University of Connecticut
DigitalCommons@UConn

Master's Theses | University of Connecticut Graduate School

9-14-2011

Differential Canopy Leaf Flushing and Site Nitrogen Status Facilitate Invasive Species Establishment in Temperate Deciduous Forest Understories

Lindsay M. Dreiss
University of Connecticut - Storrs, lmdreiss@gmail.com

Recommended Citation
Dreiss, Lindsay M., "Differential Canopy Leaf Flushing and Site Nitrogen Status Facilitate Invasive Species Establishment in Temperate Deciduous Forest Understories" (2011). *Master's Theses.* Paper 173.
http://digitalcommons.uconn.edu/gs_theses/173

This work is brought to you for free and open access by the University of Connecticut Graduate School at DigitalCommons@UConn. It has been accepted for inclusion in Master's Theses by an authorized administrator of DigitalCommons@UConn. For more information, please contact digitalcommons@uconn.edu.

Differential canopy leaf flushing and site nitrogen status facilitate invasive species establishment in temperate deciduous forest understories

Lindsay Marie Dreiss

B.A., Colby College, 2009

A Thesis

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

at the

University of Connecticut

2011

APPROVAL PAGE

Master of Science Thesis

Differential canopy leaf flushing and site nitrogen status facilitate invasive species establishment in temperate deciduous forest understories

Presented by

Lindsay Marie Dreiss, B.A.

Major Advisor _____
John C. Volin

Associate Advisor _____
Thomas H. Meyer

Associate Advisor _____
Thomas Worthley

University of Connecticut
2011

ACKNOWLEDGEMENTS

This thesis would not be possible without the tremendous creativity, support, and insight of those involved with this study and who have seen me through the past two years. In particular, my major advisor John Volin, who kept me both focused and enthusiastic about this project and who never held back from sharing his stories and pearls of wisdom. I would like to thank my advisor Tom Meyer for challenging me and expanding my knowledge on many fronts, helping me see science research from another perspective. I am also grateful to my advisor Tom Worthley for his experience and his curiosity which helped to form the questions posed in this paper as well as many others. And, of course, thank you to my family, friends, and fellow graduate students who can truly appreciate the work that went into this project.

TABLE OF CONTENTS

1. INTRODUCTION 1
2. MATERIALS AND METHODS 9
2.1 Study Sites 9
2.2 Phenology 12
2.3 Vegetation Sampling 12
2.4 Stand Characteristics 13
2.5 Data Analysis 15
3. RESULTS 16
3.1 Light Regimes Beneath Closed Canopies 16
3.2 Phenology of Canopy Dominants 20
3.3 Other Site Characteristics 20
3.4 Understory Vegetation Diversity 23
3.5 Invasive Species Status 26
4. DISCUSSION 30

APENDIX I 38
APENDIX II 38
APENDIX III 39
LITERATURE CITED 40

Abstract

Invasion by nonnative species is considered one of the greatest threats to ecosystem structure and function worldwide. The temperate forests of the northeastern United States are no exception. Human pressures of land development and fragmentation allow for increased edge environments in which invasive species can establish and colonize; however, nonnative plant species are not confined to just edges but are found throughout the temperate forests. In this study, I hypothesized that, in these interior forest understories, nonnative invasive plant species presence would depend on the environmental conditions created by the canopy trees. Specifically, nonnative invasive species would be greatest under those canopy tree species that allow higher understory light levels because of phenological differences in spring leafing as well as canopy transmission and site-nutrient availability in these understories. To test this hypothesis, six canopy species that differed in leaf phenology, understory light levels, and in their ability or not to fix atmospheric nitrogen were used. From earliest leaf expansion to latest, sampling sites included canopy stands of *Populus tremuloides* (quaking aspen), *Acer saccharum* (sugar maple), *Quercus* spp./*Carya* spp. (oak/hickory), *Fraxinus americana* (white ash), *Robinia pseudoacacia* (black locust), and the evergreen species mix, *Pinus* spp./*Tsuga canadensis* (pine/hemlock). Measures of understory light availability post-leaf expansion were significantly higher under quaking aspen than other canopies with the exception of black locust and white ash. Phenologically, black locust ≥ white ash ≥ oak/hickory > sugar maple > quaking aspen > pine/hemlock. As expected, soil analyses showed higher nitrate levels in the nitrogen-fixing black locust stands, but unexpectedly, also for the white ash stands. Across the six canopy types, invasive species

cover and relative abundance were significantly higher under late-leafing black locust and white ash canopies. Collectively, these results show significantly higher presence of nonnative plants under canopies with higher resource availability (i.e., later phenology, greater light transmission, and nitrogen fixation). Light is considered the greatest determinant of understory growth in temperate forests; however, in my study, soil nitrate was the greatest driver of nonnative species success. The results suggest that sites with late leaf phenology, relatively high understory light levels, and higher site nitrogen might allow these stands to facilitate nonnative species success and to act as islands of invasion in resource-poor forested landscapes.

1. Introduction

Current ecological research initiatives reflect concerns over the vulnerability of global ecosystems to unprecedented rates of environmental change (Lubchenco et al. 1991, Redman et al. 2004). Among changes that are well-documented worldwide and yet not fully understood are those created by the introduction of nonnative invasive plant species (Blossey 1999, Vitousek et al. 1997). Invasive plant species possess the ability to successfully establish, grow, and reproduce under a wide variety of environmental conditions and usually do so at the cost of native species diversity and composition (Alvarez and Cushman 2002, Hulme and Bremner 2006, Hunter and Mattice 2002). Among the myriad traits that allow invasive species to be successful, high physiological plasticity and relative growth rates allow many invaders, once established, to outcompete native species for critical resources such as light, water, nutrients, and space (Feng et al. 2007, Feng et al. 2008, Gordon 1998, Kolb et al. 2002, Manchester and Bullock 2000, Volin 2010). Many studies compare physiological traits among invasive species and coexisting, confamilial native species to determine differences that help explain why invasive species have an advantage outside their native ranges, but this method can only assess the potential for success after the introduced species has already become established (Baruch and Goldstein 1999, Cano et al. 2009, Feng et al. 2007, Leishman et al. 2007, Schutzenhofer et al. 2009). Studying plant traits can help determine the risk of particular plants becoming pest species; however, it provides less information concerning target areas for prevention initiatives (Daehler and Carino 2000, Gordon et al. 2008, Mehta et al. 2007). On the other hand, focusing on the response of invasive species success to differences in site characteristics, in other words the invasibility of the

environment, might provide for a greater understanding of site properties more likely to be taken advantage of by invaders. To this end, several hypotheses have been put forward to help explain why some communities are more susceptible to invasion than others, but to date no clear paradigm has emerged (Davis et al. 2000, Lonsdale 1999).

Among the many hypotheses, two prevailing mechanisms of invasibility are release from natural enemies and increased resource availability (Blumenthal 2006, Davis et al. 2000, Keane and Crawley 2002, Shea and Chesson 2002, Volin et al. 2010). The latter of these two posits that invasion is caused by availability of resources such as light, water, and soil nutrients (Davis et al. 2000). In temperate deciduous forests many variables play a role in the establishment and growth of plants, but light is most often recognized as the greatest limiting resource for both plant establishment and growth as well as for its ability to invoke strong, uniform responses from native and nonnative understory vegetation (Anderson and Swain 1969, Canham et al. 1990, Denslow et al. 1991, Gurevitch et al. 2008, Klinka et al. 1996, Messier et al. 1998). Invasive species in particular have been recognized for exhibiting higher establishment success in high light environments (Gurevitch et al. 2008, Small and McCarthy 2005, Yamashita et al. 2000). This is typical, considering that conditions which usually facilitate successful invasion include a disturbance (human or natural) in the landscape and/or augmentation of resource availability (Davis et al. 2000, Knapp and Canham 2000, Lake and Leishman 2004, Shea and Chesson 2002, Yamashita et al. 2000). In this sense, invasive species often behave like or exhibit properties of early successional species, which often helps explain why dense monospecific stands of invasive vegetation can be found in forest gaps and along edges (Durand and Goldstein 2001, Fine 2002, Gurevitch et al. 2008).

In New England, the ability of nonnative plant species to invade closed canopy temperate forests is notable given that these ecosystems are often nutrient-poor and exhibit very limited understory light availability during the growing season. Understory light environments of forest ecosystems are most often studied in terms of the amount of transmitted photosynthetically active radiation (PAR) (that light which is necessary for plant photosynthesis and life processes to occur) (Canham et al. 1990, Messier et al. 1998). Although growth and establishment of nonnative species in resource-low environments might seem unlikely, there are many reports of invasive species in closed canopy understories (Knapp and Canham 2000, Lubell and Brand 2001, Martin et al. 2009, Meekins and McCarthy 2001, Peters 2001). For example, dense stands of invasive species such as Japanese barberry (*Berberis thunbergii*) and garlic mustard (*Allaria petioloata*) are found under closed canopies where PAR at the forest floor is often less than five percent (Canham et al. 1990, Brantley and Young 2007, Gill et al. 1998).

The dominance of deciduous canopy vegetation in southern New England is another critical trait that defines the temperate forest light environment. Timing of phenological events, such as bud burst and leaf expansion, differ among tree species, and, as a result, temporal leaf cover and canopy light penetration are not uniform across forest floor environments. The temporal and spatial distributions of sun and shade in temperate deciduous forests create unique understory light regimes which reflect on species composition and growth (Bartemucci et al. 2006, Komiyama et al. 2001, Messier et al. 1998, Powers et al. 1997). Leaf emergence in the spring and senescence in autumn allow a seasonal window of high light availability in the understory, creating opportunities for understory vegetation to take advantage of essential photosynthetic resources very early

in the growing season. There are, of course, consequences that come with exposing leaves early in the season such as the increased chance of damage by herbivory or a late frost (Grime 2006, Reich et al. 1995, Williams et al. 1989). In an ecosystem with low resource availability; however, the benefits might outweigh the costs: maximum incident solar radiation flux and zenith angle are larger in the spring than in winter resulting in a greater transmission of light and a greater likelihood for photosynthetic capacity to be reached just before leaf flushing (Richardson and O'Keefe 2009). Also, studies have shown that the majority of annual carbon gained by understory vegetation is attained during the period in early spring when canopy trees are still leafless, allowing sub-canopy vegetation to fix a "spring carbon subsidy" (Givnish 1992, Harrington et al. 1989, Lopez et al. 2008, Richardson and O'Keefe 2009).

Differential phenologies among canopy species result in differing lengths of time in which high initial spring sunlight reaches the forest floor. Leaf longevity can vary within species, but in any one geographical/ecological region, the time lag between canopy species might be as much as a month (Augspurger 2008, Lechowicz 1984; Tessier 2003). In New England, observations show that maples (*Acer* spp.) and birches (*Betula* spp.) are among the first canopy species to leaf out while oak (*Quercus* spp.) and ash (*Fraxinus* spp.) species are some of the last to flush (Lechowicz 1984; Lopez et al. 2008). Taking advantage of resource availability is critical for the persistence of saplings and understory vegetation in temperate deciduous forests and this is especially so in early spring (Augspurger 2008). Literature shows that many nonnative invasive species are among those to expand leaves early on in the growing season, considerably earlier than both canopy and understory native species (Harrington et al. 1989, Pattison et al. 1998,

Schierenbeck 1992, Xu et al. 2007). For example, Xu et al. (1997) found that Japanese barberry leaves emerged up to two weeks earlier than those of native vegetation and one month earlier than canopy leaves. The overall increase in light during spring is considerable so slight differences in the timing of understory leaf expansion can have a large effect (Anderson 1964). However, the benefit of early understory leaf emergence might be relative: leaves that emerge weeks earlier in an oak canopy might only emerge days earlier when under a sugar maple canopy. Timing gives many nonnative invasive species an advantage over understory native species and, paired with canopy phenology, an opportunity to exploit the early spring period of high light availability. Thus, a question emerges, do canopy species that expand leaves later in the spring, allowing understory species to have an extended period of time for high quality light acquisition, make these pockets of forest more susceptible to nonnative establishment and act as islands of invasion in the forested landscape?

Beyond the limitations of light availability, nutrients (nitrogen in particular) are also important determinants of plant growth and survival in temperate deciduous forests (Aber et al. 1998; Gurevitch et al. 2008). In nutrient-poor systems such as temperate forests, nitrogen deposition can alter resource efficiency, nutrient composition, and stability of vegetation (Aber et al. 1995). Southern New England forests are susceptible to increases in nitrogen deposition due to various human alterations to the environment (Aber et al. 1989, Vitousek et al. 1997). Such increases in nitrogen availability have been linked with increases in nonnative species growth rates, cover, and frequency as well as declines in overall biodiversity (Gurevitch et al. 2008, Small and McCarthy 2005, Vitousek et al. 1997). A less recognized source of nitrogen deposition in northeastern

United States forests is the tree *Robinia pseudoacacia*. Commonly known as black locust, it is an invasive species of intracontinental origin which, due to assisted migration, has successfully established in many places outside of its native range, including New England (Mueller and Hellmann 2008). Its presence in temperate, nutrient-poor ecosystems is unique because of its nitrogen-fixing capabilities and therefore, its potential to alter natural communities (Mordelet and Menaut 1995). Depending on stand age, density, and certain climatic conditions, black locust fixes 35-150 kg N per hectare per year (Danso et al. 1995). In this regard, once established, it is highly likely that black locust might act as an 'ecosystem engineer' in its introduced environment (Doren et al. 2009, Jones et al. 1994). Historically, many countries around the world have introduced this species as a means of ecosystem restoration and as such have allowed it to become one of the top 100 worldwide plant invaders (Cronk and Fuller 1995). This has also led to concerns over its potential ability to facilitate the growth of other nonnative species (Altieri et al. 2010, Hunter and Mattice 2002, Von Holle et al. 2008). By creating an increase in nitrogen availability, it can promote the growth of understory vegetation, and, more notably, the growth of those nonnative species quick to take advantage of augmented resources (Davis et al. 2000, Shea and Chesson 2002). Also of interest to this study is the fact that black locust has a relatively late leaf phenology and high understory light environment in comparison to many other dominant canopy species of northeastern temperate deciduous forests. Augmenting the availability of two critical resources (understory light and soil nitrogen) might allow black locust stands to facilitate an environment more suitable to invasive plant species success, creating opportunities for

nonnative establishment and spread at these and neighboring closed canopy sites. If this hypothesis is correct, then black locust stands act as islands of invasion.

Opportunities of high resource availability allow invading species to obtain sufficient resources for successful establishment, leaving those environments which provide augmented resources more vulnerable to invasion (Davis et al. 2000, Gurevitch et al. 2008, Small and McCarthy 2005). Both understory light environment throughout the growing season as well as phenology have emerged as important factors in determining understory species composition in temperate deciduous forests (Barbier et al. 2008, Bartemucci et al. 2006, Berger and Puettmann 2000, Legare et al. 2001, Maeno and Hiura 2000, Tomita and Seiwa 2004). In some studies, phenology, in particular the timing of leaf flush in the spring, is important for total seasonal carbon gain of many understory species (Augsperger 2008, Givnish 1992, Harrington et al. 1989). Given that many problematic invasive species leaf out significantly earlier than do native understory species, advantageous leaf timing and establishment of understory invasive species might be relative to the phenology of the leaf canopy and therefore the quantity of light reaching the canopy floor before full leaf expansion. A greater disparity between understory and canopy phenologies would increase the period of resource availability to understory plants. This might potentially leave late-leafing stands more receptive to invasive species establishment. With this premise, I hypothesized that tree canopy dominants that allow greater understory light availability, both through light transmission and, in particular for this study, through later spring leaf phenologies, will result in greater invasive species presence within those stands. This relationship would suggest that establishment and survival of invasive species is relative to differential canopy leaf

phenologies: those stands which allow for a longer period of spring light availability act as islands of invasion from which introduced plant species can establish. Moreover, the additional deposition of nitrogen into temperate forest ecosystems from canopy dominant nitrogen-fixing species such as black locust might alter the environment such that the increased nitrogen availability would facilitate the successful establishment of nonnative species. Consequently, with its late leafing phenology, relatively high understory light environment and its increased site nitrogen availability, I also hypothesized that among the canopy species studied, black locust stands would have the greatest nonnative species presence in their understories. In other words, under canopies of similar phenology, a stand that has greater nitrogen availability would better support vegetative growth and success of nonnative species.

To test these hypotheses replicated stands of six canopy-dominant species common to southern New England temperate forests were studied. Canopy species were chosen to represent differences in spring leaf phenology and light transmittance and included five types of deciduous stands *Populus tremuloides, Acer saccharum, Quercus* spp.*/Carya* spp.*, Fraxinus Americana,* and *Robinia pseudoacacia* and one type of evergreen stand (*Pinus* spp.*/Tsuga canadensis*). This study examined how the understory environment, in particular the availability of early spring light and soil nitrogen, as determined by the canopy species, might effect the invasbility of a site, increasing the cover and relative abundance of nonnative plants in those stands that have greater availability of resources.

2. Materials and Methods

2.1 Study Sites

In the northeastern United States, southern New England forests are considered transitional plant communities because of the variegated vegetation mosaic that occurs as a result of being located between northern and central hardwood species ranges (Westveld 1956). A State of Connecticut forest inventory found 82 different tree and shrub species present, the most abundant canopy species being *Acer rubrum*, *A. saccharum*, *Fagus grandifolia*, *Quercus alba,* and *Q. rubra* (Wharton et al. 2004). In this region, the annual mean temperature is 10.1˚C with mean January temperature at -3.5˚C and mean July temperature at 23.3˚C. The annual mean snowfall is 127.0 cm and the total annual mean precipitation is 117.2 cm (NOAA 2009). To test the hypotheses, multiple canopy types were identified by species to represent different leafing phenologies, understory light environments, and by their ability to fix atmospheric nitrogen or not. For each canopy type 4 to 7 sites were chosen for sampling. From earliest leaf expansion to latest, sampling sites included canopy covers of *Populus tremuloides* (n=4), *Acer saccharum* (n=5), *Quercus* spp./*Carya* spp. (n=7), *Fraxinus americana* (n=4), and *Robinia pseudoacacia* (n=6) as well as one evergreen species mix, *Pinus* spp./*Tsuga canadensis* (n=6). To be considered one of the specified canopy cover types, a forest stand had to be at least 70% dominated by the tree species for which the canopy type was named. All sites were located in central and eastern portions of the State of Connecticut and grouped within the towns of Eastford (41.83˚N, 72.06˚W), Mansfield (41.81˚N 72.24˚W), Haddam (41.44˚N 72.5˚W), Ledyard (41.43˚N 72.09˚W), and Colchester, CT (41.56˚N 72.35˚W) (Figure 1). Sites were chosen with help from spatial state forest

inventory data collected and compiled by the Connecticut Department of Environmental Protection and University of Connecticut Cooperative Extension System. ArcGIS version 9.3 was used to view State Forest properties by cover type. Preliminary sites were visited to verify that they fit the desirable criteria. Criteria was specified for even-aged forest canopies (60-100 years old) as determined through 1934 aerial photography (University of Connecticut Map and Geographic Information Center: http://magic.lib.uconn.edu/), with approximate species uniformity and little canopy disturbance (natural gaps or harvesting) as well as minimal slopes and elevations. In addition, to minimize large differences in bedrock and soil types, sites were selected in a relatively narrow geographic region on the eastern side of the state. Those sites that did fit the criteria were marked using a Global Positioning System (GPS) receiver (Trimble Juno 2005 Series). GPS data were then uploaded to ArcGIS and overlayed on an aerial photograph. The ArcGIS program was useful for keeping track of attributes of the sites such as spatial coordinates, cover type, and other field notes.

Two circular plots, each with a radius of five meters, were nested at each site. Plots were marked at the center of origin with a flagged PVC stake and a flag. This design was used to assess the effect of within-site heterogeneity that might otherwise confound the relationship of native to nonnative species diversity (Shea and Chesson 2002). A measuring tape, extended to five meters in length, was used as reference for the area encompassed by the plot. Within each plot records were taken to characterize canopy type, average diameter at breast height (DBH) (measured at 1.4 m above ground), understory light environment, and understory species cover (see details below) (Appendix I).

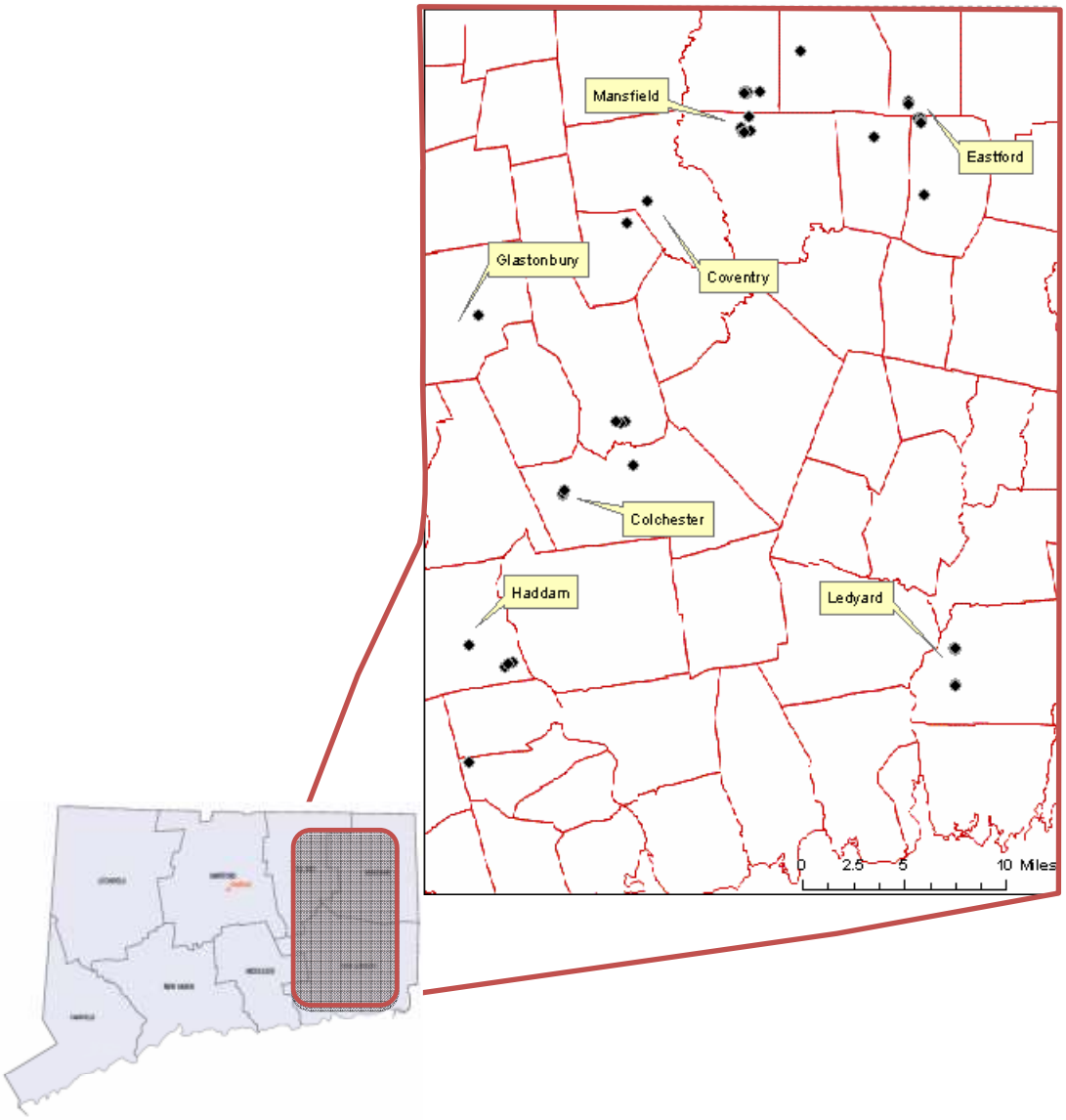


Figure 1: The 32 forest study site locations in eastern Connecticut, USA.

2.2 Phenology

Beginning in March 2010, sites were visited on a bi-weekly basis to observe and record phenology events. Two events were of particular interest to this study: the beginning of bud break or when more than 1/3 of an individual's buds had burst as well as completion of leaf expansion which was achieved when more than 2/3 of leaves were fully extended (Komiyama et al. 2001). These events were investigated by binocular observation and recorded by Julian date of occurrence. Both canopy and understory species were taken into account.

2.3 Vegetation Sampling

To characterize the understory, a 1-m^2 quadrat was used to record parameters within each plot. The quadrat was threaded with a 10-cm^2 grid for visual observation. The quadrat was placed at three randomized locations within each circular subplot. These quadrats were chosen by overlaying a virtual grid over the 5 m radius subplot. Each grid cell was 1 m^2 (the size of the quadrat) and numbered according to its position relative to the northern-most point of the plot. A random number table was generated and used to select locations of quadrats for sampling. Diameter at breast height was recorded for all tree species specific to the canopy cover type within the 5-m radius of each subplot and averaged by site.

Understory species abundance was measured as the number of stems < 1 m in height for a particular species within each quadrat. The percent cover of a species was estimated visually. Total cover within a grid might not have added to 100% due to bare patches. Sampling was replicated three times per subplot. Records were noted for the

community as a whole as well as for native and nonnative species groups. If a species could not be positively identified in the field, a sample was returned to the laboratory for later identification.

2.4 Stand Characteristics

For all subsequent variables, measurements were taken twice during the season: once in June and again in August. To explore the light environment within each subplot, light quantity was measured in terms of irradiance under full leaf flush using a quantum sensor to record photosynthetically active radiation (PAR) in the plot. Understory PAR was measured at each plot within a site with the AccuPAR photo-ceptometer held parallel to the ground at breast height and away from any low-hanging vegetation. Concurrently, a paired AccuPAR photo-ceptometer set up in a nearby open area was used to record full sunlight. The two measurements were then used together to determine the true understory PAR. Leaf area index (LAI), total growing season light, and canopy openness were determined using a Canon G10 camera fitted with a fisheye lens. The camera was leveled 1.5m above the ground and photographs were taken at both dawn and dusk for each subplot. Digital photographs were later downloaded and analyzed by Gap Light Analyzer software to calculate LAI, total growing season light, and canopy openness values (Simon Fraser University and Institute of Ecosystem Studies 1999). Canopy openness values were the percentage of the total sky area found within canopy gaps and total growing season light referred to the total amount of radiation (direct and diffuse) reaching a point in the understory throughout the entire growing season.

A digital elevation model (DEM) created from LiDAR data flown with 10-foot nominal posting spacing was downloaded from the University of Connecticut Center for Land Use Education and Research (CLEAR) website (http://clear.uconn.edu). The DEM was used in ArcGIS to calculate the slope aspect of each site. Basal area was calculated from the DBH data collected at each site using the equation: basal area = 0.00007854 x DBH^2 (Elledge and Barlow 2010).

Soil samples were recovered from every site to determine significant differences in soil chemistry across canopy types. A trowel was used to obtain a sample at least six inches in depth at each subplot. Subplot samples were mixed together in a sealed plastic bag to represent each site. Each bag was labeled and samples were sent to the University of Connecticut Nutrient Analysis Laboratory in Storrs, Connecticut and to the Kansas State University Agronomy Soil Testing Lab in Manhattan, Kansas. Quantitative soil data included pH, calcium, magnesium, potassium, copper, boron, phosphorus, manganese, aluminum, zinc, lead, iron, ammonium, and nitrate. A modified Morgan soil test was conducted to complete a standard nutrient analysis for plant available nutrients and micronutrients (Northeast Coordinating Committee for Soil Testing 2011). A separate test for nitrogen in the form of ammonium and nitrate was conducted using with 1 M KCl and 2 g of prepared soil. Cadmium reduction was used for nitrate and colorimetric procedures were run in separate channels in a flow analyzer to measure these ions simultaneously (http://agronomy.ksu.edu/soiltesting/).

2.5 Data Analysis

Data collected from vegetation sampling were used to calculate diversity measures for analysis. The total number and relative abundance of species at a site were used to compute the richness, evenness of abundance, Simpson's diversity index (Simpson 1949), and the Shannon-Wiener diversity index (Shannon 1948). Statistics package JMP v. 5.0 (The SAS Institute) was used to evaluate the distribution of variables. To test for normality, means and medians were compared as well as skewness and kurtosis. Shapiro-Wilks tests were also used to test variable distributions. Those variables which did not exhibit normal distributions were log10 transformed and re-assessed for normality. Analysis of variances were executed to determine differences in variables (both light and soil characteristics) across canopy types. Means were compared with a Tukey-Kramer test to find significant differences between canopy types. Partial correlations were also evaluated to understand the strength of relationships among variables. Regression analyses were used to determine environmental variables useful for modeling site diversity and invasive species measures. Stepwise regression analysis was initially used to determine the most significant variables and then standard least squares regressions were run to verify the significance of the models. Further analysis was done using principle components analysis (PCA) (JMP v 5.0; SAS Institute). In this PCA, sites were analyzed with reference to those environmental variables determined to be significant in the regression model analysis. However, because pine/hemlock canopies are closed all year round, dates for phenology events (bud break and full flush) were not recorded. To include phenology dates into the PCA, a random numbers table was created with the same mean and standard deviation as the combined data set of the deciduous

sites. Random numbers were assigned as dates for bud break. Because full leaf expansion naturally occurs after bud break, another random numbers table was created to represent the difference (in days) between bud break and full leaf expansion. These random numbers were added to the bud break dates to create full flush measures. By assigning random numbers to bud burst and full flush of pine/hemlock sites, the PCA could include these variables in a way that would not falsely impact the influence of phenology on the analysis. The identity and amount of principle components chosen to represent the data was a factor of maximizing the amount of data variability explained by the ordination.

3. Results

3.1 Light Regimes Beneath Closed Canopies

Two subplots (six quadrats for understory measurements) were sampled within each of the 32 sites. Each site was a representative average of June and August measurements taken at the two subplots. Sampled closed-canopy sites were distinguished by one of six different canopy dominant types, either *P. tremuloides* (quaking aspen), *A. saccharum* (sugar maple), *F. americana* (white ash), *R. pseudoacacia* (black locust), a mix of *Quercus* spp. and *Carya* spp, (oak/hickory) or a mix of *Pinus* spp. and *T. canadensis* (pine/hemlock). After analyzing the distribution of environmental variables, the majority of them were log10 transformed to achieve normality (JMP v5.0). The six canopy types selected for this study varied in understory photosynthetically active radiation (PAR), leaf area index (LAI), total growing season light, canopy openness, and basal area. Slope aspect was not significantly different across sites (Table 1). Photosynthetically active radiation averages showed significant ($p = 0.002$) differences

among canopy types (Table 1). With the exception of quaking aspen sites, average percent PAR reaching the forest understories remained below 5%. Quaking aspen light conditions had the highest PAR value at 7.9% of full sunlight which was significantly higher than all other canopies with the exception of black locust (4.3%) and white ash (3.9%) (Figure 2). White ash and black locust stands also tended to be higher than the evergreen stands ($p = 0.02$ and 0.06, respectively).

All environmental variables measured were significant across canopy cover types with the exception of aspect. As expected, other environmental light variables were positively correlated with PAR but stand variables were negatively correlated. Positive correlations included total season light and canopy openness, negative correlations included LAI and basal area ($r = 0.77$, 0.69, 0.55, -0.53, and -0.87, respectively; Appendix II). Leaf area index, which, as expected, was negatively correlated with light variables, was significantly ($p = 0.05$) higher under evergreen canopies (Table 1). Season understory light transmission values, representing percent transmission integrated over the entire growing season calculated from Gap Light Analyzer software (Simon Fraser University and Institute of Ecosystem Studies 1999), were also significantly different across canopy species ($F_{5,54} = 13.01$; $p<0.0001$, Table 1). Like PAR, quaking aspen had the highest overall seasonal understory light values.

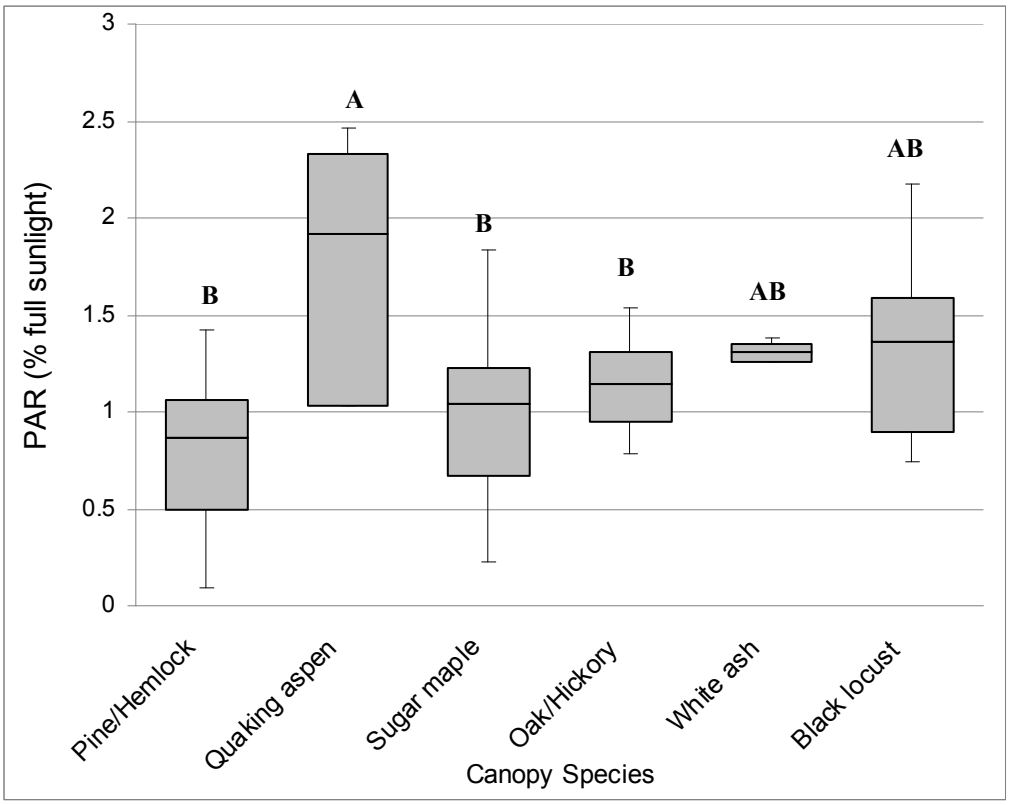


Figure 2: Box plot of log transformed photosynthetically active radiation (PAR) through canopies dominated by six major tree species on. A solid line represents the mean. Different letters denote significant differences in understory PAR among species at $p < 0.05$ (n = 6, 4, 5, 7, 4, 6, for pine/hemlock [*Pinus* spp./*Tsuga canadensis*], quaking aspen [*Populus tremuloides*], sugar maple [*Acer saccharum*], oak/hickory [*Quercus* spp./*Carya* spp.], white ash [*Fraxinus americana*], and black locust [*Robinia pseudoacacia*], respectively). Canopy species are in the order of spring phenology events and remain so throughout the paper.

Table 1: Non-transformed values of environmental variables (photosynthetically active radiation [PAR] and total season understory light) and stand/site characteristics (leaf area index [LAI], canopy openness, aspect, basal area, bud break, and full leaf flush) measured for six different canopy dominant species. Different letters within a row denote significant differences among canopy types at $p < 0.05$. (Note: Bud break and full flush dates were not recorded for pine/hemlock sites to represent these evergreen canopies being fully expanded all year round).

Light Variable	Pine/Hemlock	Quaking aspen	Sugar maple	Oak/Hickory	White ash	Black locust
PAR (% full sunlight)	2.55 ± 0.59^{b}	7.77 ± 0.83^{a}	3.23 ± 0.55^{b}	3.25 ± 0.44^{b}	3.71 ± 0.81^{ab}	4.22 ± 0.48^{ab}
LAI	3.7 ± 0.2^{a}	2.6 ± 0.3^{ab}	2.8 ± 0.2^{ab}	2.7 ± 0.2^{b}	2.5 ± 0.2^{b}	2.6 ± 0.2^{b}
Total Season ($mols/m^2/day$)	7.1 ± 0.4^{b}	10.7 ± 0.6^{a}	5.6 ± 0.4^{bc}	6.6 ± 0.3^{b}	5.1 ± 0.6^{bc}	5.3 ± 0.3^{c}
Canopy Openness (%)	6.1 ± 1.2^{ab}	9.0 ± 1.7^{ab}	9.6 ± 1.1^{a}	9.2 ± 0.9^{a}	9.4 ± 1.3^{ab}	5.2 ± 1.0^{b}
Aspect (degrees)	103 ± 44^{a}	208 ± 62^{a}	203 ± 41^{a}	165 ± 33^{a}	45 ± 63^{a}	158 ± 54^{a}
Basal Area (m^2/ha)	33.9 ± 5.93^{ab}	19.8 ± 8.38^{ab}	18.9 ± 5.59^{b}	34.8 ± 4.48^{ab}	37.9 ± 6.90^{ab}	34.6 ± 4.84^{a}
Bud Break (Julian date)	NA	93 ± 0.5^{a}	99 ± 0.3^{b}	103 ± 0.3^{c}	103 ± 0.5^{cd}	105 ± 0.3^{d}
Full Flush (Julian date)	NA	97 ± 0.3^{a}	105 ± 0.2^{b}	111 ± 0.2^{c}	112 ± 0.3^{cd}	113 ± 0.2^{d}

[a] Lowercase letters denote differences in log transformed data at the 5% level of significance across canopy types. Canopy types followed by the same lowercase letter within a variable are not significantly different.

3.2 Phenology of Canopy Dominants

Phenological differences, as measured by both bud break and full leaf flush, were significantly different ($p<0.0001$ for both) across canopy dominant species (Table 1 and Figure 2). Bud break of the six canopy species studied ranged from early April to mid April while differences in timing to full leaf flush showed a larger range, from early April to late April (Figure 3). Quaking aspen and sugar maple leafed early, and white ash and black locust leafed late (Figure 3). The canopy tree species that completed bud break early tended to also reached full leaf expansion at a faster rate than the later leafing species. Quaking aspen stands achieved full leaf flush approximately two weeks earlier than either the white ash or black locust stands. Understory vegetation flushed significantly earlier than canopy leaf expansion for all forest types, starting in the beginning of March for some invasive species (i.e. Japanese barberry) and late March for native herbaceous species and saplings (Appendix III).

3.3 Other Site Characteristics

Across canopy types, there were several significant differences in the measured soil parameters (Table 2). Those variables that differed most significantly across canopy types were pH, calcium, magnesium, potassium, iron, and nitrate (ANOVA; $p<0.0001$). Evergreen canopies were significantly and consistently lower for all measured soil values with the exception of iron and aluminum. As expected, soil nitrate levels were significantly higher on black locust sites, and unexpectedly, on white ash sites as well (Table 2).

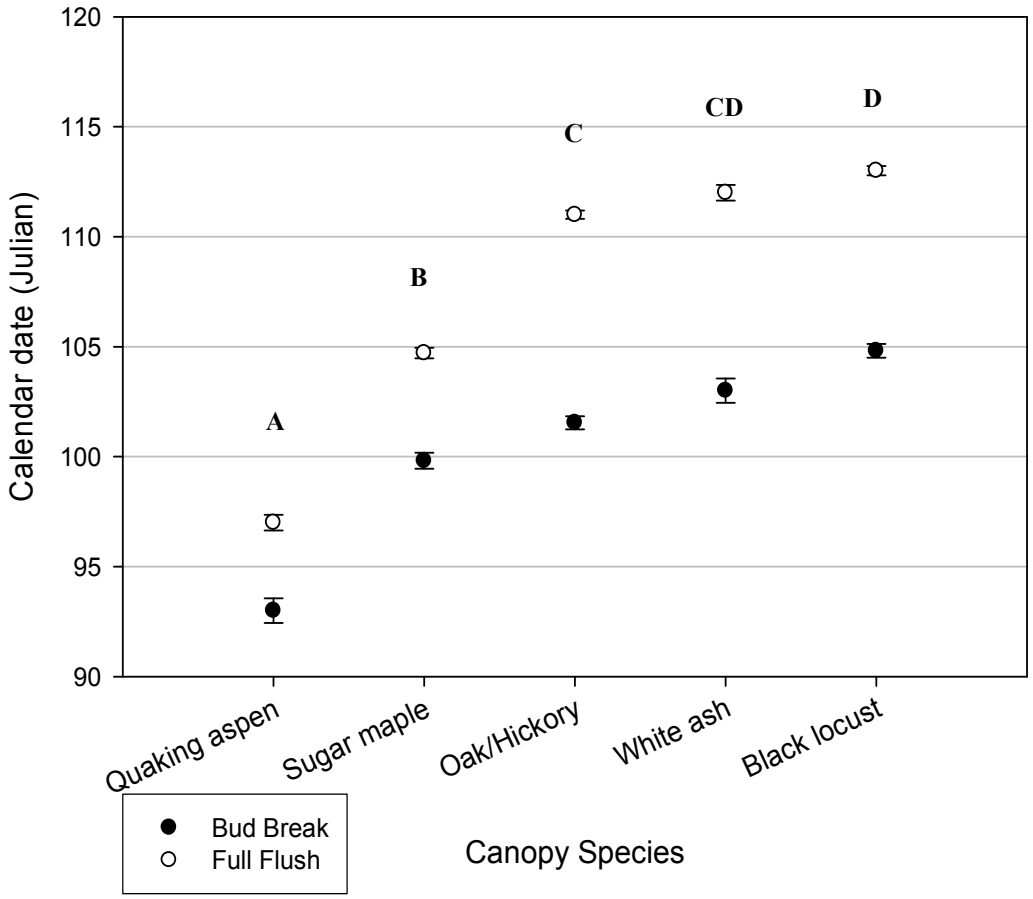


Figure 3: Average Julian date of bud break and full leaf flush ± SE for deciduous canopy species in the spring of 2010. Letters denote significant differences between canopy types. (Note: Bud break and full flush dates were not recorded for pine/hemlock sites to represent these evergreen canopies being fully expanded all year round).

Table 2: Non-transformed values of results of soil tests taken under different canopy dominant species. Letters within a row indicate significant differences between canopy types at $p < 0.05$ for variables used in statistical analyses.

Soil Property	Pine/Hemlock	Quaking aspen	Sugar maple	Oak/Hickory	White ash	Black locust
pH	4.7 ± 0.1^{b}	5.2 ± 0.1^{a}	4.5 ± 0.1^{b}	4.6 ± 0.1^{b}	5.1 ± 0.1^{a}	4.5 ± 0.1^{b}
Al (ppm)	495 ± 34^{a}	489 ± 48^{a}	381 ± 32^{a}	433 ± 26^{a}	330 ± 48^{a}	443 ± 28^{a}
B (ppm)	0.13 ± 0.02^{a}	0.15 ± 0.02^{a}	0.20 ± 0.01^{a}	0.13 ± 0.01^{a}	0.20 ± 0.02^{a}	0.13 ± 0.01^{a}
Ca (kg/ha)	175 ± 50^{d}	434 ± 72^{b}	369 ± 47^{bc}	209 ± 38^{cd}	997 ± 72^{a}	344 ± 41^{b}
Cu (ppm)	0.33 ± 0.01^{a}	0.35 ± 0.02^{a}	0.38 ± 0.01^{a}	0.39 ± 0.01^{a}	0.35 ± 0.02^{a}	0.40 ± 0.01^{a}
Fe (ppm)	33.9 ± 4.3^{ab}	20.5 ± 6.0^{bc}	54.7 ± 4.0^{a}	32.2 ± 3.2^{ab}	14.2 ± 6.0^{c}	33.8 ± 3.5^{ab}
K (kg/ha)	102 ± 18^{b}	182 ± 25^{a}	196 ± 17^{a}	160 ± 13^{a}	184 ± 25^{a}	179 ± 15^{a}
Mg (kg/ha)	52 ± 7.1^{c}	87 ± 9.8^{ab}	77 ± 6.6^{bc}	63 ± 5.5^{bc}	157 ± 9.7^{a}	62 ± 5.7^{bc}
Mn (ppm)	6.7 ± 1.2^{a}	8.1 ± 1.6^{a}	6.7 ± 1.1^{a}	4.7 ± 0.9^{a}	8.2 ± 1.5^{a}	5.7 ± 0.9^{a}
NH_4 (ppm)	28.8 ± 8.7^{b}	79.1 ± 12.3^{a}	31.2 ± 8.2^{b}	30.4 ± 6.6^{b}	24.3 ± 11.9^{ab}	25.6 ± 7.1^{b}
NO_3 (ppm)	2.2 ± 1.5^{b}	1.3 ± 2.2^{b}	3.3 ± 1.4^{b}	2.1 ± 1.2^{b}	7.6 ± 2.3^{a}	12.0 ± 1.3^{a}
P (kg/ha)	1.2 ± 1.6^{a}	1.2 ± 1.3^{a}	1.2 ± 1.5^{a}	1.2 ± 1.2^{a}	3.9 ± 2.1^{a}	5.7 ± 1.3^{a}
Zn (ppm)	2.0 ± 0.8^{b}	4.8 ± 1.1^{ab}	3.7 ± 0.7^{b}	1.9 ± 0.6^{b}	10.5 ± 1.1^{a}	3.2 ± 0.6^{b}

[a] Lowercase letters denote differences in log transformed data at the 5% level of significance across canopy types. Canopy types followed by the same lowercase letter within a variable are not significantly different.

Principal component analysis of the site environmental characteristics produced three significant axes, the first of which explained 37% of the variance. Principal component 1 was positively correlated with phenology events (r = 0.55) and negatively correlated with total growing season light (r =-0.44), where component 1 represented a gradient from early leafing species with high growing season light to late phenology and lower season totals (Figure 4). Much of the variation along component 2, which accounted for 25% of the variance in environmental data, was explained by positive correlations with canopy openness (r = 0.62) and a negative correlation with LAI (r = -0.70). Component 3 represented PAR (r = 0.78) and soil nitrate (0.42) and explained 16% of the variance (Figure 4).

3.4 Understory Vegetation Diversity

Results of the analysis of variance indicated that both richness and evenness of abundance showed no significant differences across canopy cover types (p = 0.27 and 0.14, respectively), but Simpson's and Shannon-Wiener diversity indices , showed slight differences (p = 0.06 and 0.009, respectively) (Figure 5).

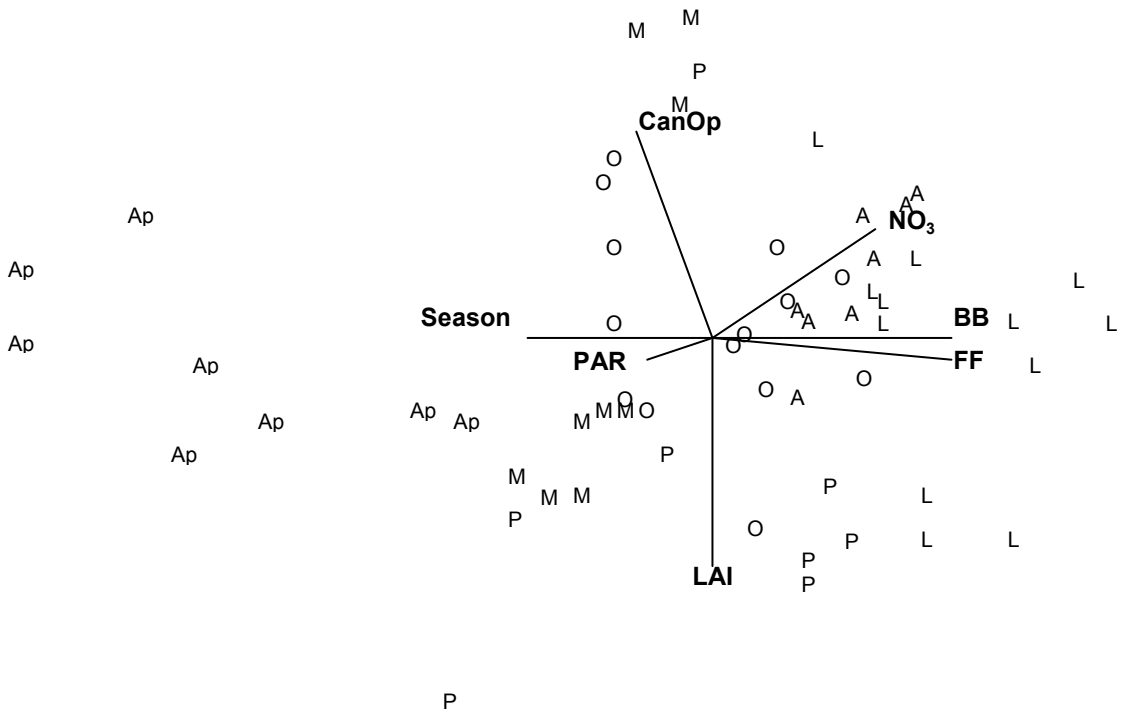


Figure 4: Principal component analysis of 32 sites (64 subplots) of six canopy cover types using environmental variables and stand/site characteristics that were significant in regression analyses. These included photosynthetically active radiation (PAR), leaf area index (LAI), total seasonal light transmission (Season), canopy openness (CanOp), and phenological events of bud break (BB) and full leaf flush (FF) by Julian date as well as soil nitrate (NO_3). Each point represents the average of June and August measurements taken at each site symbolized by canopy type (P = pine/hickory [*Pinus* spp./*Tsuga canadensis*], Ap = quaking aspen [*Populus tremuloides*], M = sugar maple [*Acer Saccharum*], O = oak/hickory *[Quercus* spp./*Carya* spp.], A = white ash [*Fraxinus americana*], L = black locust [*Robinia pseudoacacia*]). Vectors represent the strength and direction of correlation between sites and environmental variables.

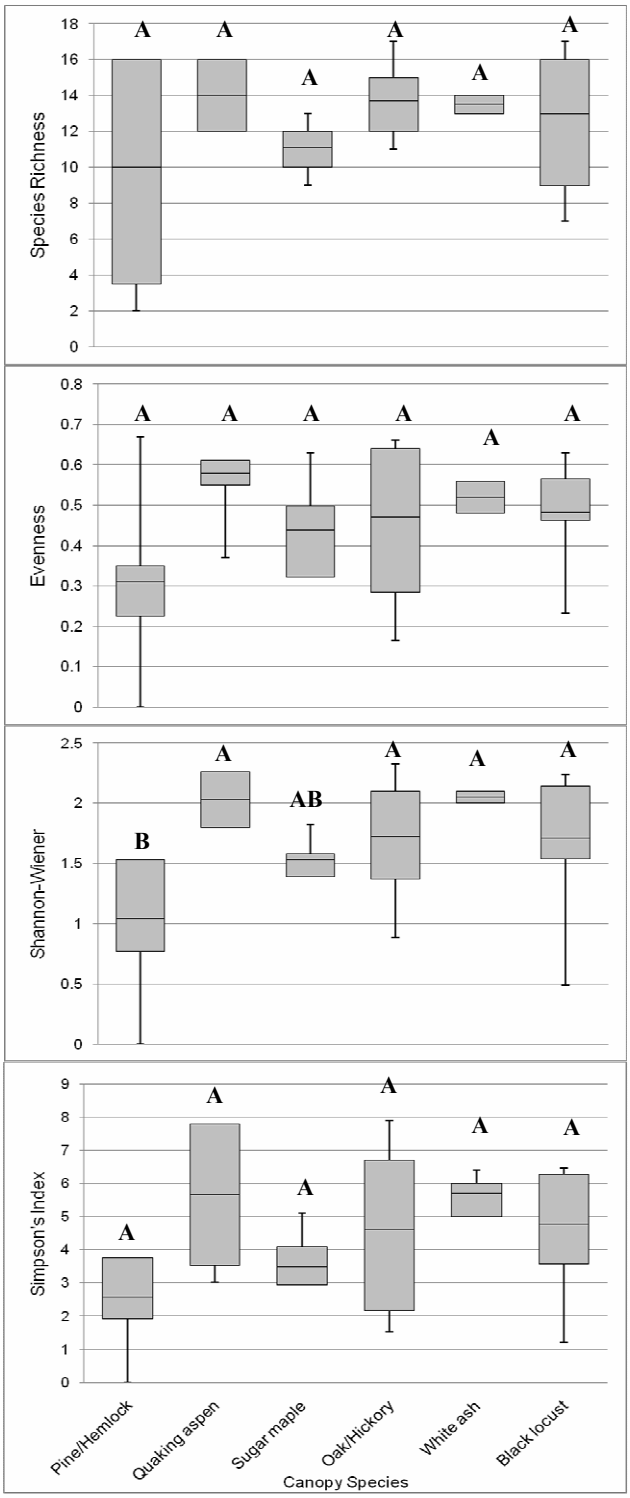


Figure 5: Box plots of diversity of understory plant species under six overstory species as measured by a) species richness, b) evenness, c) Shannon-Wiener Index, and d) Simpson's Index. A solid line represents the mean. Different letters within each box denotes a significant difference at $p<0.05$ using a Tukey test (n = 36, 24, 30, 42, 24, 36, for pine/hemlock [*Pinus* spp./*Tsuga canadensis*], quaking aspen [*Populus tremuloides*], sugar maple [*Acer saccharum*], oak/hickory [*Quercus* spp./*Carya* spp.], white ash [*Fraxinus americana*], and black locust [*Robinia pseudoacacia*], respectively).

3.5 Invasive Species Status

Eight different species of nonnative plants were recorded in understory site vegetation samples and measured in terms of both percent cover and percent relative abundance. Both variables were significantly higher under white ash and black locust canopies (Figure 6). Cover (0-97%) and abundance (0-93%) did not exceed 30% in sites that achieved bud break before 103 days or full leaf expansion prior to 110 days (with the exception of one quaking aspen sample which was due to a localized patch of Japanese barberry) (Figure 6). The majority of invasive species samples documented at white ash sites were garlic mustard (*Alliaria petiolata*) (58% of records) although samples under black locust stands were more evenly mixed (Figure 7). Regression analyses including invasive species measures and light and nitrate variables showed invasive species cover and relative abundance to be most highly correlated with soil nitrate ($r = 0.57$ and 0.60, respectively), followed by light variables, including PAR ($r = 0.45$ and 0.31, respectively) and phenology dates ($r = 0.31$ and 0.39, respectively) (Table 3).

A stepwise regression was used to determine the significant environmental variables used in standard regression analyses of percent invasive cover and relative abundance. Soil nitrate was the most significant environmental variable and, therefore, the first variable to be entered in a forward stepwise regression for both percent cover and relative abundance (Table 3). For both measures of invasive species (i.e., percent cover and relative abundance) three environmental variables were consistently found to be significant in explaining the variation: they were PAR, phenology dates, and soil nitrate (Table 4). Percent relative abundance also had LAI, canopy openness, and soil pH as significant explanatory variables in the regression. These significant environmental

variables explained 59% and 72% of the variation in invasive species cover and relative abundance, respectively (Table 4).

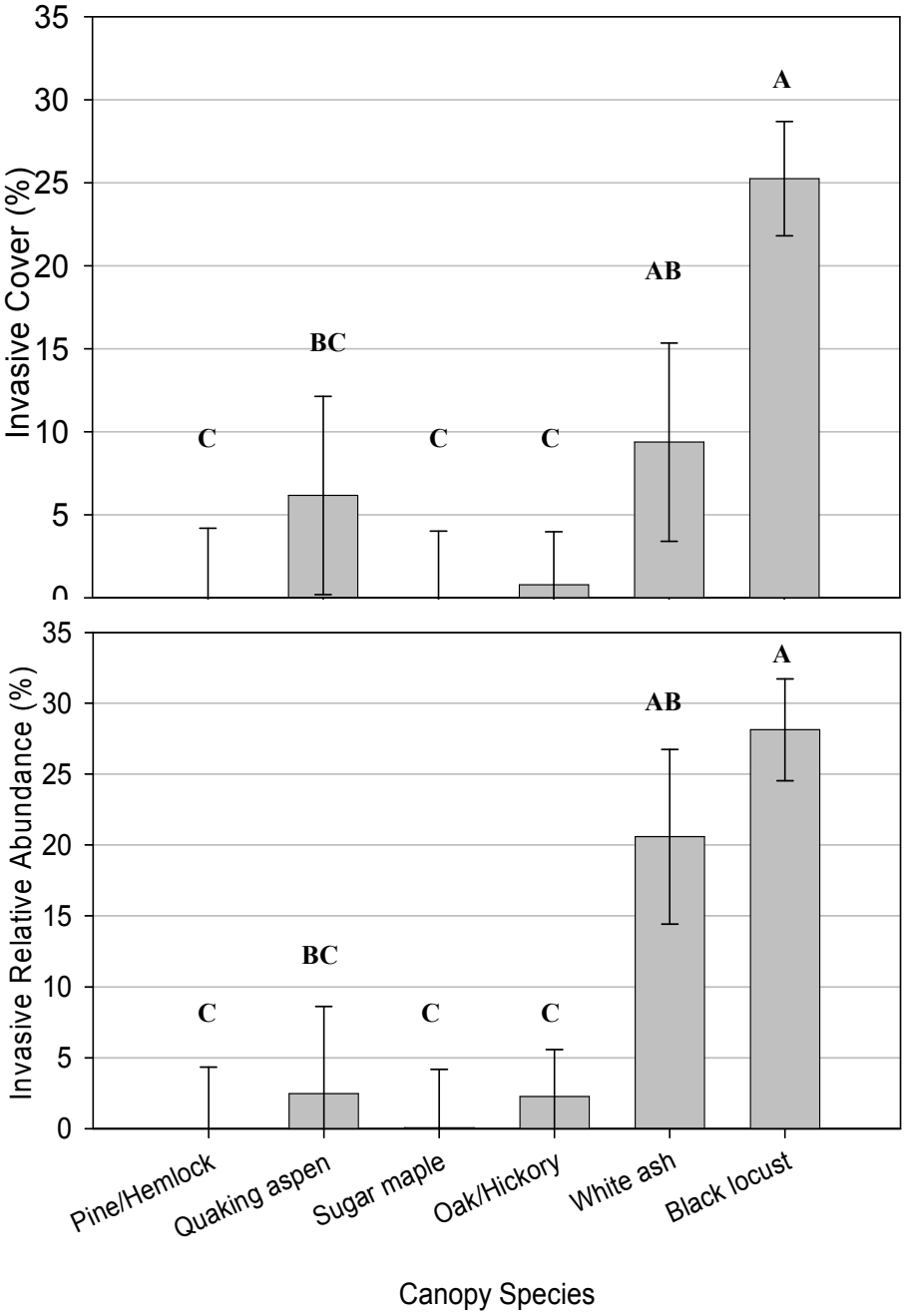


Figure 6: Understory invasive plant species presence measured by a) mean percent cover (±SE) and b) mean percent invasive relative abundance (ratio of # invasive plants to total plants) (±SE) under six canopy species. Different letters within each box indicates significant differences across canopy types using a Tukey test.

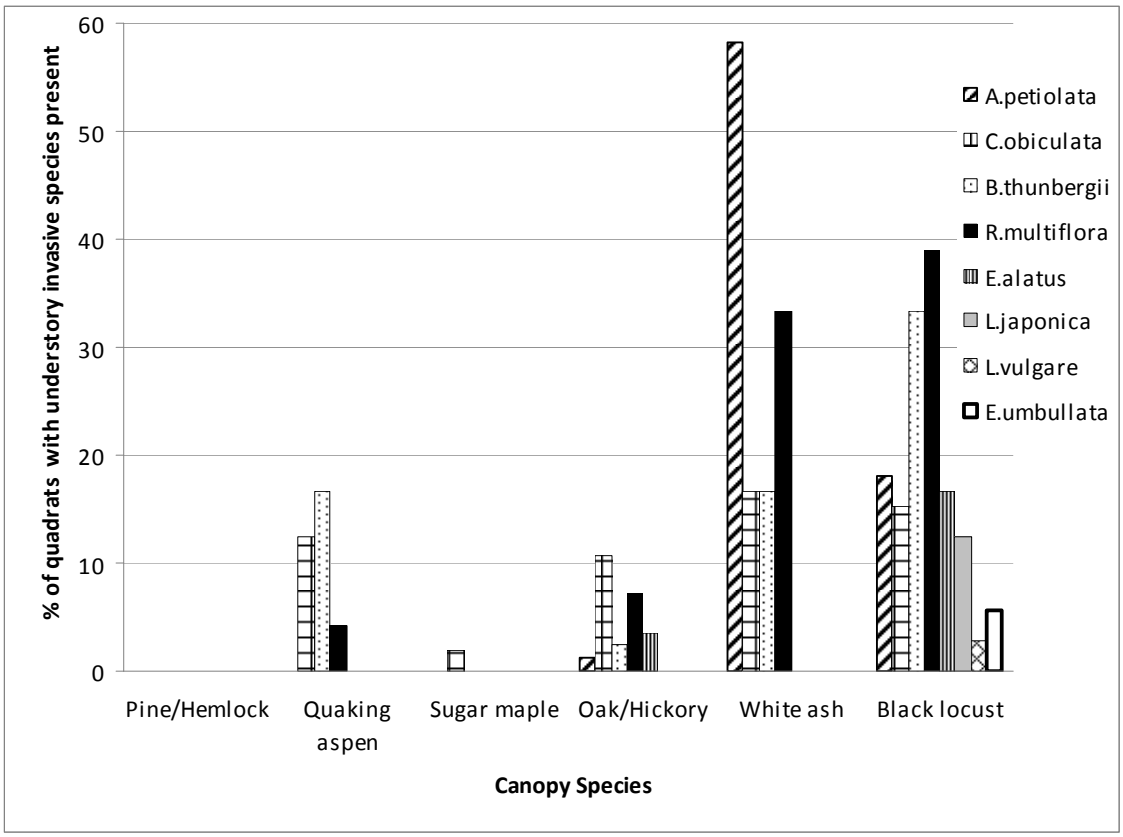


Figure 7: The presence of eight nonnative invasive plant species under six different canopy cover types (pine/hemlock [*Pinus* spp./*Tsuga canadensis*], quaking aspen [*Populus tremuloides*], sugar maple [*Acer saccharum*], oak/hickory [*Quercus* spp./*Carya* spp.], white ash [*Fraxinus americana*], and black locust [*Robinia pseudoacacia*]). Each invasive species is represented as the percent of total quadrats sampled within a given canopy type for which that the species was present. Understory invasive species included *Alliaria petiolata* (garlic mustard), *Celastrus obiculata* (oriental bittersweet), *Berberis thunbergii* (Japanese barberry), *Rosa multiflora* (multiflora rose), *Euonymous alatus* (winged euonymous), *Lonicera japonica* (japanese honeysuckle), *Ligustrum vulgare* (european privet), and *Elaeagnus umbellata* (autumn olive).

Table 3: Correlation of environmental variables in explaining the variance in invasive measures taken from a multivariate analysis. Bold numbers indicate variables that were significant ($p < 0.05$) to corresponding regression models.

Variable	Invasive Cover (%)	Invasive Relative Abundance (%)
PAR (% full sunlight)	**0.45**	**0.31**
LAI	-0.24	-0.21
Total Season (mols/m^2/day)	**0.33**	**0.46**
Canopy Openness	0.23	**0.36**
Basal Area (m^2/ha)	0.17	0.23
Full Flush (Julian date)	**0.31**	**0.39**
Bud Break (Julian date)	**0.28**	**0.31**
NO_3 (ppm)	**0.57**	**0.60**

Table 4: Significant environmental site variables remaining in a forward stepwise regression for explanation of invasive species percent cover and relative abundance used in standard least squares regression models for those response variables.

Dependent Variables	R^2	P for the factor	P for the model
Invasive Cover	0.59		<.0001
PAR		<.0001*	
Full Flush		0.0323*	
NO_3		<.0001*	
Intercept		0.011	
Invasive Relative Abundance	0.72		<.0001
PAR		0.027*	
LAI		0.0001*	
CanOp		<.0001*	
Full Flush		0.009*	
pH		0.009*	
NO_3		0.002*	
Intercept		0.12	

4. Discussion

The premise of this study was that establishment and growth of nonnative plant species within temperate forest understories of the northeastern U.S. is primarily a function of resource availability. In this case, availability of resources, both transmitted light and plant-extractable nutrients, were considered equivalent to the amount supplied, but not completely sequestered by resident communities (Davis et al. 2000). Commonly, many nonnative invasive plant species are described as high-resource species, their successful establishment in part facilitated by factors which augment resource availability (Blumenthal 2006, Davis et al. 2000, Huenneke et al. 1990, Lonsdale 1999, Mooney and Drake 1986). Although these periods of resource enrichment are fairly limited in space and time, and often associated with disturbance, they are thought to result in increased vulnerability of recipient communities to invasion (Blumenthal 2006, Davis et al. 2000). Although this study did not directly test the causes and effects of the fluctuating resource availability hypothesis (*sensu* Davis et al. 2000) it did examine the correlative relationships between invasive species in the understory and site resources (i.e. understory light and soil nitrate) and, as such, it contributes to the further elucidation of this hypothesis. Specifically, I hypothesized that establishment (cover and relative abundance) of invasive nonnative species would be connected with differences in phenology, understory light environment, and soil nitrate, which was based on the argument that invasive nonnative species will take advantage of forest understories which allow for higher resource availability (i.e., later phenology, greater light transmission, and nitrogen fixation). Overall, this hypothesis was largely supported in my study, although

with some unexpected results in regard to the canopy species studied and in the order of resource importance concerning invasive species presence.

As is consistent with other studies, I found variation in understory light availability post-leaf expansion across different canopy cover types (Bartemucci et al. 2006, Kabakoff and Chazdon 1996, Lefrancois et al. 2008). In my study, it was manifested most notably in terms of photosynthetically active radiation (PAR), LAI, total growing season light, and canopy openness. Understories under quaking aspen showed significantly higher PAR than under other canopy species with the exception of white ash and black locust. Quaking aspen understories were also significantly higher in total growing season light in comparison to the other canopy dominant tree species studied. Although he did not study quaking aspen canopies, Canham (1994) similarly found interspecific PAR and total seasonal light (GLI values) under common canopy species in New England to be: ash > oak > maple > hemlock. Collectively, my results and previous literature suggest that much of the variation in understory light levels is a predictable function of canopy composition and as such, potentially has important implications for invasive species establishment (Barbier et al. 2007, Canham 1994, Godefroid et al. 2005, Klinka et al. 1996, Messier et al. 1998).

Through principle components analysis I also found that understory site conditions were best represented along a range of light availability with like-canopy sites clumped together and correlated with LAI, total seasonal understory light, and canopy openness. In addition, of particular note was the significance of early spring canopy phenology. Consistent with previous research by others, this study documented canopy species differences in spring phenological activity from “early” species (quaking aspen

and sugar maple) to “late” species (white ash and black locust) (e.g., Lechowicz 1984, Richardson and O’Keefe 2009).

In my study, timing for both bud break and full leaf flush events were the same across canopy species, where: quaking aspen > sugar maple > oak/hickory ≥ white ash = black locust. Temporal variation in canopy closure, which occurs heterogeneously across stands, can influence understory vegetation growth, establishment, and distribution (Givnish 1992, Harrington 1989, Lopez et al. 2008, Richardson and O’Keefe 2009). Trees which expand leaves later in the spring, such as white ash and black locust in my study, allow sub-layer vegetation more time to fix carbon and accumulate resources than for individuals under earlier leafing canopies (Givnish 1992, Harrington et al. 1989, Lopez et al. 2008, Richardson and O’Keefe 2009). Many studies have found that saplings leafed out earlier than the overstory canopy thus allowing them to take advantage of this high resource opportunity (Augsperger 2008, Gill et al. 1998, Lopez et al. 2008, Rathke and Lacey 1985). More notably, as in my study, many nonnative species expand their leaves for photosynthesis well before both canopy species and coexisting understory native species (Harrington et al. 1989, Pattison et al. 1998, Schierenbeck 1992, Xu et al. 2007). In this case, strategic timing adds to the advantage many nonnative plants possess over native species in capturing an early carbon subsidy (Harrington et al. 1989).

Higher PAR under quaking aspen, white ash, and black locust canopies and later phenology in white ash and black locust stands provide higher light availability in corresponding understories. According to my hypothesis it should have been under these canopies is where invasive species establishment was most prevalent, but particularly so for the white ash and black locust stands which had significantly later leaf phenology. In

fact, invasive species cover and relative abundance were significantly higher under white ash and black locust canopies, but, even though quaking aspen stands had the highest total season light and the highest PAR in their understories, there was little evidence of invasive species. Across canopy types, analyses showed that PAR, LAI, canopy openness, and phenology (bud break and full flush) dates were able to explain a large amount of variation in invasive species cover (52%) and relative abundance (60%). On the other hand, quaking aspen canopies, while providing relatively high understory light conditions post-leaf expansion, also had the earliest phenology among the deciduous canopy species studied. Thus, at least in the case of my study, it appears that canopies with significantly later full leaf expansion dates might play a key role in allowing for invasive species to gain a foothold. Although phenology is an example of high resource availability resulting from a period of low resource use by resident species (Shea and Chesson 2002), other resources, such as soil nutrients, can also be influenced by resident species.

The temperate forests of the northeastern United States are often considered to be nitrogen limited (Aber et al. 1989, Robertson 1982, Vitousek 1984). Generally site fertility depends on a number of factors including the composition of overstory species (Augusto et al. 2002). In my study, black locust was one of the canopy dominant species. Black locust is a fast growing early successional nitrogen-fixing tree species, which is also considered to be an intracontinental invasive species (Burke and Grime 1996, Hobbs and Huenneke 1992, Maron and Connors 1996, Milchunas and Lauenroth 1995, Wedin and Tilman 1996). With the exception of the white ash stands, sites dominated with black locust had significantly higher soil nitrate than other sites. It is not clear why white ash

sites consistently had higher nitrate levels than the other non-legume sites. Some literature suggest that post-agricultural land use (Mosher et al. 2009) might provide for a residual increase in site nitrogen level, but examination of historic aerial photography revealed no evidence of past agricultural activities on my sites for at least the last 76 years. White ash sites had a notably high presence of garlic mustard (*Allaria petiolata*) in the understory, which might partly explain the increase in site soil nitrate (Rodgers et al. 2008, Stinson et al. 2007). Garlic mustard is an invasive nonnative herbaceous plant that can be found throughout the temperate forests of North America and is known for increasing nitrogen availability (Rodgers et al. 2008). Of all sites in which garlic mustard was present, one third of these understories were located under white ash canopies while the other two thirds were located under black locust (with the exception of one record under an oak/hickory canopy). Raw data of vegetation sampling beneath white ash canopies further suggested garlic mustard's prominence, where garlic mustard was present in fourteen out of twenty four white ash plots, and, in eight of these, it had the highest coverage, abundance or both of any species. Thus, it appears that late phenology conveys an advantage for the establishment of garlic mustard, which then potentially increases site nitrate levels thereby facilitating further invasion. However, further study would be needed to substantiate the possibility of this positive feedback.

Although a higher soil nitrogen level for white ash sites was a surprise, it only added to the support of my hypothesis in that sites with increased resource availability would show greater invasive species cover and relative abundance and thus be more susceptible to invasion than those sites with lower resource availabilities. In this case, both white ash and black locust stands, which were noted for having later phenology, higher understory

light availability, and higher soil nitrate levels, also had significantly greater understory invasive species cover and relative abundance than any of the other canopy species studied. Unexpectedly, when looking at a single variable in a model explaining invasive species cover or relative abundance, soil nitrate was even greater than the light variables, PAR and phenology (bud break and full flush). As a single variable, soil nitrate is also just as adequate at explaining nonnative species measures than a model with these three light variable combined, explaining from 33 - 36 % as compared to 32 - 37 %, respectively. So although light availability is commonly observed as the greatest determining factor of native vegetative growth/development in temperate forest ecosystems (Anderson and Swain 1969, Canham et al. 1990, Denslow et al. 1991, Klinka et al. 1996, Messier et al. 1998), nitrate levels, at least in my study, were more important in understanding invasive species success in these understories. It remains to be determined why white ash stands had higher soil nitrate levels, but regardless, the fertilizing effects under these canopies seem to facilitate understory invasive species establishment.

For several decades numerous studies have tested the biotic resistance hypothesis and the potential links between diversity and invasibility (e.g., Elton 1958, Naeem et al. 2000 Stohlgren et al. 1999), but the link between the two remains elusive (Richardson and Pyŝek 2006). In my study, there were no significant differences in understory species richness, evenness of abundance or Simpson's diversity regardless of significant differences in understory environmental conditions. Shannon-Wiener Index was significant, which, as found in other studies (Barbier et al. 2008, Berger and Puettmann 2000), was the result of marginally lower diversity in the evergreen sites. Instead, like has

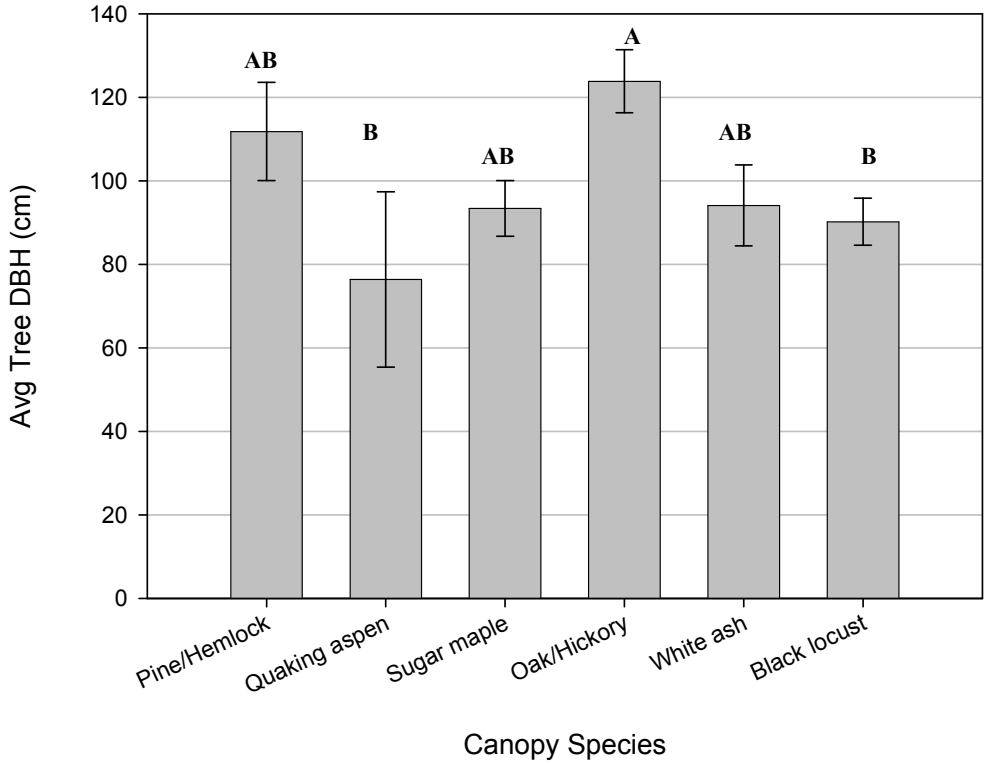
been found previously, resource availability explained more variance in invasibility than did diversity measures (Foster et al. 2002).

Historically, black locust (*R. pseudoacacia*) was used for its ability to restore nutrient-poor environments, but today is recognized globally as a serious invasion threat (Rice et al. 2004, Xiao-rong et al. 2009). It can fix 35-150 kg N per hectare per year, and the added soil nitrogen is detectable years after removal which contributes to a growing concern over its potential to promote the growth and establishment of other nonnative invasive species (Altieri et al. 2010, Danso et al. 1995, Hunter and Mattice 2002, Malcom et al. 2008, Nasir et al. 2005, Peloquin and Hiebert 1999, Vitousek and Farrington 1997, Von Holle et al. 2008). This increase in resources, nitrogen in particular, is proposed to have negative effects on native communities including greater frequencies of fast-growing nitrophilous species which might competitively exclude more "typical" understory herbs (Small and McCarthy 2005), increases in tree mortality and forest declines (Aber et al. 1995) as well as global repercussions of biodiversity loss (Bobbink et al. 1998, Tilman 1997, Vitousek et al. 1997), and transgeneration effects under climate change conditions (Cannell and Thornley 1998, Lau et al. 2008, Tilman and Downing 1994). Assisted migration of species, such as black locust, might have unintended consequences through facilitation of invasive species establishment, especially for nitrogen-limited forest ecosystems, such as those found in the northeastern United States (Kleinbauer et al. 2010).

This study shows that invasive species status in temperate forest closed canopy understories was influenced by the dominant canopy species because of its effect on resource availability. Light transmitted through the canopy, early spring light availability

(phenology) and, more notably, accessible nitrate, were all resources that were correlated with increased site invasibility. Pockets of forest underneath either white ash or black locust canopies appeared to be more invasible than other canopy dominants that were studied. Thus, it begs the question: do these canopy dominant species create islands of invasion within a temperate forest landscape? In effect, do these species act similar to forest edges in their ability to facilitate an invasive species foothold (Spellerberg 1998, Trombulak and Frissell 2000)? Further studies should continue to investigate the ability of nonnative plant species to alter resource availability. The potential for nonnative species to facilitate the success of other invasive species is important to consider for species predictive modeling and management planning in resource poor plant communities.

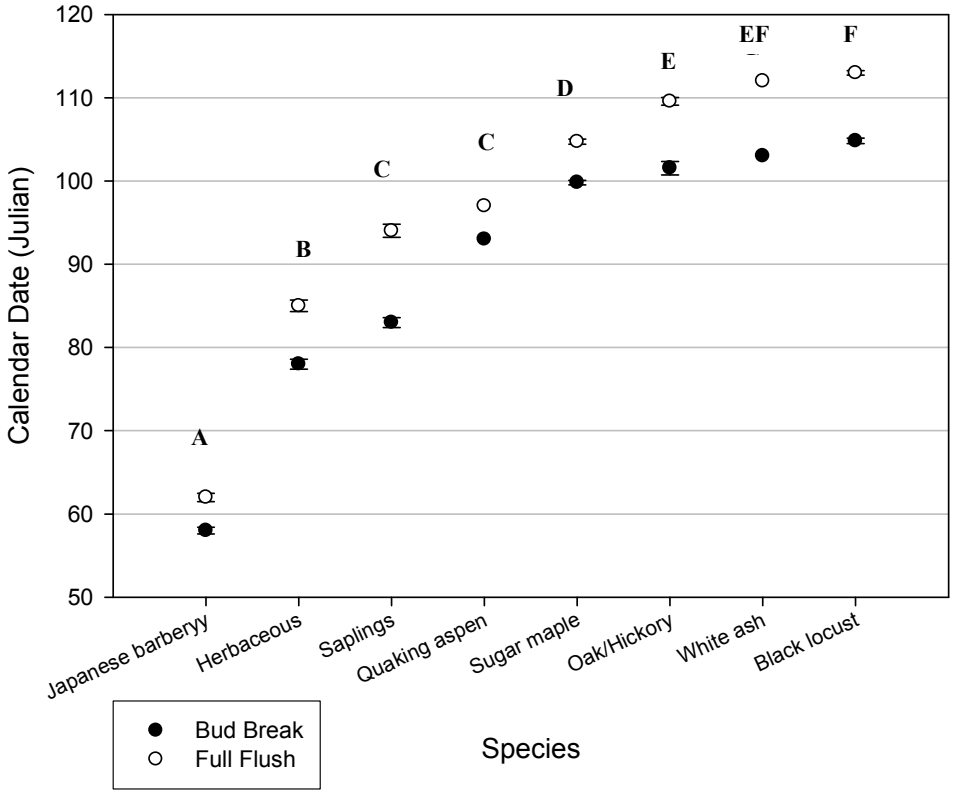
Appendix I: The average diameter at breast height in centimeters of trees measured within plot of a 5 m radius. Averages were taken by plot, each plot being one of six canopy species dominants. Error bars are 1 SE (bars with the same length are not significantly different at p =0.05)



Appendix II: Partial Correlation of site variables representing the understory light environment.

	PAR	LAI	Total Season	Canopy Openness	Aspect	Basal Area	Bud Break	Full Flush
PAR	1.00	-0.53	0.70	0.55	-0.12	-0.87	0.47	0.48
LAI	-0.53	1.00	-0.60	-0.78	0.10	0.50	-0.50	-0.51
Total Season	0.70	-0.60	1.00	0.66	-0.13	-0.69	0.15	0.16
Canopy Openness	0.55	-0.78	0.66	1.00	-0.13	-0.62	0.41	0.42
Aspect	-0.12	0.10	-0.13	-0.13	1.00	0.12	0.10	0.09
Basal Area	-0.87	0.50	-0.69	-0.62	0.12	1.00	-0.36	-0.39
Bub Break	0.47	-0.50	0.15	0.41	0.10	-0.37	1.00	0.99
Full Flush	0.48	-0.51	0.16	0.42	0.10	-0.39	0.99	1.00

Appendix III: Calendar date of bud break and full flush ± SE for deciduous canopy and understory species in the spring of 2010. Letters denote significant differences between canopy events.



Literature Cited

Aber, J.D., K.J. Nadelhoffer, P. Steudler and J.M. Melillo. 1989. Nitrogen saturation in northern forest ecosystems. BioScience 39(6): 378-386.

Aber, J.D., A. Magill, S.G. McNulty, R.D. Boone, K.J. Nadelhoffer, M. Downs, and R. Hallett. 1995. Forest biogeochemistry and primary production altered by nitrogen saturation. Water, Air and Soil Pollution 85: 1665-1670.

Aber, J., W. McDowell, K. Nadelhoffer, A. Magill, G. Berntson, M. Kamakea, S. McNulty, W. Currie, L. Rustad, and I. Fernandez. 1998. Nitrogen saturation in temperate forest ecosystems. Bioscience 43(11): 921-934.

Altieri, A.H., B.K. van Wesenbeeck, M.D. Bertness and B.R. Silliman. 2010. Facilitation cascade drives positive relationship between native biodiversity and invasion success. Ecology. 91(5): 1269-1275.

Alvarez, M.E. and J.H. Cushman. 2002. Community-level consequences of a plant invasion:effects on three habitats in coastal California. Ecologial Applications 12: 1434-1444.

Anderson, M.C. 1964. Studies of woodland light climate: II. Seasonal variance in the light climate. Journal of Ecology 52(3): 643-663.

Anderson, R.C., and A.M. Swain. 1969. Herbaceaous response to canopy cover, light intensity, and through fall precipitation in conifer forests. Ecology 50: 256-263.

Armesto, J.J. and S.T.A. Pickett. 1985. Experiments on disturbance in old-filed plant communities: impact on species richness and abundance. Ecology 66(1): 230-240.

Augspurger, C.K. 2008. Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. Oecologia 156: 281-286.

Augusto, L., J. Ranger, D. Binkley and A. Rothe. 2002. Impact of several common tree sspecies of European temperate forests on soil fertility. Annual Review of Forest Science 59: 233-253.

Barbier, S., F. Gosselin and P. Balandier. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. Forest Ecology and Management 254: 1-15.

Bartemucci, P., C. Messier, and C.D. Canham. 2006. Overstory influences on light attenuation patterns and understory plant community diversity and composition in southern boreal forests of Quebec. Canadian Journal of Forest Resources 36: 2065-2079.

Baruch, Z. and G. Goldstein. 1999. Leaf construction cost, nutrient concentration, and net CO2 assimilation of native and invasive species in Hawaii. Oecologia 121: 183-192.

Berger, A.L., Puettmann, K.J., 2000. Overstory composition and stand structure influence herbaceous plant diversity in the mixed aspen forest of northern Minnesota. Am. Midl. Nat. 143, 111–125.

Bobbink, R., M. Hornung and J.G.M. Roelofs. 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. Journal of Ecology 86: 717-738.

Brantley, S.T. and D.R. Young. 2007. Leaf-Area Index and light attenuation in rapidly expanding shrub thickets. Ecology 88(2): 524-530.

Burke, M.J.W. and J.P. Grime. An experimental study of plant community invisibility. Ecology 77(3): 776-790.

Canham, C.D., J.S. Denslow, W.J. Platt, J.R. Runkle, T.A. Spies and P.S. White. 1990 Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Resources 20: 620-631.

Canham, C.D. and D.H. Burbank. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Canadian Journal of Forest Resources 24: 337 – 349.

Cannell, M.G. and J.H. Thornley. 1998. N-poor ecosystems may respond more to elevated [CO2] than N-rich ones in the long term. A model analysis of grassland. Global Change Biology 4: 431-442.

Cano, L., J. Escarre, K. Vrieling, and F.X. Sans. 2009. Palatability to a generalist herbivore, defense and growth of invasive and native Senecio species: testing the evolution of increased competitive ability hypothesis. Oecologia 159: 95-106.

Cassidy, T.M., J.H. Fownes and R.A. Harrington. 2004. Nitrogen limits and invasive perennial shrub in forest understory. Biological Invasions 6: 113-121.

Chazdon, R.L. and R.W. Pearcy. 1991. The importance of sunflecks for forest understory plants. BioScience 41(11): 760-766.

Chen, W.J., T.A. Black, P.C. Yang, A.G. Barr, H.H. Neumann, Z. Nesic, P.D. Blanken, M.D. Novak, J. Eley, R.J. Ketler and R. Cuenca. 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Global Change Biology 5: 41-53.

Cole, P.G., and J.F. Weltzin. 2005. Light limitation creates patchy distribution of an invasive grass in eastern deciduous forests. Biological Invasions 7: 477-488.

Daehler, C.C. and D.A. Carino. 2000. Predicting invasive plant: prospects for a general screening system based on current regional models. Biological Invasions 2: 93-102.

Danso, S.K.A., F. Zapata and K.O. Awonaike. 1995. Measurement of biological N2 fixation in field-grown *Robinia pseudoacacia* L. Soil Biology and Biochemistry 27(4): 415-419.

Davis, M.A., J.P. Grime and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. Journal of Ecology 88: 528-534.

Denslow, J.S., E.A. Newell and A.M. Ellison. 1991. The effect of palms on growth and survival of tree seedlings in a rain forest understory. Biotropica 23: 225-234.

Durand, L.Z. and G. Goldstein. 2001. Photosynthesis, photoinhibition and nitrogen use efficiency in native and invasive tree ferns in Hawaii. Oecologia 126: 345-354.

Elledge, J. and B. Barlow. 2010. Basal area: a measure made for management. Alabama Cooperative Extension System: ANR-1371.

Elton, C. S. 1958. The ecology of invasions by animals and plants. - Methuen, London.

Feng, Y., J. Wang, and W. Sang. 2007. Irradiance acclimation, capture ability, and efficiency in invasive and non-invasive alien plant species. Photosynthetica 45(2): 245-253.

Feng, Y., G.L. Fu, and Y.L. Zheng. 2008. Specific leaf area relates to the differences in leaf construction cost, photosynthesis, nitrogen allocation, and use efficiencies between invasive and noninvasive alien congeners. Planta 228: 383-390.

Fine, P.V. 2002. The invisibility of tropical forest by exotic plants. Journal of Tropical Ecology 18(5): 687-705.

Finzi, A.C., C.D. Canham and N. Van Breemen. 1998. Canopy tree-soil interaction within temperate forests: species effects on pH and cations. Ecological Applications 8(2): 447-452.

Finzi, A.C., N. Van Breemen and C.D. Canham. 1998. Canopy tree-soil interaction within temperate forests: species effects on soil carbon and nitrogen. Ecological Applications 8(2): 440-446.

Gill, D.S., J.S. Amthor and F.H. Bormann. 1998. Leaf phenology, photosynthesis and the persistence of saplings and shrubs in a mature northern hardwood forest. Tree Physiology 18: 281-289.

Givnish, T.J. 2002. Ecological constraints on the evolution of plasticity in plants. Evolutionary Ecology 16: 213-242.

Godefroid, S., S.S. Phartyal, G. Weyembergh and N. Koedam. 2005. Ecological factors controlling the abundance of non-native invasive black cherry (Prunus serotina) in deciduous forest understory in Belgium. Forest Ecology and Management 210, 91-105.

Gordon, D.R. 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. Ecological Applications 8(4): 975-989.

Gordon, D.R., D.A. Onderdonk, A.M. Fox, R.K. Stocker and C.Gantz (2008b) Predicting invasive plants in Florida using the Australian Weed Risk Assessment system. Invasive Plant Science and Management 1, 178–195.

Grime, P.J. 2006 Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. Journal of Vegetation Science 17 (2): 255-260.

Gurevitch, J., T.G. Howard, I.W. Ashton, E.A. Leger, K.M. Howe, E. Woo and M. Lerdau. 2008. Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. Biological Invasions 10: 821-831.

Harrington, R.A., B.J. Brown, and P.B. Reich. 1989. Ecophysiology of exotic and native shrubs in Southern Wisconsin: Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia 80(3): 356-367.

Harrington, R.A., B.J. Brown, and P.B. Reich. 1989. Ecophysiology of exotic and native shrubs in Southern Wisconsin: annual growth and carbon gain. Oecologia 80(3): 368-373.

Hobbs, R.J. and L.F. Huenneke. 1992. Disturbance, diversity and invasion: implications for conservation. Conservation Biology 6: 324-337.

Hulme, P.E. and E.T. Bremner. 2006. Assessing the impact of Imatients flandulifera on riparian habitats: partitioning diversity components following species removal. Journal of Applied Ecology 43: 43-50.

Hunter, J.C. and J. Mattice. 2002. The spread of woody exotics into the forests of a northeastern landscape, 1938-1999. Journal of Torrey Botanical Society 129: 220-227.

Kleinbauer, I., S. Dullinger, J. Peterseil and F. Essi. 2010. Climate change might drive the invasive tree Robinia pseudoacacia into nature reserves and endangered habitats. Biological Conservation. 143: 382-390.

Klinka, K., H.Y. Chen, Q. Wang and L. de Montigny. 1996. Forest canopies and their influence on understory vegetation in early seral stands on West Vancouver Island. Northwest Science 70(3): 193-200.

Knapp, L.B. and C.D. Canham. 2000. Invasion of an old-growth forest in New York by Ailanthus altissima: sapling growth and recruitment in canopy gaps. Journal of the Torrey Botanical Society 127(4): 307-315.

Kolb, A., P. Alpert, D. Enters, C. Holzapfel. 2002. Patterns of invasion within a grassland community. Journal of Ecology 90(5): 871-881.

Komiyama, A., S. Kato and M. Teranishi. 2001. Differential overstory leaf flushing contributes to the formation of a patchy understory. Journal of Forest Restoration 6: 163-171.

Lake, J.C. and M.R. Leishman. 2004. Invasion success of exotic plants in natural ecosystems: the role of disturbance, plant attributes and freedom from herbivores. Biological Conservation 117: 215-226.

Lau, J.A., J. Peiffer, P.B. Reich, and P. Tiffin. 2008. Transgenerational effects of global environmental change: long-term CO2 and nitrogent treatments influence offspring growth response to elevated CO2. Oecologia 158: 141-150.

Lechowicz, M.J. 1984. Why do temperate deciduous trees leaf out at different times Adaptation and ecology of forest communities. The American Naturalist 124(6): 821-842.

Leishman, M.R., T. Haslehurst, A.Ares, and Z. Baruch. 2007. Leaf trait relationships of native and invasive plants: community- and global- scale comparisons. New Phytologist 176: 635-643.

Legare, S., Y. Bergeron, A. Leduc and D. Pare. 2001. Comparison of the understory vegetation in boreal forest types in southwest Quebec. Canadian Journal of Botany 79:1019-1027.

Lopez, O.R., K. Farris-Lopez, R.A. Montgomery and T.F. Givnish. 2008. Leaf phenology in relation to canopy closure in southern Appalachian trees. American Journal of Botany. 95(11): 1395-1407.

Maeno, H. and T. Hiura. 2000. The effect of leaf phenology of overstory trees on the reproductive success of an understory shrub, Staphylea bumalda DC. Canadian Journal of Botany 78L 781-785.

Malcolm, G.M., D.S. Bush, and S.K. Rice. 2008. Soil nitrogen conditions approach pre-invasion levels following restoration of nitrogen-fixing black locust (Robinia pseudoacacia) stands in a pine-oak ecosystem. Restoration Ecology 16(1): 70-78.

Manchester, S.J. and J.M. Bullock. 2000. The impacts of non-native species on UK biodiversity and the effects of control. Journal of Applied Ecology 37(5): 845-864.

Maron, J.L and P.G Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. Oecologia 105: 302-312.

Martin, P.H., C.D. Canham and P.L. Marks. 2009. Why forests appear resistant to exotic plant invasionsL intentional introguctions, stand dynamics and the role of shade tolerance. Frontiers in Ecology and the Environment 7: 142-149.

Mehta, S.V., R.G. Haight, F.R. Homans, S. Polasky, and R.C. Venette. 2007. Optimal detection and control strategies for invasive species management. Ecological Economics 61: 237-245.

Messier, C., S. Parent and Y. Bergeron. 1998. Effectos of overstory and understory vegetation on the understory light environment in mixed boreal forests. Journal of Vegetation Science 9(4): 511-520.

Milchunas, D.G. and W.K. Lauenroth. 1995. Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. Ecological Applications 5(2): 452-458.

Mordelet, P. and J.C. Menaut. 1995. Influence of trees on above-ground production dynamics of grasses in a humid savanna. Journal of Vegetation Science 6(2): 223-228.

Mosher, E.S., J.A. Silander and A.M. Latimer. 2009. The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biological Invasions 11: 2317-2328.

Mueller, J.M. and J.J. Hellmann. 2008. An assessment of invasion risk from assisted migration. Conservation Biology 22 (3): 562-567.

Naeem, S., J.M.H. Knops, D. Tilman, K.M. Howe, T. Kennedy and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. OIKOS 91: 97-108.

Nasir, H., Z. Iqbal, S. Hiradate, and Y. Fujii. 2005. Allelopathic potential of Robinia pseudoacacia. Journal of Chemical Ecology 31(9): 2179-2192.

Northeast Coordinating Committee for Soil Testing. 2011. Recommended soil testing procedures for the northeastern United States. Northeastern Regional Publication No. 493, 3rd Edition: NEC-1012.

Pattison, R.R., G. Goldstein and A. Ares. 1998. Growth, biomass allocation and photosynthesis of invasive and native Hawaiian rainforest species. Oecologia 117: 449-459.

Peoloquin, R.L., and R.D. Hiebert. 1999. The effects of black locust (Robinia pseudoacacia L.) on species diversity and composistion of black oak savanna/woodland communities. Natural Areas Journal 19(2): 121-131.

Powers, J.S., J.P. Haggar and R.F. Fisher. 1997. The effect of overstory composition on understory woody regeneration and species richness in 7-year-old plantations in Costa Rica. Forest Ecology and Management 99: 43-54.

Rathke, B. and E.P. Lacey. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16: 179-214.

Reich, P.B., T. Koike, S.T. Gower and A.W. Schoettle. 1995. Causes and consequences of variation in conifer leaf life-span, in *Ecophysiology of Coniferous Forests*: pp.225-254. Academic, San Diego, CA.

Rice, S.K., B. Westerman, and R. Federici. 2004. Impacts of the exotic, nitrogen-fixing black locust (Robinia pseudoacacia) on nitrogen-cycling in a pine-oak ecosystem. Plant Ecology 174: 97-107.

Richardson, A.D. and J. O'Keefe. 2009. Phenological differences between understory and overstory: a case study using the long-term Harvard Forest Records Book Pp. 87-117 from *Phenology of Ecosystem Processes*. Springer, New York, NY.

Richardson D.M. and P. Pyšek. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. Progress in Physical Geography 30:409–431

Robertson, G.P. 1982. Nitrification in forested ecosystems. Philosophical Transactions of the Royal Society of London B: Biological Sciences 296: 445-457.

Rodgers, V.L., B.E. Wolfe, L.K. Werden and A.C. Finzi. 2008. The invasive species Alliaria petiolata (garlic mustard) increases soil nutrient availability in northern hardwood-conifer forests. Oecologia 157: 459-471.

Schierenbeck KA (1992) Comparative ecological and genetic studies between a native (Lonicera sempervirens L.) and and introduced congener (L. japonica Thunb.). PhD thesis, Washington State University, Pullman

Schutzenhofer, M.R., T.J. Valone, and T.M. Knight. 2009. Herbivory and population dynamics of invasive and native Lespedeza. Oecologia 161: 57-66.

Shannon, C.E. 1948. A mathematical theory of communication. Bell System Technical Journal 27: 379-423.

Shea, K. and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. Trends in Ecology and Evolution 17(4): 170-176.

Simpson, E.H. 1949. Measurement of diversity. Nature (London) 163:688.

Small, C.J. and B.C. McCarthy. 2005. Relationship of understory diversity to soil nitrogen, topographic variation and stand age in an easter oak forest, USA. Forest Ecology and Management 217(2-3): 229-243.

Spellerberg, I.F. 1998. Ecological effects of roads and traffic: A literature review. *Global Ecology and Biogeography Letters* 7:317-333.

Stinson, K., S. Kaufman, L. Durbin, and F. Lowenstein. 2007. Impacts of garlic mustard invasion on a forest understory community. Northeastern Naturalist 14(1): 72-88.

Stohlgren, T.J., D. Binkley, G.W. Chong, M.A. Kalkhan, L.D. Schell, K.A. Bull, Y. Otsuki, G. Newman, M. Bashkin and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs 69: 25-46.

Tessier, J.T. 2003. Leaf habitat, phenology and longevity of 11 forest understory plant species in Algonquin State Forest, northwest, Connecticut, USA. Botany 86: 457-465.

Tilman, D. 1997. Community invisibility, recruitment limitations and grassland biodiversity. Ecology 78: 81-83.

Tilman, D. and J.A. Downing. 1994. Biodiversity and stability in grasslands. Nature 57: 189-214.

Tomita, M. and K. Seiwa. 2004. Influence of canopy tree phenology on understorey populations of Fagus crenata. Journal of Vegetation Science 15: 379-388.

Trombulak, S.C. and C.A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14:18-30.

Vitousek, P.M. 1984. Nutrient cycling and nutrient use efficiency. The American Naturalist 119: 553-572.

Vitousek, P.M. and H. Farrinton. 1997. Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37: 63-75.

Vitousek, P.M., J.D. Aber, R.W. Howarth, G.E. Likens, P.A. Matson, D.W. Schindler, W.H. Schlesinger and D.G. Tilman. 1997. Human alteration of the global nitrogen cycle: sources and consequences. Ecological Applications 7(3): 737-750.

Volin, J.C. 2010. Gestalt of an invader. *Current Conservation* 4:29-32.

Volin, J.C., E.L. Kruger, V.C. Volin, M.F. Tobin and K. Kitajima. 2010. Doe release from natural belowground enemies help explain the invasiveness of Lygodium microphyllum? A cross-continental comparison. Plant Ecology 208(2): 223-234.

Von Holle, B., K.A. Joseph, E.F. Largay, and R.G. Lohnes. 2006. Facilitations between the introduced nitrogen-fixing tree Robinia pseudoacacia and non-native plant species in the glacial outwash updland ecosystem of Cape cod, MA. Biodiversity and Conservation 15: 2197-2215.

Wedin, D.A. and D. Tilman 1996. Influence of nitrogen loading and species composition on the carbon balance of grasslands. Science 274: 1720-1723.

Westveld, M. 1956. Natural Forest Vegetation Zones of New England. *Journal of Forestry,* 54:332-338.

Wharton, Eric H.; Widmann, Richard H.; Alerich, Carol L.; Barnett, Charles H.; Lister, Andrew J.; Lister, Tonya W.; Smith, Don; Borman, Fred 2004. The forests of Connecticut. Resour. Bull. NE-160. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 35 p..

Williams, K., C.B. Field and H.A. Mooney. 1989. Relationsips among leaf construction cost, leaf longevity and light environment in rain-forest plants of the genus Piper. The American Naturalist 133(2): 198-211.

Xiao-rong, W., S. Ming-an, Z. Xing-chang, and S. Hong-bo. 2009. Landform affects on profile distribution of soil properties in black locusts land in loessial gully region of the Chinese Loess Plateau and its implications for vegetation restoration. African Journal of Biotechnology 8(13): 2984-2992.

Xu, C.Y., K.L. Griffin and W.S.F. Schuster. 2007. Leaf phenology and seasonal variation of photosynthesis of invasive Berberis thunbergii (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. Oecologia 154:11-21.

Yamashita, N., A. Ishida, H. Kushima and N. Tanaka. 2000. Acclimation to sudden increase in light favoring an invasive over native trees in subtropical islands, Japan. Oecologia 125: 412-419.