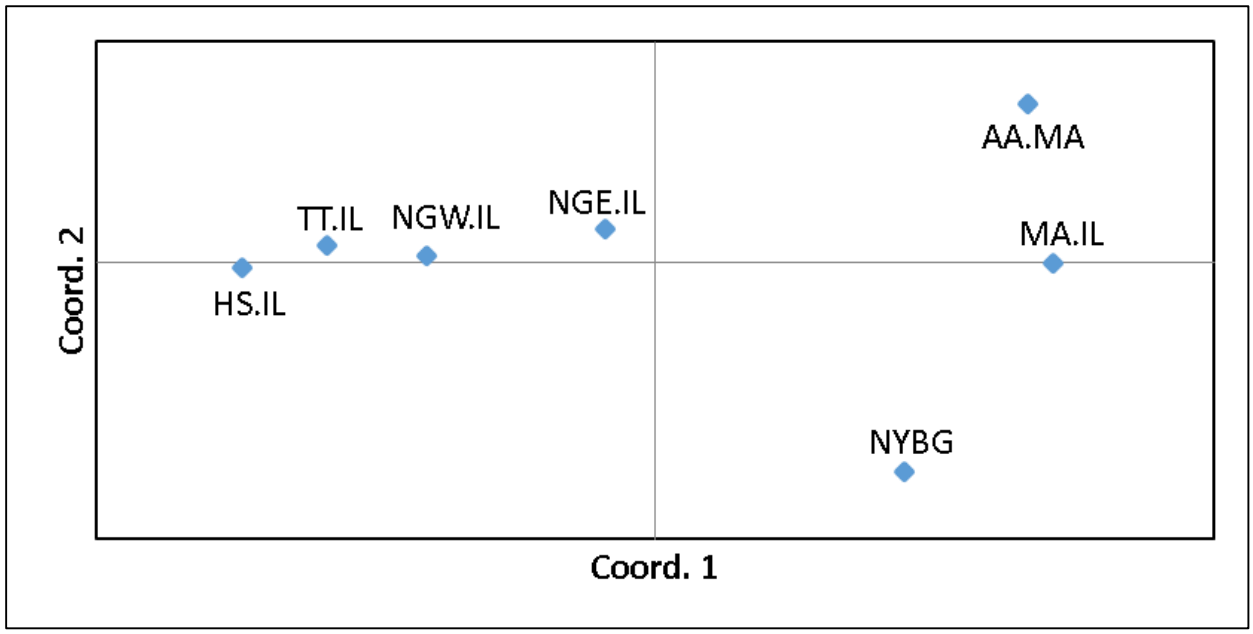

Figure 73. Principal Coordinates Analysis (PCoA) via covariance matrix with standardized Nei's genetic distance data. The two axes explain a cumulative 72.80% of the variation in genetic distance. Graph produced using GenAlEx 6.501.

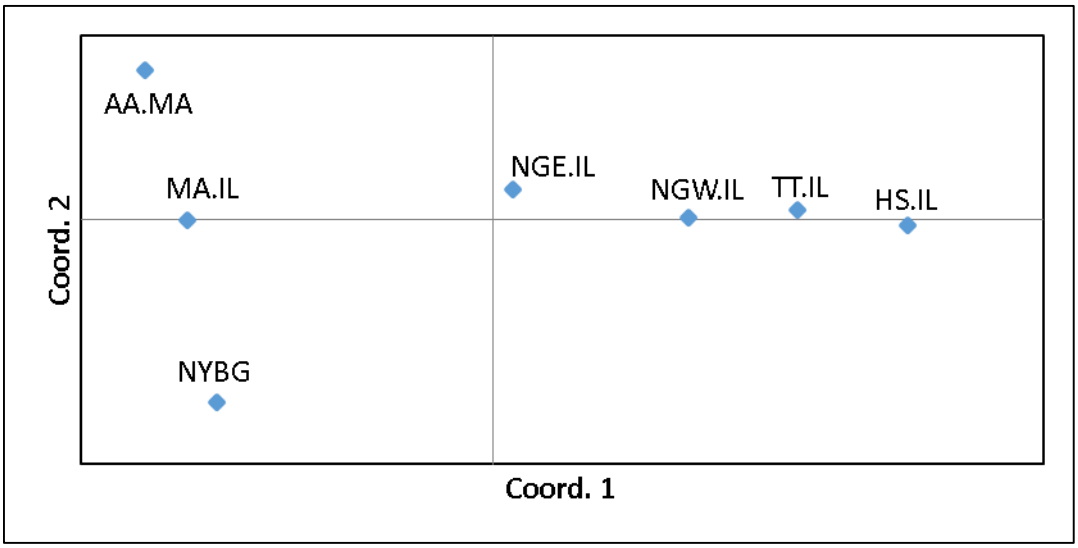

Figure 74. Principal Coordinates Analysis (PCoA) via covariance matrix with standardized F_{ST} data (999 permutations). Cumulatively, the two axes explain 77.52% of the variation in genetic distance. Graph produced using GenAlEx 6.501.

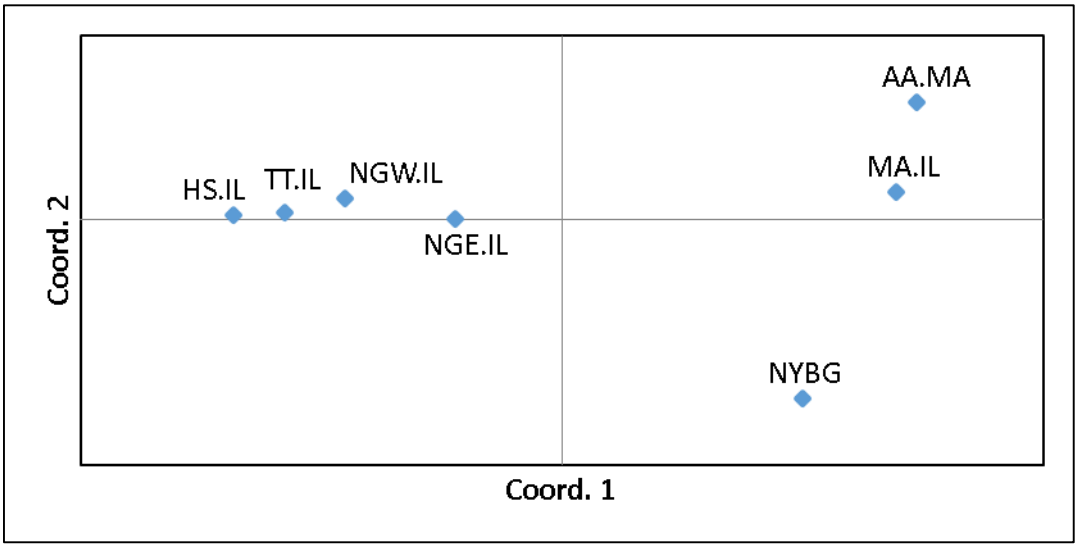

Figure 75. Principal Coordinates Analysis (PCoA) via covariance matrix with standardized Shannon Diversity Index ($^5H_{ua}$) data. Cumulatively, the two axes explain 63.02% of the variation in genetic distance. Graph produced using GenAlEx 6.501.

An additional PCoA was used to visualize an individual-by-individual (N x N) genotypic distance (GD) matrix created in GeneAlEx 6.501 software, to determine whether individual Amur honeysuckle samples (rather than overall subpopulations) displayed patterns of genetic differentiation (Figure 76). No clear pattern emerged from the genotypic distance PCoA, which cumulatively explained only 23.95% of the genetic variation.

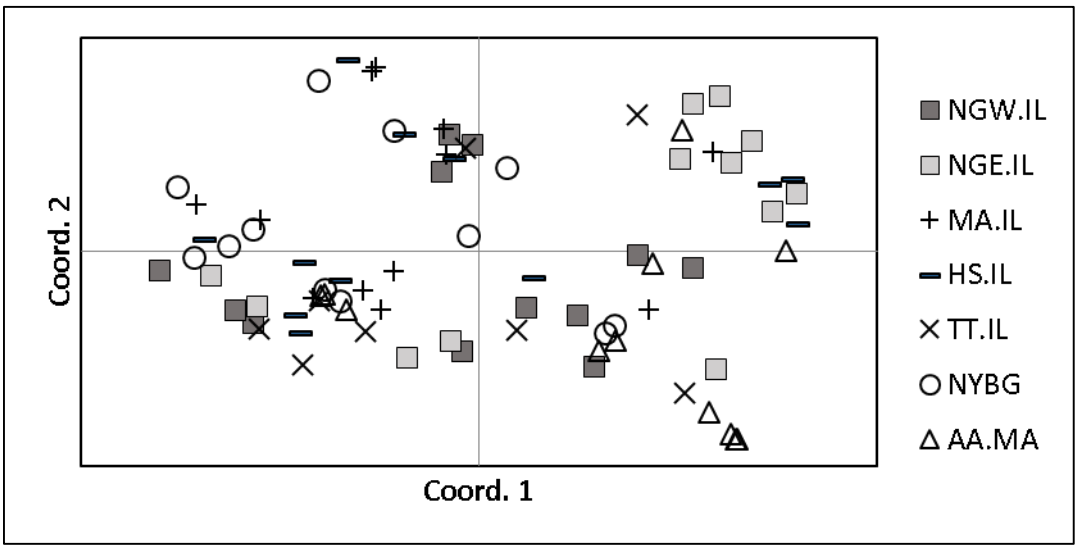

Figure 76. Principal Coordinates Analysis (PCoA) via covariance matrix with standardized codominant genotypic distance data. Cumulatively, the two axes explain 23.95% of the variation in genetic distance. Graph produced using GenAlEx 6.501.

The Mantel correlation test comparing the geographic distances (km) to the genetic differentiations (F_{ST}) of all seven subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL, NYBG, AA.MA) revealed a significant positive correlation (coefficient =0.548, $p<0.05$), indicating significant isolation by distance since genetic differentiation increased with geographic distance (Figure 77). Furthermore, the significant positive correlation held when a mantel test was used to compare linearized genetic distance

((Fst/(1-Fst)) as proposed by Rousset 1997) and natural log of geographic distance (km) (coefficient =0.628, $p<0.01$) (Figure 78). When the Illinois subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL) were analyzed separately, no significant correlation between the geographic distances (km) and the genetic differentiations (F_{ST}) (Figure 79), or linearized genetic distance and natural log of geographic distance (Figure 80) were detected by the mantel correlation test. The mean geographic distance when all seven subpopulations were taken into account was 927.2 ± 196.6 km, while the mean geographic distance for the five Illinois populations was 73.8 ± 18.1 km.

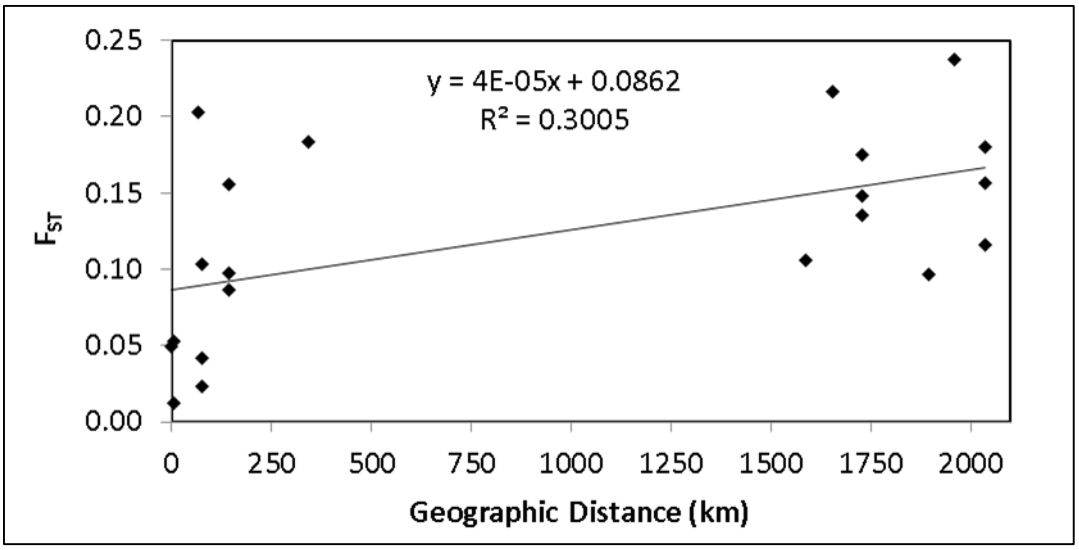

Figure 77. Mantel test relationship between genetic differentiation (Fst) and geographic distance of all seven subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL, NYBG, AA.MA). Strong positive correlation found, denoted by trend line with accompanying formula and R^2 value reported. Graph produced using GenAlEx 6.501.

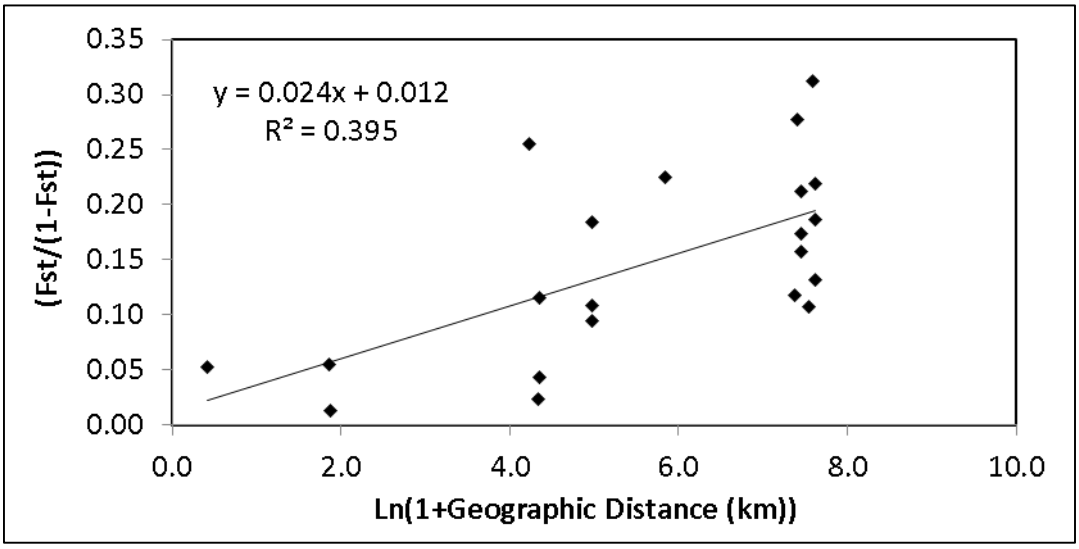

Figure 78. Mantel test relationship between linearized genetic differentiation (Fst/(1-Fst))) and Ln(1+geographic distance) of all seven subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL, NYBG, AA.MA). Strong positive correlation found, denoted by trend line with accompanying formula and R^2 value reported. Graph produced using GenAlEx 6.501.

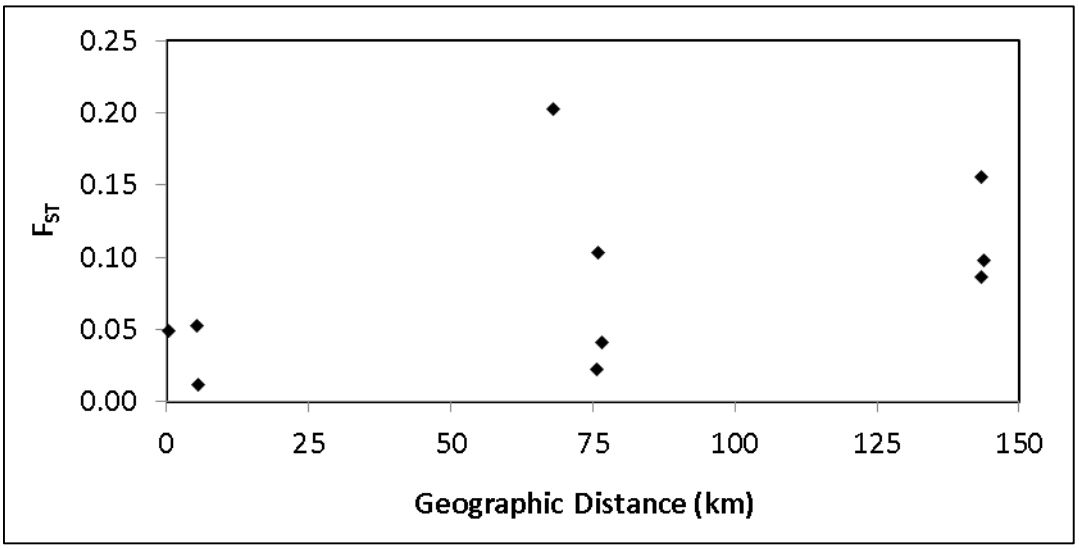

Figure 79. Mantel test relationship between genetic differentiation (Fst) and geographic distance of the five Illinois subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL). No significant correlation was found. Graph produced using GenAlEx 6.501.

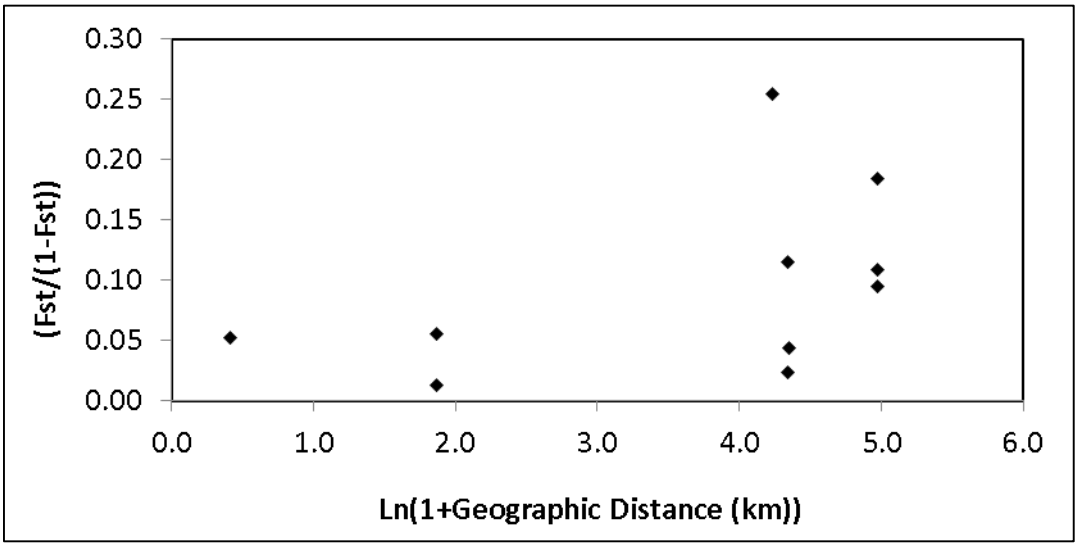

Figure 80. Mantel test relationship between linearized genetic differentiation (Fst/(1-Fst))) and Ln(1+geographic distance) of the five Illinois subpopulations (i.e. NGW.IL, NGE.IL, MA.IL, HS.IL, TT.IL). No significant correlation was found. Graph produced using GenAlEx 6.501.

7.7 DISCUSSION

Ultimately, the goal of this chapter was to investigate the underlying evolutionary mechanisms associated with the spatial-temporal long distance dispersal patterns of Amur honeysuckle, as inferred by population genetics, to better understand the mechanisms and pathways by which Amur honeysuckle has spread throughout the United States. More specifically, this research explored whether Amur honeysuckle spread via natural and/or anthropogenically facilitated long-distance dispersal followed by outward expansion through local and/or regional dispersal, based on the notion that the number and source of individuals establishing new populations, along with gene flow (or pattern of dispersal) and geographic distance, determine the extent of genetic differentiation between populations at a landscape level (Whitlock and McCauley 1999).

Three proposed invasion pathways were identified based on historical records. The first hypothesized pathway for the spread of Amur honeysuckle to and throughout Illinois was west via anthropogenically facilitated long-distance dispersal from *The New York Botanical Garden, NY and/or The Arnold Arboretum of Harvard University, MA.* The New York Botanical Garden was the first U.S. location to record successful cultivation of Amur honeysuckle obtained from Washington D.C. in 1898, followed by The Arnold Arboretum at Harvard University in 1903 (Luken and Thieret 1996). The second hypothesized pathway was west from *The Morton Arboretum, Lisle, IL.* The Morton Arboretum was the first location to document the ability of Amur honeysuckle to reproduce and spread beyond the point of its introduction in the U.S. in the mid-1920s, and reports of naturalized populations within the United States began appearing by the

late 1950s (Luken and Thieret 1996; Cipollini and Dorning 2008). The final hypothesized pathway for the spread of Amur honeysuckle throughout Illinois was via regional dispersal between Illinois State Forests, including *Hidden Springs State Forest, Strasburg, IL and Trail of Tears State Forest, Jonesboro, IL* (EDDMapS 2015). Both of these State Forests were identified as being located in and near areas with a high number of reported sightings of mature Amur honeysuckle encroachment (EDDMapS 2015).

Ultimately, this research found slightly lower levels of heterozygosity and slightly higher levels of inbreeding than previous research exploring populations of Amur honeysuckle throughout Ohio (McNutt 2010; Barriball 2012; Barriball et al. 2015), suggesting that Amur honeysuckle subpopulations in Illinois and on the east coast might be more self-compatible and experience fewer outcrossing events than Amur honeysuckle populations in Ohio. Beyond that, however, the findings from this research supported existing studies on the genetic population structure of Amur honeysuckle. For example, like other studies (McNutt 2010; Barribal 2012; Rocha et al. 2014; Barriball et al. 2015), a major proportion of the genetic differentiation that was found in Amur honeysuckle occurred within subpopulations, rather than among them. Previous research has suggested that the high within-subpopulation genetic variation found for Amur honeysuckle was, in part, explained by the long distances over which Amur honeysuckle seed distributers (i.e. birds) can travel, as well as by the localized and shorter distances over which pollinations of Amur honeysuckle by bees and insects ensues (McNutt 2010; Barriball et al. 2015).

Inherent traits possessed by successful plant invaders often include longer range seed dispersal as compared to their native counterparts (Luken 1997a; Reichard and Hamilton 1997; Collier et al. 2002; Lieurance 2004). The introduction and expansion of invasive species are often also accelerated by human dispersal and expansion of disturbed habitats (Collier et al. 2002). Ultimately, the spread of Amur honeysuckle populations has been hypothesized as being limited only by competitive pressures and distribution efficiency, although anthropogenic distribution has made it so distribution efficiency is less of a hindrance (Luken and Thieret 1996; Bauer et al. 2012). Given the history of Amur honeysuckle, human dispersal has played a role in its spread over long distances, as specimens and seeds were exchanged and shared between herbaria, commercial nurseries, and distributed by the USDA Section of Foreign Seed and Plant Introduction (Luken and Thieret 1996).

Multiple expansion pathways and the existence of several different cultivars resulting from manipulations to Amur honeysuckle by the Natural Resources Conservation Services (i.e. selecting genotypes from naturalized populations that enhance fruit production; Luken and Thieret 1996) were also identified as potential factors that would increase the likelihood that new populations of Amur honeysuckle were initially established from multiple seed sources, which would in turn increase overall genetic diversity and decrease the divergence of one population from another (McNutt 2010). At minimum, Amur honeysuckle was distributed seven different times between 1898 and 1927, and was available from about eight commercial nurseries by 1931 (Luken and Thieret 1996). Between 1960 and 1984, the Natural Resources

Conservation Services distributed the manipulated cultivars throughout the United States (i.e. Maryland in 1970, Mississippi in 1979, Texas in 1980, North Dakota in 1983, and Michigan in 1984), so that they could be used to achieve soil stabilization and reclamation, in addition to improving ornamental landscapes and bird habitats (Luken and Thieret 1996).

Like other studies (McNutt 2010), the high level of genetic differentiation within each subpopulation was phenotypically undetectable during field identification and collection in this study. The size and abundance of Amur honeysuckle shrubs from subpopulation to subpopulation (attributed to the length of time since invasion, with areas having an abundant amount of large shrubs having the longest invasion period) were noted as the only observable difference among sampled subpopulations in previous studies, and therefore hypothesized as potentially contributing to the high within-subpopulation genetic differentiation (McNutt 2010). Findings from this research contradict that hypothesis, since within-subpopulation genetic differentiation still constituted a high proportion of the significant genetic differentiation detected in this study, which restricted sampling to only reproductively mature Amur honeysuckle shrubs (i.e. with evidence of flowering or fruiting). Variations in environmental factors from site to site (e.g. landscape topography, soil, microsite climate conditions, etc.) has also been hypothesized as potentially influencing genetic variation within-subpopulations (McNutt 2010), and as this study did not assess environmental factors within each subpopulation, it could not support or reject that assertion and should therefore be explored further in future research.

Based on the clustering patterns found in the Principal Coordinate Analyses for three genetic differentiation variables in this study, long distance regional dispersal events of up to about 74 km have likely occurred throughout Illinois, given the low genetic differentiation between the regional subpopulations located in southern (TT.IL), central (HS.IL) and northern Illinois (predominantly NGW.IL and NGE.IL to a lesser extent). These regional dispersal events have likely contributed to the high within-subpopulation genetic differentiation detected in this research. Without additional research into the details of this dispersal, however, it is difficult to determine, strictly from the genetic population analyses, whether the mode by which the dispersal between these subpopulations was via anthropogenic activity or by the migratory pathways of the birds known to disperse Amur honeysuckle; specifically: European starlings (*Sturnus vulgaris*), American robins (*Turdus migratorius*), hermit thrushes (*Catharus guttatus*), cedar waxwings (*Bombycilla cedrorum*), and northern mockingbirds (*Mimus polyglottus*) (Bartuszevige and Gorchov 2006).

No correlation between genetic distance and geographic distance was found when the Illinois subpopulations were isolated, even though the subpopulation from The Morton Arboretum was shown to have a large genetic differentiation when compared to other Illinois subpopulations. The lack of correlation found in this study for the Illinois subpopulations suggest that they do not display genetic isolation or similarity with increasing or decreasing distance, which is consistent with the finding that there has been active gene flow between these subpopulations via regional long distance dispersal events. This is contrary to previous research that found stronger relationships

between genetic and geographic distances for subpopulations in Ohio as the geographic radius within which subpopulations were compared was reduced (Barriball 2012; Barriball et al. 2015).

When all subpopulations from this research were analyzed together (increasing the mean distance to about 927 km), strong positive correlations were found between genetic and geographic distance. The strong positive correlation between the genetic distance and geographic distance in this research supports previous research and suggests that Amur honeysuckle may experience genetic isolation across a variety of distances, in addition to possessing well-defined population structures (attributable to more than just random sampling of genes from each subpopulation) across a wide range of geographic landscapes (McNutt 2010; Barriball 2012; Barriball et al. 2015). Specifically, the patterns found in the Principal Coordinate Analyses for three genetic differentiation variables in this study suggest that The New York Botanical Garden subpopulation was most genetically isolated from all other subpopulations. The Arnold Arboretum at Harvard University and The Morton Arboretum also displayed patterns of genetic isolation from the other subpopulations, more so than from each other, suggesting that these two subpopulations have experienced some form of anthropogenic long distance dispersal events, given the large geographic distance (approx. 1,614 km) and the east-west orientation (an orientation and geographic distance unlikely to been enabled by birds, which tend to follow north-south migratory paths; Bartuszevige and Gorchov 2006) that separates them.

Furthermore, the subpopulation from the eastern half of the oak savanna restoration study site seemed to act as an intermediary between the genetically isolated subpopulations and the genetically similar subpopulations found in this research. The relatively close geographic distance, but high genetic differentiation (along with the findings from the Shannon Diversity Indices analysis) of The Morton Arboretum subpopulation to the other Illinois subpopulations, suggests that it might be a sink (i.e. accumulating genetically distinct propagules, thereby increasing genetic differentiation from other Illinois subpopulations) and not a source for the spread of Amur honeysuckle, except potentially for the Nachusa Grasslands subpopulation in northern Illinois and the Trail of Tears State Forest subpopulation in southern Illinois to which it shares some genetic connection. Ultimately, all of these relationships should be explored further with larger sample sizes from additional subpopulations along a more expansive geographic gradient, before they can be confirmed.

Once the mechanisms by which invasive species spread to their current range distributions are understood, predictions can be made about where and in what way the invasive species might spread in the future, which can ultimately inform and guide management strategies meant to control any future expansion (Castellano and Gorchov 2013). If, for example, an invasive species is spreading through local dispersal from an expanding front, and subsequent propagule recruitment continually occurs from outside the newly established patch from neighboring populations, then management strategies would be best served targeting the edge of the invasive specie’s current range (Gorchov and Henry 2013). If, on the other hand, an invasive species is spreading through long-

distance dispersal, and subsequent propagule recruitment occurs from the matured individuals that have established themselves within the new patch after the initial long-distance dispersal event, then management strategies would be best served targeting individual colonists; preferably before they begin to propagate after establishment (Gorchov and Henry 2013). It is important to note, however, that invasion models suggest that as the number of reproductively immature invasive species decrease in a location, the more the invasion becomes scattered (Iannone et al. 2014)

Based on findings from this and previous research (McNutt 2010; Gorchov et al. 2014; Barriball et al. 2015), Amur honeysuckle displays characteristics of a stratified dispersal model, also referred to as stratified diffusion (coined by Hengeveld in1989), with gene flow (dispersal) patterns that spread from multiple locations through local and regional diffusion across the landscape in combination with long distance, “jump” dispersal events that range in distance from around four km to as much as 1,614 km (i.e. approximate distance between The Morton Arboretum and The Arnold Arboretum at Harvard University). Given this information, this research supports the suggested management recommendations of Gorchov et al. (2014) for the most efficient use of resources when designing strategies to control the expansion of Amur honeysuckle. More specifically, Gorchov et al. (2014) asserts that it is important to locate newly colonized Amur honeysuckle shrubs in neighboring sites (especially within about 5 km) before they reach reproductive maturity, which may seem like a daunting, time-consuming task until the lag between establishment and development to reproductive maturity of Amur honeysuckle is taken into account. This lag in reproductive maturity

can range from three to eight years for Amur honeysuckle (Deering and Vankat 1999), therefore sweeps for new colonizers need only occur about every three years according to Gorchov et al. (2014).

7.8 CONCLUSIONS

As Amur honeysuckle and other invasive species continue to spread into the United States, it is important to understand invasion dynamics, such as range expansion and colonization patterns to further guide management strategies with an aim to control abundant and aggressive invasive species (Gorchov et al. 2014; Iannone et al. 2014). Based on this and previous research, microsatellite markers and other molecular methods have been successfully used in a variety of studies inferring plant demographic processes, including genetic population structure and understanding dispersal patterns (Cain et al. 2000;Davis and Shaw 2001; Diochon et al. 2003; DeWoody et al. 2004; Hu et al. 2010). With specific relevance to Amur honeysuckle, this and previous research conducting landscape genetic population structure analyses have been able to identify geographic and genetic differentiation and variation between populations, which can be used to estimate dispersal distances, colonization patterns, and infer potential sources of both founding and newly established individuals (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015). Long-distance dispersal events in particular have been identified as important features of populations, especially given the role it plays in the biological aspects of non-native plant species invasions, including metapopulation dynamics, diversity and dynamics of ecological communities,

population dynamics, evolution of populations, and colonization probabilities (Ouborg et al. 1999; Cain et al. 2000).

Ultimately, the combination of genetic methods and geographic knowledge in the research presented in this chapter promotes and validates the importance of integrating geographic perspective into molecular research on invasive species population dynamics. More research that utilizes the known invasion history of Amur honeysuckle and redefines long-distance dispersal to include potential anthropogenic influences is necessary to more accurately determine the general geographic and evolutionary patterns associated with Amur honeysuckle's range expansions throughout the eastern and central United States, as well as to locate potential source populations for use in targeted *in situ* removal management strategies.

CHAPTER 8:

SUMMARY AND CONCLUSIONS

The dynamic nature of Midwest oak savannas are ideal for exploring regeneration and recruitment mechanisms of white oak, as they naturally exhibit range contraction in unfavorable years and range expansion in favorable years (Brudvig and Asbjornsen 2009). Throughout Eastern and Central North America the aggressive and abundant invasive plant species, *Lonicera maackii* (Rupr.) Maxim (Amur honeysuckle), has encroached upon the understory canopies of many oak forests and open oak savannas at high environmental and economic costs (Pimentel et al. 2000; Collier et al. 2002; Pimentel et al. 2005; Lodge et al. 2006). Nachusa Grasslands is a Nature Conservancy preserve with 1,255 hectares of prairie, wetland and woodland located in north-central Illinois straddling the border of Ogle and Lee Counties. Nachusa Grasslands has devoted time and effort on various restoration projects, including oak savanna restorations. Throughout Lee County, Amur honeysuckle is the most common invasive species (Illinois Department of Natural Resources, 2003), and the extensive encroachment of Amur honeysuckle throughout the oak savanna restoration study site at Nachusa Grasslands is an ongoing restoration hurdle.

As plant invasions increase within Midwest oak savannas, competition for limited understory resources (e.g. space, soil moisture, nutrients, light, etc.) intensifies, which may constrain the regeneration, growth, recruitment, and survival of white oak seedlings

(Bowles and McBride 1998; Albrecht and McCarthy 2006; Meiners 2007; Brudvig and Asbjornsen 2008; Kuebbing et al. 2014). Additionally, as Amur honeysuckle and other invasive species continue to spread into the United States, it is important to understand invasion dynamics, such as range expansion and colonization patterns to further guide management strategies with an aim to control abundant and aggressive invasive species (Gorchov et al. 2014; Iannone et al. 2014).

Past studies have explored the role of Amur honeysuckle in altering a variety of aboveground and belowground community dynamics associated with native tree seedlings (e.g. regeneration, recruitment, growth, composition, mortality, soil dynamic properties, etc.), with conflicting findings concerning the ecological impact of invasive species on belowground ecosystem properties (Hutchinson and Vankat 1997; Gould and Gorchov 2000; Collier et al. 2002; Gorchov and Trisel 2003; Hartman and McCarthy 2004; Bartuszevige et al. 2006; McEwan et al. 2009; McEwan et al 2012; Wilson et al. 2013; Iannone et al. 2014; Iannone et al. 2015). Additionally, genetic population structure analyses have been successfully used to identify geographic and genetic differentiation and variation between subpopulations of Amur honeysuckle throughout Ohio, as a way to estimate dispersal distances, colonization patterns, and infer potential sources of both founding and newly established individuals (McNutt 2010; Barriball 2012; Rocha et al. 2014; Barriball et al. 2015). Few studies, however, have explicitly addressed how Amur honeysuckle impacts white oak regeneration and recruitment, in relation to carbon assimilation, soil quality, soil moisture, soil temperature, and plant available nutrients; nor have they utilizes the known invasion history of Amur

honeysuckle in order to assess whether anthropogenic influences should be considered when defining long-distance dispersal events of invasive species.

The objectives of this study were to better understand how the encroachment of *Lonicera maackii* (Amur honeysuckle) impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration project located in Lee County, Illinois, USA, with particular focus on mechanisms required for successful oak regeneration and recruitment (i.e. adequate carbon assimilation, soil quality, soil moisture, soil temperature, and plant available nutrients). This study also aims to explore the spatial-temporal long distance dispersal patterns of Amur honeysuckle, as inferred by population genetics, in order to better understand the mechanisms and pathways by which Amur honeysuckle has spread throughout Illinois.

The following summary addresses each of the research questions posed in Chapter 1, beginning first by assessing the ecological impact of the extended leaf phenology and invasive encroachment of Amur honeysuckle on understory light environments and seasonal carbon assimilation rates; followed by an examination of soil quality, moisture, temperature, and nutrient characteristics in areas with and without Amur honeysuckle; and concluding with a description of the general geographic and evolutionary patterns associated with Amur honeysuckle's historic range expansion throughout the eastern and central United States, with implications for identifying past and future invasion pathways and potentially redefining our understanding of long distance dispersal with regards to invasive species.

8.1 ECOLOGICAL IMPACTS RELATED TO LIGHT AND CARBON ASSIMILATION

The first set of research questions concerned the ecological impact of the invasive encroachment and extended leaf phenology of Amur honeysuckle on understory light environments and seasonal carbon assimilation totals of both Amur honeysuckle and white oak seedlings. In answering these questions, the current stand structure of the oak savanna restoration study site at Nachusa Grasslands, IL was also characterized. The specific questions were as follows: What role does the extended leaf phenology of Amur honeysuckle play in its leaf-level seasonal carbon gain? What are the existing *in situ* light levels above and below Amur honeysuckle canopies and do those light levels inhibit the ability of *in situ* white oak seedlings to maintain a positive net leaf-level seasonal carbon balance?

This research found that by the time bud swell initiated for white oak seedlings in the understory of the oak savanna restoration study site at Nachusa Grasslands, the leaves of Amur honeysuckle shrubs were already fully open, creating a dense midstory canopy. Additionally, the dominant overstory tree species in the oak savanna restoration study site at Nachusa Grasslands reached leaf open phase before white oak seedlings, which in turn further reduced the amount of light reaching the white oak seedlings in the understory. Overall, the Amur honeysuckle shrubs in the oak savanna restoration study site at Nachusa Grasslands experienced about 48 more days with leaves open than white oak seedlings. On average, however, the extended leaf phenology of Amur honeysuckle that was observed in this study did not significantly increased the amount of total seasonal carbon gained by photosynthetically average Amur honeysuckle

shrubs when compared to the total seasonal carbon gained by a photosynthetically average white oak seedlings, no matter the light scenario.

The average midday light level from leaf open to leaf senescence phenology phases for the one meter understory light scenario was 98.8 ± 3.2 mol/m^2 (8.68 percent of midday full sun measured at Nachusa Grassands), while the midday average for the same phenology period in the understory light scenario with and without Amur honeysuckle encroachment was 65.0 ± 2.8 mol/m^2 (5.71 percent of midday full sun measured at Nachusa Grassands) and 28.4 ± 2.1 mol/m^2 (2.49 percent of midday full sun measured at Nachusa Grassands), respectively. The total seasonal light measured at one meter above the ground in the oak savanna restoration study site understory did not significantly differ from the total seasonal light measured at 30 cm above the ground, both with and without the presence of Amur honeysuckle, which indicates that the current dense overstory tree canopy in the oak savanna restoration study site at Nachusa Grasslands played a significant role in the amount of seasonal light received by the understory.

In the end, the low light levels in the understory of the oak savanna restoration study site at Nachusa Grasslands yielded marginal seasonal carbon assimilation totals for white oak seedlings, especially when compared to the high seasonal carbon assimilation totals that were estimated for white oak seedlings had they been growing in full sun light conditions. In all light scenarios, the white oak seedlings that survived until the end of the study period (indicating a higher level of fitness) had significantly higher daily average carbon assimilation than the white oak seedlings that died at some point

before the end of the study. This was especially pronounced in the daily carbon assimilation rates of white oak seedlings growing in the understory of the oak savanna restoration study site with Amur honeysuckle encroachment, where surviving white oak seedlings had a marginally positive average daily carbon assimilation rate, as compared to the negative average daily carbon assimilation of white oak seedlings that died during the study.

8.2 ECOLOGICAL IMPACTS RELATED TO SOIL DYNAMIC PROPERTIES

The second set of research questions concerned detecting whether there were ecological differences in belowground soil dynamic properties associated with the presence and absence of Amur honeysuckle, with implications for belowground resource competition with white oak seedlings. In answering these questions, general soil variability throughout the oak savanna restoration study site at Nachusa Grasslands, IL was also characterized. The specific questions were as follows: Do aggregate stability, soil moisture/temperature, carbon/nitrogen ratios, and levels of other soil nutrients significantly different in soil found under and away from Amur honeysuckle?

The study site was found to be primarily composed of Mollic Hapludalfs, a soil subgroup representative of savanna vegetation communities, given its mixture of soil characteristics associated in part with forest communities and prairie communities. White oak is adapted to all soil textures except fine textured soils (USDA 2015d), and all soils found in the study site were well within the range of ideal soil textures for white oaks, and were therefore not considered an inhibiting factor for the regeneration and

recruitment of white oak in the oak savanna restoration study site at Nachusa Grasslands. Likewise, Amur honeysuckle was found thriving across multiple soil textures within the oak savanna restoration study site, suggesting that soil texture was also not a limiting factor for Amur honeysuckle at Nachusa Grasslands.

The overall soil moisture measured in the oak savanna restoration study site at Nachusa Grasslands was higher than soil moisture reported by previous research for other oak savanna communities (Tang et al. 2005). Additionally, no significant differences in soil moisture or soil temperature were found in the oak savanna restoration study site across a gradient of Amur honeysuckle encroachment (i.e. near stem under canopy, near canopy dripline, and at least one meter away from Amur honeysuckle). As a result, soil moisture was also determined not to be a limiting factor for the regeneration and recruitment of white oak in this study, especially given the medium drought tolerance and medium moisture usage of white oak (Larson and Whitmore 1970; USDA 2015d).

The high nutrient availability found at Nachusa Grasslands indicates that nutrients are not a limiting factor for white oak in the oak savanna restoration site, especially given their adaptations to low fertility sites (USDA 2015d). The average soil pH measured in the oak savanna restoration study site at Nachusa Grasslands fell within the optimal pH range for white oak seedlings. Furthermore, no significant differences in any soil nutrient or acidity were found in the oak savanna restoration study site under or away from Amur honeysuckle, which suggests that the shallow root system and extended leaf phenology of Amur honeysuckle does not represent direct

belowground competition for white oak regeneration and recruitment a Nachusa Grasslands.

With regards to soil quality, as inferred by wet-aggregate soil stability, all soils analyzed in the oak savanna restoration study site at Nachusa Grasslands (including those collected under Amur honeysuckle) had a high soil macro-aggregate (4-0.25 mm) stability, with the highest proportion of stable sand-free aggregates occurring in the 4-2 mm size fraction. No significant differences were detected in soil stability under and away from Amur honeysuckle. This suggests that even given the high level of disturbance cause by Amur honeysuckle, the soil in the uncultivated oak savanna restoration study site at Nachusa Grasslands has a high quality, given the highly stable macro-aggregates.

8.3 EVOLUTIONARY INVASION DYNAMICS OF AMUR HONEYSUCKLE

The final set of research questions investigated the underlying evolutionary mechanisms associated with the spatial-temporal long distance dispersal patterns of Amur honeysuckle, as inferred by population genetics, to better understand the mechanisms and pathways by which this species is spreading throughout the Midwestern United States. The specific questions were as follows: Did Amur honeysuckle spread into Illinois via natural and/or anthropogenically facilitated long-distance dispersal followed by outward expansion through local and/or regional diffusion? Do the results from a genetic structure analysis support any of the three proposed invasion pathways, identified based on historical records?

The first hypothesized pathway for the spread of Amur honeysuckle to and throughout Illinois was west via anthropogenically facilitated long-distance dispersal from *The New York Botanical Garden, NY and/or The Arnold Arboretum of Harvard University, MA.* The New York Botanical Garden was the first U.S. location to record successful cultivation of Amur honeysuckle obtained from Washington D.C. in 1898, followed by The Arnold Arboretum at Harvard University in 1903 (Luken and Thieret 1996). The second hypothesized pathway was west from *The Morton Arboretum, Lisle, IL.* The Morton Arboretum was the first location to document the ability of Amur honeysuckle to reproduce and spread beyond the point of its introduction in the U.S. in the mid-1920s, and reports of naturalized populations within the United States began appearing by the late 1950s (Luken and Thieret 1996; Cipollini and Dorning 2008). The final hypothesized pathway for the spread of Amur honeysuckle throughout Illinois was via regional dispersal between Illinois State Forests, including *Hidden Springs State Forest, Strasburg, IL and Trail of Tears State Forest, Jonesboro, IL* (EDDMapS 2015). Both of these State Forests were identified as being located in and near areas with a high number of reported sightings of mature Amur honeysuckle encroachment (EDDMapS 2015). Ultimately, this portion of the research was based on the notion that the number and source of individuals establishing new populations, along with gene flow (or pattern of dispersal) and geographic distance, determine the extent of genetic differentiation between populations at a landscape level (Whitlock and McCauley 1999).

This study found that a major proportion of the genetic differentiation that was found in Amur honeysuckle occurred within subpopulations, rather than among them.

Similar to other studies (McNutt 2010), the high level of genetic differentiation within each subpopulation was phenotypically undetectable during field identification and collection in this study. Based on the clustering patterns found in the Principal Coordinate Analyses for three genetic differentiation variables in this study, long distance regional dispersal events occurring across an average of about 74 km (up to as much as 490 km) have likely occurred throughout Illinois, given the low genetic differentiation between the regional subpopulations located in southern (TT.IL), central (HS.IL) and northern Illinois (predominantly NGW.IL and NGE.IL to a lesser extent). The lack of correlation for the Illinois subpopulations suggest that they do not display genetic isolation or similarity with increasing or decreasing distance, which is consistent with the finding that there has been active gene flow between these subpopulations via regional long distance dispersal events.

These regional dispersal events between the Illinois subpopulations have likely contributed to the high within-subpopulation genetic differentiation detected in this research. Without additional research into the details of this dispersal, however, it is difficult to determine, strictly from the genetic population analyses, whether the mode by which the dispersal between these subpopulations was via anthropogenic activity or by the migratory pathways of the birds known to disperse Amur honeysuckle; specifically: European starlings (*Sturnus vulgaris*), American robins (*Turdus migratorius*), hermit thrushes (*Catharus guttatus*), cedar waxwings (*Bombycilla cedrorum*), and northern mockingbirds (*Mimus polyglottus*) (Bartuszevige and Gorchov 2006).

When all subpopulations from this research were analyzed together (increasing the mean dispersal distance to about 927 km), a strong positive correlation between the genetic distance and geographic distance was found. The New York Botanical Garden subpopulation was found to be most genetically isolated from all other subpopulations (based on patterns found in three Principal Coordinate Analyses using genetic differentiation variables), indicating that very little, if any, propagule exchange has occurred between The New York Botanical Garden and the other subpopulations. The Arnold Arboretum at Harvard University and The Morton Arboretum also displayed patterns of genetic isolation from the other subpopulations, more so than from each other, suggesting that these two subpopulations have experienced some form of anthropogenic long distance dispersal events, given the large geographic distance (approx. 1,614 km) and the east-west orientation (an orientation and geographic distance unlikely to been enabled by birds, which tend to follow north-south migratory paths; Bartuszevige and Gorchov 2006) that separates them.

Furthermore, the subpopulation from the eastern half of the oak savanna restoration study site seemed to act as an intermediary between the genetically isolated subpopulations and the genetically similar subpopulations found in this research. The relatively close geographic distance, but high genetic differentiation (supported by findings from the Shannon Diversity Indices analysis) of The Morton Arboretum subpopulation to the other Illinois subpopulations, suggests that it might be a sink (i.e. accumulating genetically distinct propagules, thereby increasing genetic differentiation from other Illinois subpopulations) and not a source for the spread of Amur

honeysuckle, except potentially for the Nachusa Grasslands subpopulation in northern Illinois and the Trail of Tears State Forest subpopulation in southern Illinois to which it shares some genetic connection.

Ultimately, the results of this research support the stratified dispersal model, meaning that it spreads from multiple locations through local and regional diffusion across the landscape in combination with long distance, “jump” dispersal events (Hengeveld in1989; Gorchov et al. 2014). Although more research should be conducted with larger sample sizes from additional subpopulations along a more expansive geographic gradient, before any major conclusions are drawn from these results.

8.4 CONCLUSION AND MANAGEMENT RECOMMENDATIONS

Dominance of white oaks throughout Midwest oak savanna is vital to maintaining composition and species habitat (Rogers 1990; Abrams 2005; Brudvig and Evans 2006; Wang and Bauerle 2006). Without a competitive advantage over encroaching species, Schulte et al. (2011) predicts that oaks will lose their historical dominance within the next few decades. Restoration (defined as the removal of large shrubs and mesophytic trees) of oak savannas has been shown to be a viable way to promote white oak regeneration and recruitment (Brudvig and Asbjornsen 2008, 2009; Craig 2012) and information concerning white oak responses to individual site characteristics and invasive species can benefit these restoration activities, given their ability to provide guidance for site specific goals and management practices.

Evidence suggests that low light levels and average carbon assimilation totals play a significant role in the white oak regeneration and recruitment gap found in the oak savanna restoration study site at Nachusa Grasslands. The low seasonal carbon assimilation totals estimated for white oak seedlings growing in the understory of the oak savanna restoration study site, both with and without Amur honeysuckle encroachment, would most likely not be sufficient to provide enough resources for the white oak seedlings to survive and recruit to the overstory canopy. The low light saturation point found for white oak seedlings at Nachusa Grasslands suggest that there would be no added benefit to opening or increasing light environments any higher than 24 percent of full sun (equivalent to about 273.2 μmol /m^2/s using the full sun measured at Nachusa Grasslands), which is slightly above the average light saturation point of the white oak seedlings surveyed in the oak savanna restoration study site. To achieve 24 percent full sunlight, the light level within the understory needs to be increase by between 15 to 21.5 percent. Finally, when considering where to focusing attention and resources when reducing the basal area in the oak savanna restoration study site at Nachusa Grasslands, mesophytic overstory trees should also be targeted, along with reduction of Amur honeysuckle encroachment. While the removal of overstory canopy trees is recommended as an important management strategy for increasing light levels within oak savanna restorations to promote the regeneration and recruitment of white oak seedlings, precautions (i.e. focusing management resources on invasive shrubs growing in canopy gaps) should be built into management strategies to minimize the counteractive consequences potentially caused by canopy thinning (i.e. increased spread of invasive species; Iannone et al. 2014) .

In relation to belowground properties, this study found no significant differences between any of the soil characteristics (i.e. wet macro-aggregate soil stability, soil moisture, soil temperature, carbon nitrogen ratios, and nutrient levels) measured in adjacent soil samples collected under and away from Amur honeysuckle throughout the western half of the oak savanna restoration study site. As a result, this research concludes that competition by and/or presence of Amur honeysuckle had minimal impact on the soil dynamic properties (i.e. wet macro-aggregate soil stability, soil moisture, soil temperature, carbon nitrogen ratios, and nutrient levels) in the oak savanna study site at Nachusa Grasslands. Management efforts to increase white oak seedlings regeneration and recruitment in the oak savanna restoration study site at Nachusa Grasslands should therefore be focused on other understory resource competition dynamics beyond belowground properties. These findings expand our general understanding of dynamic soil and forest floor properties (e.g. soil moisture, carbon, nitrogen, and available plant nutrient levels) in relation to the environmental impacts of Amur honeysuckle encroachment, and provide further support that impact of soil characteristics may differ spatially from one site to another. Additionally, these findings facilitates a more accurate discussion about how the encroachment of Amur honeysuckle impacts the Midwest native *Quercus alba* (white oak) population in a Nature Conservancy oak savanna restoration study site located at Nachusa Grasslands in Lee County, Illinois, with particular focus on ecological mechanisms required for successful oak regeneration and recruitment.

With regard to the underlying evolutionary mechanisms associated with the spatial-temporal long distance dispersal patterns of Amur honeysuckle, the findings from this research provide support for the stratified dispersal model, also referred to as stratified diffusion (coined by Hengeveld in1989), currently associated with Amur honeysuckle (McNutt 2010; Gorchov et al. 2014; Barriball et al. 2015). Meaning that dispersal (as inferred by gene flow) of Amur honeysuckle was found to occur from multiple locations through regional diffusion across the landscape, in combination with longer distance dispersal events that range in distance from around four km (Gorchov et al. 2014) to as much as 1,614 km (i.e. approximate distance between The Morton Arboretum and The Arnold Arboretum at Harvard University). As a result, this research supports the suggested management recommendations of Gorchov et al. (2014) for the most efficient use of resources when designing strategies to control the expansion of Amur honeysuckle. More specifically, Gorchov et al. (2014) asserts that it is important to locate newly colonized Amur honeysuckle shrubs in neighboring sites (especially within about 5 km) before they reach reproductive maturity, which may seem like a daunting, time-consuming task until the lag between establishment and development to reproductive maturity of Amur honeysuckle is taken into account. This lag in reproductive maturity can range from three to eight years for Amur honeysuckle (Deering and Vankat 1999), therefore sweeps for new colonizers need only occur about every three years according to Gorchov et al. (2014).

Future work will continue to explore the ecological impact and evolutionary invasion mechanisms of *Lonicera maackii*, as it relates to the regeneration and

recruitment gap of *Quercus alba*. Continued long-term observations of leaf phenology for white oak trees, saplings, and seedlings across spatial and temporal scales would benefit the understanding of seasonal carbon assimilation. Furthermore, scaling seasonal carbon assimilation from leaf-level to plant- and community- level would provide added information about the role of invasive species in the regeneration and recruitment gap of white oak. Future studies would also benefit from larger scale replications of the soil analyses with added monitoring stations across an oak restoration chronosequence to represent a wider range of environmental gradients and invasion stages, so as to better understand the role of invasive species in belowground ecosystem properties. Moreover, future studies exploring how site environmental factors (e.g. landscape topography, soil, microsite climate conditions, etc.) influence genetic variation within-subpopulations are necessary, coupled with expanded genetic population analyses using larger sample sizes from additional subpopulations along a more expansive geographic gradient. Finally, it is important to establish long-term monitoring studies that assess the impact of implemented restoration strategies on oak regeneration, establishment, growth, and mortality rates, with the aim of improving conservation efforts for white oak into the future.

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APPENDIX A

LEAF PHENOLOGY OBSERVATION DATES

Table A-1. Table listing dates associated with the leaf phenology stages of all species surveyed in study site for the 2011 growing season. Bold, red dates indicate estimated dates based on other observations.

Species	Swell (2)	Break (3)	Leaves unfolding (4)	Open (5)	Leaves Changing (>5, <7)	Senesced (7)	GS (# Days)	GD (# Days)
Carya cordiformis	22-Apr-11	29-Apr-11	8-May-11	15-May-11	2-Oct-11	27-Oct-11	188	140
Carya ovata	2-May-11	9-May-11	12-May-11	15-May-11	2-Oct-11	14-Oct-11	165	140
Celtis occidentalis	27-Apr-11	2-May-11	11-May-11	15-May-11	2-Oct-11	17-Nov-11	204	140
Lonicera maackii	**5-Apr-11**	7-Apr-11	10-Apr-11	16-Apr-11	27-Oct-11	**20-Dec-11**	259	181
Prunus serotina	11-Apr-11	13-Apr-11	16-Apr-11	29-Apr-11	2-Oct-11	17-Nov-11	220	156
Ptelea trifoliata	11-Apr-11	16-Apr-11	6-May-11	15-May-11	2-Oct-11	10-Oct-11	182	140
Quercus alba (seedlings)	**7-May-11**	**14-May-11**	**21-May-11**	**1-Jun-11**	**25-Sep-11**	**21-Nov-11**	198	116
Quercus alba (trees)	22-Apr-14	7-May-11	12-May-11	20-May-11	2-Oct-11	27-Oct-11	188	135
Quercus rubra	23-Apr-11	2-May-11	9-May-11	15-May-11	2-Oct-11	17-Nov-11	208	140
Ulmus rubra	8-Apr-11	16-Apr-11	29-Apr-11	15-May-11	2-Oct-11	27-Oct-11	202	140

Table A-2. Table listing dates associated with the leaf phenology stages of all species surveyed in study site for the 2012 growing season. Bold, red dates indicate estimated dates based on other observations.

Species	Swell (2)	Break (3)	Leaves unfolding (4)	Open (5)	Leaves Changing (>5, <7)	Senesced (7)	GS (# Days)	GD (# Days)
Carya cordiformis	24-Mar-12	4-Apr-12	18-Apr-12	11-May-12	3-Sep-12	19-Oct-12	209	115
Carya ovata	3-Apr-12	16-Apr-12	24-Apr-12	11-May-12	3-Sep-12	28-Oct-12	208	115
Celtis occidentalis	21-Mar-12	24-Mar-12	31-Mar-12	14-Apr-12	3-Sep-12	28-Oct-12	221	142
Lonicera maackii	18-Mar-12	20-Mar-12	23-Mar-12	8-Apr-12	9-Sep-12	9-Dec-12	266	154
Prunus serotina	**15-Mar-12**	18-Mar-12	22-Mar-12	24-Mar-12	3-Sep-12	3-Nov-12	233	163
Ptelea trifoliata	21-Apr-12	28-Apr-12	1-May-12	4-May-12	3-Sep-12	14-Oct-12	176	122
Quercus alba (seedlings)	**11-Apr-12**	**18-Apr-12**	**25-Apr-12**	**6-May-12**	3-Sep-12	3-Nov-12	206	120
Quercus alba (trees)	23-Mar-12	30-Mar-12	16-Apr-12	28-Apr-12	3-Sep-12	19-Oct-12	210	128
Quercus rubra	20-Mar-12	24-Mar-12	3-Apr-12	28-Apr-12	3-Sep-12	28-Oct-12	222	128
Ulmus rubra	20-Mar-12	23-Mar-12	28-Mar-12	8-Apr-12	3-Sep-12	6-Oct-12	200	148

Table A-3. Table listing dates associated with the leaf phenology stages of all species surveyed in study site for the 2013 growing season. Bold, red dates indicate estimated dates based on other observations.

Species	Swell (2)	Break (3)	Leaves unfolding (4)	Open (5)	Leaves Changing (>5, <7)	Senesced (7)	GS (# Days)	GD (# Days)
Carya cordiformis	29-Apr-13	2-May-13	4-May-13	16-May-13	17-Sep-13	7-Nov-13	192	124
Carya ovata	1-May-13	6-May-13	10-May-13	30-May-13	17-Sep-13	24-Oct-13	176	110
Celtis occidentalis	29-Apr-13	3-May-13	7-May-13	11-May-13	17-Sep-13	7-Nov-13	192	129
Lonicera maackii	18-Apr-13	22-Apr-13	28-Apr-13	4-May-13	10-Oct-13	**16-Dec-13**	242	159
Prunus serotina	22-Apr-13	28-Apr-13	1-May-13	4-May-13	17-Sep-13	7-Nov-13	199	136
Ptelea trifoliata	14-Apr-13	20-Apr-13	4-May-13	16-May-13	17-Sep-13	1-Nov-13	201	124
Quercus alba (seedlings)	7-May-13	12-May-13	18-May-13	30-May-13	14-Sep-13	26-Nov-13	203	107
Quercus alba (trees)	29-Apr-13	6-May-13	10-May-13	16-May-13	24-Sep-13	7-Nov-13	192	131
Quercus rubra	27-Apr-13	1-May-13	4-May-13	16-May-13	24-Sep-13	16-Nov-13	203	131
Ulmus rubra	27-Apr-13	1-May-13	4-May-13	11-May-13	17-Sep-13	1-Nov-13	188	129

Table A-4. Table listing dates associated with the leaf phenology stages of all species surveyed in study site for the 2014 growing season. Bold, red dates indicate estimated dates based on other observations.

Species	Swell (2)	Break (3)	Leaves unfolding (4)	Open (5)	Leaves Changing (>5, <7)	Senesced (7)	GS (# Days)	GD (# Days)
Carya cordiformis	27-Apr-14	4-May-14	8-May-14	20-May-14	26-Sep-14	1-Nov-14	188	129
Carya ovata	4-May-14	9-May-14	12-May-14	20-May-14	26-Sep-14	1-Nov-14	181	129
Celtis occidentalis	26-Apr-14	2-May-14	6-May-14	14-May-14	26-Sep-14	1-Nov-14	189	135
Lonicera maackii	10-Apr-14	13-Apr-14	19-Apr-14	1-May-14	8-Oct-14	14-Dec-14	248	160
Prunus serotina	16-Apr-14	21-Apr-14	26-Apr-14	1-May-14	26-Sep-14	1-Nov-14	199	148
Ptelea trifoliata	1-May-14	20-May-14	24-May-14	28-May-14	26-Sep-14	1-Nov-14	184	121
Quercus alba (seedlings)	4-May-14	12-May-14	19-May-14	28-May-14	26-Sep-14	1-Nov-14	181	121
Quercus alba (trees)	3-May-14	9-May-14	13-May-14	28-May-14	26-Sep-14	1-Nov-14	182	121
Quercus rubra	23-Apr-14	4-May-14	8-May-14	14-May-14	26-Sep-14	1-Nov-14	192	135
Ulmus rubra	15-Apr-14	26-Apr-14	1-May-14	8-May-14	26-Sep-14	1-Nov-14	200	141

APPENDIX B

SOIL CORE DESCRIPTIONS

Table B-1. Soil description of 5m soil core collected at grid point 9 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #9
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'51.31"N, 89°22'8.51"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 04/18/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	12	10 YR 2/2	10 YR 3/2					2	c	sbk							fr	c	vf			
								3	c/m	gr												
ABt	19	10 YR 2/2	10 YR 2/2					3	c/m/f/vf	gr							fr	c	f/vf/vc			
											clf	10 YR 3/4	c	th	c	pf						
Bt1	39	10 YR 3/5						3	c/m/f	sbk	org	10 YR 2/2	c			sc/sp	fi	c	m/f/vf			
											clf	10 YR 3/2	m	th	c	pf						
Bt2	61	10 YR 3/6						2	m	abk	org	10 YR 3/2	f			sp/sc	fi	c	f/vf		a	
								3	f/vf	abk	clf	10 YR 3/4	m	th	c	pf						
2Bt/Cr	80	10 YR 3/5						3	c/f	sbk	clf	10 YR 3/4	c	th	c	pf	fr	f	vf	st	a	
		10 YR 5/8								m												

Few lithocranic mottles found from 59-80 cm

Table B-2. Soil description of 5m soil core collected at grid point 10 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #10
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'51.38"N, 89°22'5.88"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 05/27/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	12	10 YR 2/2	10 YR 5/2					3	c/m/f/vf	gr							fr	c	f/vf			
BAt	26	10 YR 4/4	10 YR 5/3					3	c/m/f/vf	sbk	org	10 YR 3/2	c (25%)			sp/sc	fi	c	c/f/vf			
											clf	10 YR 4/4	m	th	c	pf						
Bt1	40	10 YR 3/6						1	c/m	abk	org	10 YR 3/2	f (6%)			sp/sc	fi	c	f/vf			
								2	f/vf	sbk	clf	10 YR 4/4	m	th	c	pf						
Bt2	56	10 YR 3/6						3	m	sbk	org	10 YR 3/1	vf (4%)			sp/sc	fi	c	c/f/vf			
								1	f/vf	abk	clf	10 YR 4/6	m	th	c	pf						
Bt3	80	10 YR 3/6		2.5 YR 3/6	f	c	p	1	m	abk	org	10 YR 3/1	vf (2%)			sp/sc	fi	c	f			
								2	f/vf	abk	clf	10 YR 3/4	m	th	c	pf		f	vf			
2Bt/Cr	86	10 YR 4/6		10 YR 2/1	c	m	d	2	m	sbk							fi	c	f/vf	vsl		
		10 YR 6/6								m	clf	10 YR 3/6	c	th	c	pf						

Table B-3. Soil description of 5m soil core collected at grid point 11 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #11
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'51.40"N, 89°22'3.22"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 05/23/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A1	8	10 YR 2/2	10 YR 3/2					2	m/f	sbk							fi	c	f/m/vf			
								2	f/vf	gr												
A2	15	10 YR 2/2	10 YR 3/2					2	c/m/f/vf	gr	clf	10 YR 3/4	f	th	c	pf	fr	c	vf			
Bt1	32	10 YR 3/6						3	m/f/vf	sbk	org	10 YR 3/1	f			sp/sc	fi	c	vf			
											clf	10 YR 3/4	c	th	c	pf						
Bt2	51	10 YR 3/6		10 YR 2/1	c (3%)	m	d	3	c/m	sbk	clf	10 YR 3/4	m	th	c	pf	fi	c	vf	sl		
				7.5 YR 5/8	c (10%)	m	d	3	f/vf	abk	org	10 YR 3/1	vf			sp/sc						
2Bt/Cr	68	10 YR 3/4						2	f	sbk							fi	c	vf	st		
		10 YR 7/6		10 YR 4/6	c (10%)	c	d			m	clf	10 YR 3/6	c	th	c	pf						
2Cr/Bt	84	10 YR 7/8								m							fi	c	vf	st		
		10 YR 5/4		10 YR 6/8	c (5%)	m	d	2	m	sbk	clf	10 YR 3/4	f	th	c	pf						
2Cr	91	2.5 Y 7/4								m										st		
				10 YR 7/8	c (5%)	m	d				clf	10 YR 4/6	vf	th	c	ff						

Table B-4. Soil description of 5m soil core collected at grid point 12 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #12
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'51.44"N, 89°22'0.60"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 03/16/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	6	10 YR 2/1	10 YR 4/2					2	m/f	sbk							fr	m	vf/f			
								3	f/vf	gr												
ABt	12	10 YR 2/1	10 YR 4/2					2	m/f	sbk							fr	c	f/vf			
								2	m/f	gr	clf	10 YR 3/3	c (40%)									
Bt1	21	10 YR 3/4						3	m/f/vf	sbk	org	10 YR 3/1	m (50%)			sp/sc	fi	f	f			
											clf	10 YR 3/4	m (80%)	th	c	pf		c	vc			
Bt2	30	10 YR 3/4						2	m/f/vf	sbk	org	10 YR 2/1	c			sp/sc	fi	f	vf			
											clf	10 YR 3/3	m	th	c	pf						
Bt3	38	10 YR 3/4						3	m/f/vf	abk	org	10 YR 3/1	c (25%)			sp/sc	fi	f	f/vf			
											clf	10 YR 3/4	m (85%)	th	c	pf						
2Bt/Cr	47	10 YR 3/6						3	m/f	abk							fi	f	f	st		
		10 YR 5/8								m	clf	10 YR 3/4	m	th	c	pf						

Table B-5. Soil description of 5m soil core collected at grid point 13 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #13
PROFILE CLASSIFICATION: Typic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'51.50"N, 89°21'57.98"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 04/26/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	13	10 YR 2/1	10 YR 3/2					2	m	sbk							fi	c	f/vf			
								2	f/vf	gr												
ABt	23	10 YR 3/3	10 YR 3/2					3	m	sbk	org	10 YR 3/1	m (50%)			sp/sc	fi	c	f/vf			
								2	m/f/vf	gr	clf	10 YR 3/3	c	th	c	pf						
BAt	40	10 YR 3/3	10 YR 3/3					3	c	sbk	org	10 YR 2/1	c (30%)			sp/sc	fi	f	f/vf			
								1	f/vf	sbk	clf	10 YR 3/3	m	th	c	pf						
Bt	52	10 YR 3/4						3/2	m	sbk	org	10 YR 2/1	f (10%)			sp/sc	fi	c	m	vsl	a	
								2	f/vf	abk	clf	10 YR 3/1	m	th	c	pf						
2Cr/Bt	73.5	2.5 Y 6/8						2	m/f	sbk	clf	10 YR 3/3	c (25%)	th	c	pf	fr	f	f/vf	st	a	
		10 YR 3/3								m	org	10 YR 3/1	f (5%)			sp/sc						

Tubers found in common abundance throughout top two horizons (0-23 cm)
Organic coatings found in 2Cr/Bt horizon (52-73.5 cm) were from roots decomposing in place, rather than organic accumulations

Table B-6. Soil description of 5m soil core collected at grid point 18 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #18
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'49.35"N, 89°22'8.50"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 03/16/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	11	10 YR 2/1	10 YR 4/1					3	f/m/vf	gr							fr	m	f/vf			
ABt	19	10 YR 3/4	10 YR 4/2					3	m	sbk	org	10 YR 2/1	m (85%)			sp/sc	fi	c	m/f/vf			
								3	m/f	gr	clf	10 YR 3/3	m (50%)	th	c	pf						
Bt	26	10 YR 4/6						2	m/f/vf	sbk	org	10 YR 2/1	m (50%)			sp/sc	fi	c	f			
											clf	10 YR 3/4	m (70%)	th	c	pf						
2Bt/Cr	32	10 YR 3/4						2	m/f	sbk								f	f	vsl		
		10 YR 5/6								m	clf	10 YR 3/4	m (50%)	th	c	pf		c	m/c			

Dry color of organic coatings in ABt horizon (11-19 cm): 10 YR 4/3

Table B-7. Soil description of 5m soil core collected at grid point 19 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #19
PROFILE CLASSIFICATION: Typic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'49.42"N, 89°22'5.87"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 03/15/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	7	10 YR 3/1	10 YR 4/2					2	vf/f	sbk							fr	c	vf/f			
								3	f/m	gr												
BAt	17.5	10 YR 4/6	10 YR 6/3					3	f/m	sbk	org	10 YR 3/1	vm			sp/sc	fr	c	f			
								2	f/m	gr												
Bt1	25	10 YR 3/4						3	f/vf	sbk	org	10 YR 3/1	m (50%)			sp/sc	fi	c	f/vf			
											clf	10 YR 3/4	m	th	c	pf		f	c			
Bt2	47.5	10 YR 3/6						3	f/vf	sbk	org	10 YR 3/1	c (30%)			sp/sc	fi	c	f/vf			
											clf	10 YR 4/3	m	th	c	pf						
Bt3	58.5	10 YR 4/6		10 YR 3/1	f (10%)		d	2	m/f	sbk							fi	c	f			
											clf	10 YR 3/4	m (80%)	th	c	pf						
Bt4	75.5	10 YR 3/6						3	f/m	sbk							fi	c	vf/f/m			
											clf	10 YR 3/2	m (75%)	th	c	pf						
2Cr/Bt	80	10 YR 5/6								m								c	f	vsl		
		10 YR 3/4						2	m	sbk	clf	10 YR 3/2	c	th	c	pf		f	vf			

Dry color of organic coatings in BAt horizon (7-17.5 cm): 10 YR 5/2

Table B-8. Soil description of 5m soil core collected at grid point 20 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #20
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'49.47"N, 89°22'3.26"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 05/23/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A1	9	10 YR 2/2	10 YR 4/2					3	f/vf	gr							fr	c	vf			
A2	19	10 YR 3/3	10 YR 4/2					2	m	sbk	org	10 YR 2/2	m (50%)			sp/sc	fr	c	f/vf/c			
								3	f/vf	gr												
BAt	28	10 YR 3/4	10 YR 5/3					2	m/f	sbk	org	10 YR 3/1	c			sp/sc	fi	c	vf			
											clf	10 YR 3/4	c	th	c	pf						
Bt1	38.5	10 YR 3/6						2	f	sbk							fi	c	f/vf			
								2	f/vf	abk	clf	10 YR 3/4	m	th	c	pf						
Bt2	54	10 YR 3/4						3	m/f/vf	abk							fi	c	vf			
											clf	10 YR 3/4	m	th	c	pf						
2Bt/Cr	61	10 YR 3/4						2	m	abk	clf	10 YR 3/4	c	th	c	pf	fi	c	f/vf	sl		
		10 YR 5/7								m												

Table B-9. Soil description of 5m soil core collected at grid point 21 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #21
PROFILE CLASSIFICATION: Lithic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'49.57"N, 89°22'0.62"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 05/23/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	11.5	10 YR 2/2	10 YR 4/2					3	m/f/vf	gr							fr	c	f/vf/m			
ABt1	18	10 YR 3/3	10 YR 4/3					3	m	sbk	org	10 YR 3/1	f (20%)			sp/sc	fr	c	f/vf/m			
								3	f/vf	gr	clf	10 YR 3/3	m	th	c	pf						
ABt2	30	10 YR 3/3	10 YR 4/4					2	m	sbk	org	10 YR 3/2	c			sp/sc	fi	c	vf			
								3	f/vf	abk	clf	10 YR 3/3	m	th	c	pf						
Bt	38	10 YR 4/6						2	m	abk							fi	c	vf			
								3	f/vf	abk	clf	10 YR 3/3	m	th	c	pf						
2Bt/Cr	50	10 YR 3/4								m							fi	f	vf	vsl		
		2.5 Y 6/4						2	m	sbk	clf	10 YR 3/4	c	th	c	pf		c	vc			

2 large pieces of root found in the 2 Bt/Cr horizon from 38 cm to 50 cm

Table B-10. Soil description of 5m soil core collected at grid point 22 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #22
PROFILE CLASSIFICATION: Typic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'49.57"N, 89°21'57.99"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 07/08/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	5	10 YR 2/1	10 YR 4/2					2	m/f/vf	sbk							fr	c	f/vf			
ABt	14	10 YR 3/1	10 YR 5/2					3	m/f/vf	sbk	clf	10 YR 3/4	f (20%)	th	c	pf	fr	c	f/vf			
BAt	31	10 YR 3/3						2	m/f	abk	clf	10 YR 3/4	c (40%)	th	c	pf	fr	c	f/vf/c			
								3	vf	sbk												
Bt1	40	10 YR 3/4						2	m/f	sbk	clf	10 YR 3/4	m (80%)	th	c	pf	fr	c	f/vf			
								2	f/vf	abk	org	10 YR 3/2	c (25%)			sp/sc						
Bt2	55	10 YR 3/4		7.5 YR 4/6	c (10%)	c	d	1	m/f	abk	clf	10 YR 3/3	m (80%)	th	c	pf	fi	c	f/vf			
				10 YR 2/1	c (5%)	f	d	3	vf	abk	org	10 YR 3/1	f (20%)			sp/sc						
2Bt/Cr	58.5	10 YR 3/4						2	m/f	sbk	clf	10 YR 3/4	c (25%)	th	c	pf	fi	c	f/vf	sl		
		10 YR 5/8		10 YR 2/1	f (1%)	f	d				org	10 YR 2/1	vf (4%)			sp/sc						

Table B-11. Soil description of 5m soil core collected at grid point 27 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #27
PROFILE CLASSIFICATION: Typic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'47.50"N, 89°22'8.52"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 05/02/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	13	10 YR 2/2	10 YR 4/2					2	m/f	sbk								c	m/f/vf			
								2	vf	gr												
BAt	24	10 YR 3/3	10 YR 5/3					2	c/m	sbk	org	10 YR 2/2				sp/sc	fr	c	m/f/vf			
								2	m/f/vf	gr	clf	10 YR 3/3	c (25%)	th	c	pf						
Bt1	40	10 YR 3/3						3	m/f	sbk							fr	c	f/vf			
								2/1	f/vf	abk	clf	10 YR 3/3	c (30%)	th	c	pf						
Bt2	64	10 YR 3/4		10 YR 2/1	c (2%)	2	d	2	c/m	sbk							fi	c	vc/c/m/f/vf			
				7.5 YR 3/3	c (5%)	3	d	2	m/f/vf	abk	clf	10 YR 3/3	m (60%)	th	c	pf						
Bt3	79	10 YR 4/6		10 YR 2/1	c (2%)	2	d	2	c/m/f/vf	abk							fi	c	f/vf			
											clf	10 YR 3/2	m (70%)	th	c	pf						
2Cr/Bt	83	10 YR 5/6								m	clf	10 YR 2/1	c (25%)	th	c	pf	fi	c	vf	st		
		10 YR 3/4						2	c/m	sbk												

Table B-12. Soil description of 5m soil core collected at grid point 28 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #28
PROFILE CLASSIFICATION: Typic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'47.53"N, 89°22'5.90"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 03/08/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	7.5	10 YR 2/2	10 YR 4/2					3	f/vf	gr							vfr	c	vf/f		a	
BEt	16.5	10 YR 3/3	10 YR 5/3					3	f	sbk	org	10 YR 2/1	m (40%)			sp/sc	vfr	c	f/vf		a	
								3	f/vf	gr	clf	10 YR 3/2	m	th	c	pf						
Bt1	24.5	10 YR 3/3						2	f/vf	sbk	org	10 YR 2/1	f (15%)			sp/sc	fr	f	f/vf		c	
											clf	10 YR 3/2	m	th	c	pf						
Bt2	33	10 YR 3/4						2	f/m	sbk	org	10 YR 3/1	c			sp/sc	fi	f	f/vf		a	
											clf	10 YR 3/3	m	th	c	pf						
Bt3	50	10 YR 3/5						2	m/f	sbk	clf	10 YR 3/4	c	th	c	pf	fi	f	vf		c	
											org	10 YR 3/3	f			sp/sc		c	m			
Bt4	57	10 YR 4/6		7.5 YR 5/6	f	vf	d	3	m/f	sbk	clf	10 YR 3/4	c	th	c	pf	fi	f	f/vf		v	
											org	10 YR 3/3	f			sp/sc						
2Cr/Bt	64	10 YR 5/6								m	clf	10 YR 3/4	c	th	d	pf		f	f/vf	vsl		
		10 YR 3/4																				

Biopores filled with organics from 7.5 cm to 33 cm

Table B-13. Soil description of 5m soil core collected at grid point 29 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #29
PROFILE CLASSIFICATION: Lithic Hapludoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: None
COUNTY: Lee County
LOCATION: Nachusa Grasslands
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 07/08/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	8	10 YR 2/2	10 YR 2/2					2	c/m	sbk							fr	c	f/vf			
								3	f/vf	gr												
2A/Cr	13	10 YR 2/2	10 YR 3/2					3	m/f	sbk							fr	c	vf	vsl		
		10 YR 5/6						3	f/vf	gr												
2Cr	16.5	10 YR 6/6								m	org	10 YR 2/2	m (60%)			sp/sc	fr			vsl		

Table B-14. Soil description of 5m soil core collected at grid point 30 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #30
PROFILE CLASSIFICATION: Typic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'47.61"N, 89°22'0.63"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 07/06/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A1	10	10 YR 2/2	2.5 Y 4/2					3	m/f/vf	gr							fr	c	f/vf/m			
A2	19	10 YR 2/2	2.5 Y 4/2					1	f	sbk							fr	c	f/vf/c			
								3	f/vf	gr												
ABt	28	10 YR 3/3	2.5 Y 3/3					2	m/f	sbk	clf	10 YR 3/1	c (30%)	th	c	pf	fr	c	vf			
								2	f/vf	gr												
Bt1	37	10 YR 3/3						3	m/f/vf	sbk	clf	10 YR 3/1	m (60%)	th	c	pf	fi	c	vf			
											org	10 YR 3/2	m (50%)			sp/sc						
Bt2	52	10 YR 3/4						3	m/f	sbk	clf	10 YR 3/3	m (80%)	th	c	pf	fi	c	f/vf			
								1	vf	abk	org	10 YR 2/1	f (6%)			sp/sc						
2Bt/Cr	64	10 YR 4/6						2	m/f/vf	sbk	clf	10 YR 3/2	m (50%)	th	c	pf	fi	c	f/vf	sl		
										m	org	10 YR 3/1	vf (4%)			sp/sc						

Table B-15. Soil description of 5m soil core collected at grid point 31 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #31
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'47.65"N, 89°21'58.00"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 07/11/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	6	10 YR 2/1	10 YR 4/2					2	m/f	sbk							fr	c	f/vf			
								1	vf	sbk												
ABt	15	10 YR 2/1	10 YR 4/2					3	m/f/vf	sbk	clf	10 YR 4/3	c (25%)	th	c	pf	fr	f	vf			
BAt	23	10 YR 4/3	10 YR 4/3					3	m/f	sbk	clf	10 YR 3/3	c (40%)	th	c	pf	fr	c	f/vf			
								1	vf	abk	org	10 YR 3/2	c (25%)			sp/sc						
Bt1	46	10 YR 3/5						2	m/f	abk	clf	10 YR 3/4	m (50%)	th	c	pf	fi	c	f/vf			
								1	vf	abk	org	10 YR 3/1	f (20%)			sp/sc						
Bt2	66	10 YR 3/6		10 YR 2/1	c (5%)	m	d	2	m/f	sbk	clf	10 YR 3/4	m (80%)	th	c	pf	fi	c	f/vf			
				7.5 YR 4/6	m (25%)	c	d	1	vf	abk												
2Cr/Bt	75	10 YR 6/8								m	clf	7.5 YR 3/2	f (20%)	th	c	pf	fr	c	f/vf	sl		
		10 YR 3/5						1	m/f/vf	sbk												

Table B-16. Soil description of 5m soil core collected at grid point 36 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #36
PROFILE CLASSIFICATION: Typic Argiudoll
EPIPEDON: Mollic
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'45.57"N, 89°22'8.53"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 07/10/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	14	10 YR 2/1	10 YR 4/2					3	c/m/f/vf	gr							fr	m	vf			
																		c	f			
Abt	30	7.5 YR 3/2	10 YR 4/3					3	c/m	sbk	clf	7.5 YR 3/1	f (20%)	th	c	pf	fr	c	f/vf			
								2	f/vf	gr												
Bt1	56	10 YR 3/4						3	m/f/vf	sbk	clf	10 YR 3/3	c (45%)	th	c	pf	fi	c	c/m/f/vf			
											org	10 YR 2/2	f (5%)			sp/sc						
Bt2	75	10 YR 3/4						3	m	sbk	clf	10 YR 3/4	m (50%)	th	c	pf	fi	c	f/vf			
								1	f/vf	abk	org	10 YR 3/2	f (20%)			sp/sc						
Bt3	88	10 YR 3/6		10 YR 2/1	c (5%)	2	d	2	m	sbk	clf	10 YR 3/4	m (80%)	th	c	pf	vfi	c	f/vf			
				7.5 YR 5/8	c (10%)	2	d	1	f/vf	abk												
2Bt/Cr	100	7.5 YR 3/2		10 YR 2/1	c (2%)	2	d	1	m	abk	clf	10 YR 3/2	m (80%)	th	c	pf	vfi	c	f/vf			
		10 YR 6/8		7.5 YR 5/8	m (20%)	2	d	2	f/vf	abk	org	10 YR 2/1	f (20%)			sp/sc						
2Cr	102	10 YR 6/8								m							vfi	c	vf	sl		

Table B-17. Soil description of 5m soil core collected at grid point 37 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #37
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'45.61"N, 89°22'5.88"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 04/18/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist	Dry Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	Matrix color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	9	10 YR 2/1	10 YR 4/2					2	c/m	sbk							fr	c	m/f/vf			
								2	f/vf	gr												
ABt	16	10 YR 3/3	10 YR 4/2					2	m	sbk	org	10 YR 2/2	m (50%)			sp/sc	fr	c	m/f/vf			
								2	f/vf	gr	clf	10 YR 3/4	c	th	c	pf						
Bt1	35.5	10 YR3/4						1	c/m	abk	org	10 YR 2/2	f (10%)			sp/sc	fr	c	f/vf			
								1	f/vf	sbk	clf	10 YR 3/3	m	th	c	pf						
Bt2	49.5	10 YR3/4						2	c/m	sbk							fi	c	c/f/vf			
								3/2	f/vf	abk	clf	10 YR 3/2	m	th	c	pf						
2Bt/Cr	70	10 YR 3/4						3	c/m/f	abk							fi	c	vc/vf	vsl		
										m	clf	10 YR 3/3	c	th	c	pf						

Table B-18. Soil description of 5m soil core collected at grid point 38 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #38
PROFILE CLASSIFICATION: Typic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'45.66"N, 89°22'3.27"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 03/16/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist Matrix	DRY Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	9	10 YR 2/1	10 YR 3/2					1	vc	gr								c	vf/f			
								2	m/f	sbk												
AB	15	10 YR 3/4	10 YR 5/3					2	m/f/vf	sbk	org	10 YR 2/2	m (80%)			sp/sc		c	vf/m			
BAt	25	10 YR 3/4						2	m/f	sbk	org	10 YR 3/1	m (50%)			sp/sc		c	vf/c			
											clf	10 YR 3/4	m	th	c	pf						
Bt1	33	10 YR 3/6						3	m/vf	sbk	org	10 YR 3/1	c (35%)			sp/sc		c	vf			
											clf	10 YR 3/2	m	th	c	pf						
Bt2	45	10 YR 3/4						3	m/f/vf	abk	clf	10 YR 3/2	m	th	c	pf		c	vf	vsl	a	
2Cr/Bt	62	2.5 Y 6/6						2	c	sbk/abk	clf	10 YR 3/4	f (25%)	th	c	pf				st		
		10 YR 3/4								m												

Weak, very coarse granulars in A horizon (0-9 cm) break to 3 coarse/medium granular structure
Moderate, medium/fine/very fine subangular blocky structure in AB horizon (9-15 cm) broke to weak, fine granular structure
Weird organic layer found between 22 to 25 cm with large wood chip chunk (> 10 mm)

Table B-19. Soil description of 5m soil core collected at grid point 39 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #39
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'45.68"N, 89°22'0.65"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 05/02/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist Matrix	DRY Matrix	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)	color	color	Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	6	10 YR 2/2	10 YR 4/2					2	c/m/f/vf	gr							fr	c	c/f/vf			
AB	17	10 YR 2/1	10 YR 4/2					3	m	sbk							fr	c	c			
		10 YR 3/3						3	f/vf	gr								f	f/vf			
Bt1	37	10 YR 3/4						3	c/m/f/vf	sbk	org	10 YR 3/1				sp/sc	fr	c	vc			
											clf	10 YR 3/3	c			pf/bg		f	m/f/vf			
Bt2	64	10 YR 4/4						2	c/m	abk/sbk							fi	f	vf			
								2	f/vf	abk	clf	10 YR 3/4	c			bg						
Bt3	83	10 YR 5/6						1	m/f	sbk							fr	f	vf		g	
								1	f/vf	gr	clf	10 YR 4/6	c			bg						
Bt4	96	10 YR 4/6		10 YR 2/1	c	3	d	2	m	sbk							vfi	c	m			
				10 YR 4/6	f	1	d				clf	10 YR 3/4	m			bg		f	vf			

A (0-6 cm) and Bt3 (64-83 cm) horizons were condensed during sampling
10 YR 2/1 comprises 70% of the AB horizon
10 YR 3/3 comprises 30% of the AB horizon

Table B-20. Soil description of 5m soil core collected at grid point 40 in the east half of the oak savanna restoration study site at Nachusa Grasslands, IL, USA. Field sampling and soil morphology were described using methods and nomenclature of Schoeneberger et al. (1998) and the updated Schoeneberger (2002). Soil taxonomy was described based on Soil Survey Staff (1975, 1999).

PROFILE: GRID #40
PROFILE CLASSIFICATION: Mollic Hapludalf
EPIPEDON: Ochric
SUBSURFACE HORIZONS/FEATURES: Argillic
COUNTY: Lee County
LOCATION: Nachusa Grasslands (41°53'45.71"N, 89°21'58.03"W)
ELEVATION: 225-250 meters
DATE SAMPLED: 12/12/2011
SAMPLED BY: McCarragher, Osterloh, Konen
DATE DESCRIBED: 02/23/2012
DESCRIBED BY: McCarragher
VEGETATION: Oak Savanna Restoration

Horizon	Lower Depth	Moist Matrix color	DRY Matrix color	Redox Features				Structure			Coatings						Con	Roots		Eff	Boundary	
	Interval (cm)			Color	Amount	Size	Contrast	Grade	Size	Shape	Type	Color	Abun	Thickns	Cont	Location		Amount	Size		Dist	Shape
A	11.5	10 YR 3/2	10 YR 5/2					3	f/vf	gr							vf	m	f/vf		a	
																		c	c			
BEt	28	10 YR 3/3	10 YR 6/3					2	m	sbk	clf	10 YR 3/2	c (50%)	th	c	pf	vf	c	f/vf		a	
								2	f/m	gr								c	c			
Bt1	54	10 YR 3/4						2	m/f	sbk	clf	10 YR 3/2	m	th	c	pf	fi	f	m		c	
																			f			
Bt2	73	10 YR 3/4						2	m/f	sbk	clf	10 YR 3/2	m	th	c	pf	fi	f	f		a	
																			c			
Bt3	98	10 YR 3/4		10 YR 2/1	c	m	d	2	m/f	sbk							vfi	f	f		a	
				7.5 YR 5/8	m	f/m	d				clf	10 YR 3/2	m	th		pf						
Bt/Cr	108	10 YR 3/3		10 YR 6/8	c	f	d	2	m	sbk	clf	10 YR 3/2	m	th		ff	fi	f	f	vsl		
		10 YR 6/6								m												