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The Role of Phenology in Invasive Plant Species Success in Temperate Forest Understories

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The Role of Phenology in Invasive Plant Species Success in Temperate Forest Understories

Lindsay Marie Dreiss, PhD

University of Connecticut, 2016

Mechanisms underlying the ability of invasive exotic plant species (IES) to establish outside of their native ranges and outcompete native species (NS) are not yet fully understood, especially in low-resource environments. In deciduous forest understories, where light availability is low, but seasonally variable, one potential contributor to success of IES is extended leaf phenology, which may result from earlier leaf flush or later leaf abscission compared to that of NS. If either is the case, IES would tend to exploit a broader temporal niche for assimilating resources, which is particularly beneficial if it results in photosynthetic activity when the canopy is leafless (*i.e.*, when light availability is high and competition low). Therefore, the role of phenology with respect to the hypothetical growth advantage of IES is twofold; extended leaf phenology may allow IES to take advantage of a vacant niche and canopy phenology may mediate the amount of resources available during that niche. Despite growing efforts to understand the mechanistic basis of IES success in low-light environments, relatively little is known regarding influences of overstory phenology on understory IES and NS carbon gain and physiological responses. The goal of my research was to explore the role of community-level phenological interactions in the success of IES, focusing on mechanistic causes for their hypothesized growth advantage over NS in deciduous forest understories in Connecticut.

Strong relationships characterized seasonal growth and traits associated with overstory and understory phenology, including a positive linkage with the extension of seedling leaf phenology beyond canopy leaf lifespan. Compared to NS, IES generally exhibited greater phenological extension and achieved greater seasonal growth. This advantage was most pronounced under canopies that allowed greater cumulative understory light across the growing season. After accounting for phenology, growth differences between IES and NS were explained by a number of intrinsic growth determinants, including greater specific leaf area and more efficient whole-plant photosynthesis. However, photosynthetic

capacities and their temperature responses were also temporally dependent and greater in IES than in NS during spring and summer. This contributed to a greater importance of pre-canopy periods with respect to IES growth. These findings demonstrate the significance of a community-level understanding of phenological interactions and environmental conditions in elucidating IES growth advantages over NS in deciduous forest understories.

The Role of Phenology in Invasive Plant Species Success in Temperate Forest Understories

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B.A., Colby College, **2009**

M.S., University of Connecticut, **2011**

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APPROVAL PAGE

Doctor of Philosophy Dissertation

The Role of Phenology in Invasive Plant Species Success in Temperate Forest Understories

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INTRODUCTION

Current ecological research initiative reflects concerns over the vulnerability of global ecosystems to unprecedented rates of environmental change. Among changes that are well documented worldwide and yet not fully understood are those created by the introduction of invasive exotic plant species (IES). IES 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 (NS) abundance (Alvarez & Cushman 2002; Hunter & Mattice 2002; Hulme & Bremner 2006). Studies and efforts to model exotic plant invasions often focus on species-specific traits (Baker, Baker & Stebbins 1965; Bossdorf *et al.* 2005; van Kleunen, Weber & Fischer 2010) and, more recently, site-specific factors influencing site invasibility (Gilbert & Lechowicz 2005; Leishman & Thomson 2005). One such trait is phenology – the timing of life events - , which may mediate 1) the myriad physiological, morphological, and allocational traits that allow IES to be successful outside of their native ranges (Baruch & Goldstein 1999; Feng, Wang & Sang 2007; Leishman *et al.* 2007; Cano *et al.* 2009; Schutzenhofer, Valone & Knight 2009), and 2) the environmental conditions leading to invasion vulnerability.

Phenology affects nearly all aspects of ecology and evolution, as many biological phenomena, from individual physiology to global nutrient fluxes, have annual cycles influenced by the timing of abiotic events (Forrest & Miller-rushing 2010). For plant species or communities, phenology is tied to many characteristics that are important to competitive ability, including those associated with resource availability and acquisition. Often conceptualized as a temporal niche, phenology limits species ranges (Chaine & Beaubien 2001), facilitates species coexistence (Fargione & Tilman 2005), and is adaptive (Volis 2007), making it a major indicator of community assembly, climate change (Fitter & Fitter 2002; Cleland *et al.* 2007; Sherry *et al.* 2007), and ultimately, species success. In particular, for plants, leaf budburst and abscission strongly correlate with the beginning or end, respectively, of the growing season and with a plant's temporal niche for acquiring soil and light resources (Wolkovich & Cleland 2011).

Phenology from a community perspective can indicate periods of species vulnerability to herbivory (Hunter 1990), opportunities for pollination (Kudo *et al.* 2008), and competition for resources (Davis, Grime & Thompson 2000).

There is growing recognition that distinct phenologies or phenological sensitivities of IES could facilitate their success in introduced environments (Harrington, Brown & Reich 1989; Wolkovich & Cleland 2011; Fridley 2012). IES may gain an advantage over NS by extending their leaf lifespan through earlier spring leaf flush (Harrington, Brown & Reich 1989) or delayed autumnal abscission (Zotz, Franke & Woitke 2000; Fridley 2012). In this context, phenology may be used to exploit resources through several means, including an extension of niche breadth (Richards *et al.* 2006; Wolkovich & Cleland 2011), and the occupancy of a “vacant niche” to utilize resources that are not being used by resident species (Elton 1958; Mack *et al.* 2000). Although theories regarding fluctuating resources (Davis *et al.* 2000) and “windows of invasion opportunity” (Drake *et al.* 2006; Caplat, Anand & Bauch 2010; Wolkovich & Cleland 2011) suggest that community-level phenology may play a critical role in growth success of IES, relatively little is known on this topic. Particularly in deciduous forests, where resource availabilities are low, but seasonally variable, overstory phenology may play an important role in understory survival: IES that exhibit extended leaf lifespan and photosynthetic activity in pre- and post-canopy periods may benefit from access to periods of higher resource availability and lower competition. Therefore, the role of phenology in growth advantage of IES in temperate deciduous forest understories is twofold; extended understory leaf lifespan may allow IES to take advantage of a vacant niche (Wolkovich & Cleland 2011) and community-level phenology may control the amount and fluctuation of unused resources during that niche (Davis *et al.* 2000).

In the temperate deciduous forests of New England, overstory phenology can create a complex patchwork of fluctuating resources, allowing windows of high light availability in the understory in the early spring and late autumn when the canopy is leafless. These opportunities for understory vegetation to take advantage of essential resources are critical for the persistence of understory vegetation and are

common in temperate forest seedlings (Seiwa 1998), saplings (Gill, Amthor & Bormann 1998; Seiwa 1999), understory trees (DePhamphillis & Neufeld 1989), and shrubs (Gill, Amthor & Bormann 1998). Many IES flush leaves early on in the growing season, considerably earlier than canopy and co-occurring understory NS (Harrington, Brown & Reich 1989; Schierenbeck 1992; Pattison, Goldstein & Ares 1998; Xu, Griyn & Schuster 2007), and abscise leaves later in the fall (Harrington, Brown & Reich 1989; Asshoff, Zotz & Körner 2006; Fridley 2012). For example, Japanese barberry leaves flush up to one month earlier than those of native species and two weeks earlier than do canopy leaves (Xu, Griyn & Schuster 2007). Understory light availability is considerably higher when the canopy is leafless, such that slight differences in the time of understory leaf flush can have a large effect on seasonal light absorption and carbon gain (Anderson 1964) and outweigh the consequences that come with extending leaf exposure to risk (*e.g.*, increased chance of damage by frost or herbivory) (Williams, Field & Mooney 1989; Reich 1995; Grime 2006). However, the timing of phenophases such as bud burst, leaf flush, and leaf abscission also differ among overstory tree species, and as a result, light availability is not uniform throughout the forest or within the growing season (Kato & Komiyama 2002; Dreiss & Volin 2013). As such, the potential advantage of extended leaf lifespan in the understory is mediated by composition of overstory species. Understory IES with extended leaf lifespans may gain an advantage over NS under canopies with later spring phenophases, higher light transmission, and shorter leaf lifespans.

Exploration of community-level phenology also affords investigation of critical periods of IES advantage over NS in terms of plant carbon gain. Given that conditions are favorable for photosynthesis (*e.g.*, air temperatures > 5°C), understory plants should benefit from extending leaf photosynthetic activity beyond that of canopy species and understory competitors. However, irradiance in spring is not equivalent to that in autumn as maximum incident solar radiation flux and zenith angle are larger in the spring and decline toward the winter months. This results in a greater transmission of light and a greater likelihood for photosynthetic capacity to be reached before canopy leaves flush (Richardson & O'Keefe 2009). The majority of annual carbon gained by understory vegetation is attained in early spring when

canopy trees are still leafless, allowing sub-canopy vegetation to fix a “spring carbon subsidy” (Harrington, Brown & Reich 1989; Givnish 1992; Lopez *et al.* 2008; Richardson & O ’Keefe 2009). Although post-canopy activity may not be the greatest contributor to annual carbon gain, it may be disproportionately more common in IES, potentially providing an advantage over NS in the understory (Fridley 2012). In either case, a community-level assessment of phenology, and its influence on the biomass growth and physiology responses of IES and NS, may help to elucidate the success of IES in deciduous forest understories.

Given the apparent influence of overstory phenology on understory growth, and the incomplete knowledge regarding IES and NS growth responses to seasonal light availability, the objectives of my dissertation were to evaluate the role of community-level phenology on the success of IES and the underlying mechanistic basis for IES and NS growth differences in deciduous forest understories. In Chapter One, I examined how community-level interactions in canopy phenology and understory leaf lifespans affected relative seasonal growth of IES and NS seedlings when grown over two growing seasons and under three canopy types differing in light transmission and phenology. In Chapter Two, I quantified physiological, morphological, and allocational determinants of growth to identify mechanisms of IES and NS carbon capture in low-light environments. In Chapter Three, I developed a stochastic model of photosynthesis based on physiological responses to seasonal temperature and light to examine IES and NS annual carbon gain and proportional contributions from pre- and post-canopy photosynthetic activity. Overall, I hypothesized that 1) annual carbon gain and growth of IES exceeds that of NS, 2) IES growth advantage over NS is most pronounced under canopies that allow greater understory light availability (*i.e.*, later spring phenophases, higher transmittance, and shorter leaf lifespans), 3) growth variation among IES and NS is related to differences in intrinsic growth determinants, and 4) IES advantage is more greatly influenced by spring than autumn phenological variation. Collectively, my findings stress the importance of community-level interactions mediated by the phenological structure of overstory and understory vegetation and the seasonal variation of environmental conditions for IES

growth in temperate forest understories. Furthermore, this dissertation elucidates the role of community-level predictors such as canopy species composition, plant phenology, and environmental site characteristics under different growing conditions and emphasizes their importance in understanding differences in understory growth and development between IES and NS.

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CHAPTER ONE

INFLUENCES OF OVERSTORY PHENOLOGY AND UNDERSTORY NICHE BREADTH ON GROWTH OF INVASIVE AND NATIVE SPECIES IN TEMPERATE DECIDUOUS FOREST UNDERSTORIES

ABSTRACT

When competing with native species (NS) in deciduous forest understories, invasive exotic species (IES) may benefit from extended leaf lifespan, through earlier leaf flush or delayed autumnal abscission. However, the potential advantage of extended leaf activity is mediated by overstory species composition, which determines understory light availability through canopy phenology and transmittance. I examined how community-level interactions in canopy phenology and understory leaf lifespans affect relative growth (RG) of IES and NS seedlings. Common gardens containing four IES and four NS were replicated under each of three canopy types - sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), and white ash (*Fraxinus americana*). Seasonal light availability was greatest under white ash canopies due to higher transmittance, later spring phenophases, and shorter leaf lifespans. In the understory, IES leaves generally flushed earlier and abscised later than did NS leaves, resulting in greater access to light during the growing season. As a result, IES, as a group, exhibited greater RG than did NS under all canopy types, but more so under white ash canopies. Most of the variation in IES and NS RG was explained by variation in light availability, driven by dates of canopy flush, abscission, and transmittance. These findings support the hypothesis that longer leaf lifespans afford IES a growth advantage over NS under deciduous canopies allowing greater access to light. As such, community-level phenological events are critical for mediating understory light availability and IES growth success in temperate forest understories.

ABBREVIATIONS

IES – Invasive Exotic Species;

NS – Native Species;

PAR – Photosynthetically Active Radiation;

RG – Relative Growth

INTRODUCTION

Invasive exotic plant species (IES) pose a serious threat to forest ecosystem structure and function worldwide, but the causes for success in introduced environments are often unclear. In temperate deciduous forests of eastern North America, the ability of IES to colonize understories is notable given intense competition for light and other resources. Although often referred to as highly resistant to invasion due to the deep shade cast during the growing season (Pimm 1989), interior forest understories are not without IES (Canham *et al.* 1990; Martin & Marks 2006; Dreiss & Volin 2013; Heberling & Fridley 2013). In these ecosystems, the common tendency of IES to rapidly colonize and dominate forest understories has been attributed to myriad factors (*e.g.*, Martin, Canham & Marks 2009; Funk 2013). One of several widely cited mechanisms facilitating invasion is an extended duration of annual photosynthetic activity in invasive foliage, due to early leaf flush in the spring or delayed autumnal abscission (*e.g.*, Harrington, Brown & Reich 1989; Xu, Griyn & Schuster 2007; Fridley 2012). Extended leaf lifespan commonly occurs in temperate forest seedlings (Seiwa 1998), saplings (Gill, Amthor & Bormann 1998; Seiwa 1999), understory trees (DePhamphillis & Neufeld 1989), and shrubs (Gill, Amthor & Bormann. 1998), and is particularly beneficial to understory species if it results in photosynthetic activity when the canopy is leafless. Given favorable conditions for photosynthesis (*e.g.*, air and soil temperatures $> 5^{\circ}\text{C}$), pre- and post-canopy periods of high light exposure and low competition may result in a significant amount of carbon gain for growth and survival in heavily shaded understories (Gill, Amthor & Bormann 1998; Davis *et al.* 2000; Augspurger 2008). Consequently, extended leaf lifespans allow IES to exploit resources over an extended period of time (*i.e.*, broader temporal niche; Richards *et al.* 2006) and when they are not being used by resident species (*i.e.*, vacant niche; Mack *et al.* 2000; Wolkovich & Cleland 2011).

Importantly, however, the breadth of that niche and, thus, the potential advantage in carbon gain of IES over NS in interior forest understories, is mediated by overstory canopy transmittance and phenology. Light is one of the most limiting resources for understory growth, and is a function of both

transmission (quantity and quality) and seasonality (timing of availability; *e.g.*, Anderson 1964). The importance of greater light transmission for the success of understory plants, and for IES in particular, is well documented (Pattison *et al.* 1998; Yamashita *et al.* 2000; Sanford, Harrington & Fownes 2003; Gurevitch *et al.* 2008; Knight *et al.* 2009; Schulte, Mottl & Palik 2011). However, less is known regarding overstory phenological influences on integrated light availability and their potential role in IES success (Fridley 2012; Dreiss & Volin 2013). In deciduous forests of the northeastern United States, the period of deep shade during the growing season is offset by high light transmittance prior to canopy closure in the spring and after canopy abscission in the fall. Extension of a temporal niche into pre- and post-canopy periods through early leaf flush or delayed abscission is critical for understory plants to access and assimilate light; the greater the extension of a temporal niche during favorable environmental conditions, the more carbon gained (Gill, Amthor & Bormann 1998; Davis *et al.* 2000; Augspurger 2008). In interior forest communities, however, light availability may be driven by phenological interactions among strata (Baldocchi *et al.* 1984; Kawamura *et al.* 2001). Although the growth benefits of longer leaf lifespans in the understory are clear, they may be relative: leaves that flush weeks earlier under a late-leaving canopy might only flush days earlier when under a canopy with early spring leaf phenophases.

Both transmittance and phenology differ considerably among deciduous tree species. For example, transmittance during the growing season differed from 2.6 – 7.8% of full sunlight among common overstory constituents of deciduous broadleaf forests in eastern North America, such as sugar maple, red oak, white ash, black locust, and quaking aspen (Dreiss & Volin 2013). In temperate forests, daily carbon gain by understory plants is correlated with total daily light availability, which is greatest during pre- and post-canopy periods due to the deciduous nature of the overstory (Kuppers 1984; Ellsworth & Reich 1993). Alteration of understory phenology to match these periods of high light availability results in maximum carbon gain (Iwasa & Cohen 1989; Kikuzawa 1991). However, overstory phenology also differs by species with spring leaf flush in sugar maple (*Acer saccharum*) typically occurring 1-3 weeks earlier than in red oak (*Quercus rubra*) or white ash (*Fraxinus americana*; Salisbury 1916; Lechowicz 1984; Dreiss & Volin 2013). Moreover, the latter species has a relatively short leaf

lifespan; in the fall, its canopy usually abscises at about the same time as that of sugar maple, and up to four weeks before red oak. Connecticut forests with overstories dominated by canopies allowing higher light transmittance and later spring leaf phenophases had the greatest abundance and coverage of understory IES (Dreiss & Volin 2013). These findings align with the general theory that the risk of invasion rises with increasing quantities of unused resources (Davis *et al.* 2000). Notably, phenology was more important than transmittance in determining the differences in IES and NS abundance across canopy types. Although Dreiss & Volin (2013) suggested that canopy phenology may facilitate plant invasion and establishment, continued plant success in temperate forest understories is dependent on sufficient plant growth through carbon assimilation.

My objective was to examine how community-level interactions in overstory phenology and understory leaf lifespans affect variation in relative growth (RG) of IES and NS seedlings in deciduous forest understories. I used replicated common gardens under each of three canopy cover types (*i.e.*, sugar maple, white ash, and red oak) to investigate the effects of canopy phenology, seasonality, and associated environmental conditions (*i.e.*, light availability) on growth of IES and NS in the understory. The common garden design afforded the opportunity to test mechanisms related to concepts regarding ecosystem susceptibility to species invasions; specifically, the fluctuating resource availability hypothesis (Davis *et al.* 2000), and the hypothesized importance of phenology in mediating temporal niche breadth (*e.g.*, Wolkovich & Cleland 2011). Since IES are often noted for earlier spring leaf flush and delayed abscission, my first hypothesis was that IES, occupying a broader temporal niche, would exhibit greater annual growth than that of NS in the understory. Moreover, because light is generally the greatest limiting resource for growth in temperate forest understories (*e.g.*, Finzi & Canham 2000; Zhang *et al.* 2009), my second hypothesis was that the growth advantage of IES would be most pronounced under canopies that allow greater understory light availability through higher transmittance, late spring phenophases, and short durations of leafy canopies. Finally, my third hypothesis was that contrasts between IES and NS under the three canopy types would remain consistent within and across plant functional groups of understory species.

METHODS

Study Sites

All sites were on tracts in the University of Connecticut Forest (41.80° N, 72.25° W; Fig. 1). Approximately 82 tree and shrub species are present in Connecticut, the most abundant canopy species are *Acer rubrum*, *Acer saccharum*, *Fagus grandifolia*, *Quercus alba*, and *Quercus rubra* (Wharton et al. 2004). In this region, the annual mean temperature is 8.89° C with mean January and July temperature being -3.5° C and 21.3° C, respectively. The annual mean snowfall is 109.2 cm and the total annual mean precipitation is 116.8 cm (NOAA 2010). I established three sites under each of three dominant canopy types: *A. saccharum* (sugar maple), *Q. rubra* (red oak) (n = 3), and *Fraxinus americana* (white ash) (n = 3). Together, the three canopy species represent a range in phenological traits and light transmittance (Dreiss & Volin 2013). To be considered one of the specified canopy cover types, percent canopy cover of the target species needed to exceed 70% of total overstory cover. Sites were even-aged forests greater than 75 years old (as determined from aerial photography between 1934 and 2010 from the University of Connecticut Map and Geographic Information Center: <http://magic.lib.uconn.edu/>).

Common Gardens

Common gardens containing seedlings of four IES and four NS were constructed under each of the nine sites. Gardens consisted of 4 x 4 m fenced enclosures in which 0.33 m of topsoil was excavated and replaced with a common experimental soil (5:1 volume mixture of sand and soil extracted and mixed from all forest sites). The eight understory species were chosen because they are common to the region and because they represent three functional groups: shrub, subshrub, and vine, as defined by the USDA Plant database (http://plants.usda.gov/growth_habits_def.html). The four IES included two shrubs, *Euonymus alatus* (burning bush) and *Berberis thunbergii* (Japanese barberry), a subshrub, *Rosa multiflora* (multiflora rose), and a vine, *Celastrus orbiculatus* (oriental bittersweet). Similarly, four commonly co-occurring NS included two shrubs, *Kalmia latifolia* (mountain laurel) and *Lindera benzoin* (spicebush), a

subshrub, *Rubus allegheniensis* (blackberry), and a vine, *Parthenocissus quinquefolia* (Virginia creeper). Between twenty and thirty-five individuals of each species were transplanted into each site. Individuals were collected from the field during the summer of 2013, transplanted in a stratified random manner with regards to canopy type and site, and labeled in each garden matrix (1,665 plants total). Initial plant sizes ranged from 0.02 – 0.48 g. Over the course of the study, all gardens were watered as needed to maintain field capacity and fertilized with a 15:9:12 slow-release fertilizer (The Scotts Company, Marysville, OH, USA) on a bi-monthly basis during the growing seasons.

Garden Characteristics

Critical phenophases in overstory and understory vegetation were tracked for every species with monitoring every other day in all gardens as described by Dreiss & Volin (2013). This included dates of initial and full leaf flush in spring, leaf color, and leaf abscission in fall. Chlorophyll loss was measured weekly from August to January in 2014 and 2015 using a SPAD chlorophyll meter (Konica-Minolta Laboratory USA, San Mateo, CA, USA). Garden environments were characterized through monitoring of understory photosynthetically active radiation (PAR) and air temperature at 10-minute intervals using fixed-position *Hobo* H21-002 sensors and dataloggers (Onset, Inc., Cape Cod, MA, USA) positioned at understory plant crown height.

Growth Measurements

Comparisons of annual relative growth (RG) among IES and NS seedlings under the various canopy types were based on a combination of destructive harvests and nondestructive measurements to estimate plant biomass (*i.e.*, height and diameter, *sensu* Kaelke *et al.* 2001). At the beginning of the growing season in 2014 and 2015, two leafless individuals per species were harvested in each garden, and all harvested as well as non-harvested plants were measured for stem basal diameter (D , 2 cm above the soil surface) and total height (H , from ground line to the base of the terminal bud). Nondestructive

measurements were taken again at the end of the 2014 growing season and at the beginning and end of the 2015 growing season.

Roots and shoots of harvested plants were separated, and roots were rinsed free of soil. Plant tissues were oven-dried at 70° C to a constant mass and weighed. For each species separately, regression equations were developed based on allometric measurements ($R^2 = 0.62 - 0.88$, Table S1), using data from both years, in which the total dry mass of harvested plants was regressed against a stem volume index (D^2H , cm^3) *sensu* Kaelke *et al.* (2001). Harvest data were coupled with allometric estimates of initial mass for individual seedlings in a particular year to calculate annual RG as:

$$\text{RG} = [\ln(\text{final mass}) - \ln(\text{initial mass})]$$

Data Analysis

Prior to hypothesis testing, a regression analysis was conducted to examine the influence of the natural log of initial plant mass on RG (McConnaughay & Coleman 1999; Volin, Kruger & Lindroth 2002; Kruger & Volin 2006; Soti *et al.* 2015). Regression analysis indicated a negative relationship between RG and the natural log of initial plant mass ($\text{RG} = -0.58 \cdot \ln(\text{initial mass}) - 0.64$, $P < 0.001$ for data pooled across all species and sites). Moreover, there was no significant variation in the slope of this relationship across species and sites ($P = 0.32$). Given the relationship, predicted values of RG and residuals (observed – predicted) were calculated for each seedling. RG was then adjusted based on the average initial mass of all seedlings and individual seedling residuals. Relationships between RG and other variables were analyzed using adjusted RG values.

Statistical analyses were performed using JMP v. 5.0 and SAS v. 9.3 (The SAS Institute). The total amount of potentially utilizable light available to each seedling was calculated based on its leaf flush date, abscission date, and cumulative understory PAR during that time. Dates of observed understory and overstory phenophase were also used to calculate, for each seedling, leaf lifespan and extension of temporal niche (in days) into pre- and post-canopy periods. The latter two were calculated as canopy flush

date minus seedling flush date and seedling abscission date minus canopy abscission date, respectively. To compare canopies with respect to total light availability during the growing season, understory PAR was summed for days when temperatures were favorable for photosynthesis. The total number of days for this calculation was the same for every canopy type, as there were no significant differences in understory air temperatures among canopy types (Fig. S1).

To determine differences in leaf lifespan among species ($n = 24$), IES and NS groups ($n = 6$), and functional groups ($n = 9$), foliar phenophases were compared across canopy types and years using mixed-effects, two-way ANOVAs. Statistically, values across years did not differ significantly and therefore an average across both years is reported in the results. Across species, treatment main effects and interactions were tested using analysis of variance techniques appropriate for a 3x8 factorial split-plot completely randomized design. Tukey-Kramer tests were used to determine pairwise mean differences in environmental characteristics across canopy types ($n = 3$). Within species and functional groups, treatments were tested using a randomized complete-block design. Similarly, to test for differences in growth response, RG was compared among species, IES and NS groups, and functional groups using ANOVAs. Relationships between plant growth and key environmental factors, such as total season understory PAR, were also examined with polynomial regression.

To gain a better understanding of the plant attributes and environmental factors driving differences in RG, partial correlations and partial least squares regression analyses were conducted. These determined variables useful for modeling RG responses between IES and NS groups. Predictor variables included total seasonal light, extra spring and fall days, dates of canopy phenophases (*i.e.*, leaf flush and abscission), and dates of understory phenophases (*i.e.*, budbreak, leaf flush, autumn color, and abscission). Models explaining RG of each species, pooled IES and NS groups, and pooled functional groups were analyzed. A principal components analysis (PCA) with varimax rotation provided analysis of the positions of IES and NS seedlings along indirect environmental gradients using phenological components of niche breadth *sensu* Dreiss & Volin (2013). These included extra spring and fall days, total

season light, leaf lifespan, and RG. The identity and number of principal components representing the data were those that resulted in the maximum the amount of data variability explained by the ordination.

RESULTS

Garden Environments

For both 2014 and 2015, spring and autumn phenophases, canopy light transmittance, and total light availability were significantly different among canopy types (Fig. 2). Sugar maple canopies were the first to flush leaves in the spring, followed by red oak and white ash canopies ($F_{2,8} = 53.7$, $P < 0.001$). In the fall, red oak canopies abscised 26-35 days later than did sugar maple and white ash canopies ($F_{2,8} = 42.9$, $P < 0.001$). Across the entire growing season, white ash understories had access to significantly more PAR ($2,229 \pm 57 \text{ mol m}^{-2}$) than did understories of red oak ($1,926 \pm 54 \text{ mol m}^{-2}$), each of which was significantly greater than in sugar maple understories ($1,593 \pm 61 \text{ mol m}^{-2}$; $F_{2,8} = 30.6$, $P < 0.001$). For white ash, this was in part due to higher transmittance when canopies were fully flushed, with $3.9 \pm 0.5\%$ of full sunlight reaching the understory during midday, which was significantly higher than that in red oak ($2.6 \pm 0.3\%$) and sugar maple ($2.1 \pm 0.2\%$) canopies, and allowed for more total seasonal light in the understory when canopies were flushed ($F_{2,8} = 25.8$, $P = 0.001$). Air temperature did not significantly differ across canopy types at any point in the growing season (Fig. S1).

Understory Phenology

In general, understory vegetation flushed earlier than the corresponding overstory (Fig. 2, Table 1). The exceptions were three of the four NS growing under sugar maple canopies (Fig. 2). Leaf flush for some IES (*i.e.*, *Berberis thunbergii*, *Euonymus alatus*, and *Rosa multiflora*) and the NS subshrub (*i.e.*, *Rubus alleghiensis*) was, on average, two weeks earlier than canopy leaf flush. Understory vegetation also abscised significantly later than canopies of white ash and sugar maple ($P < 0.001$ for each), but not red oak ($P = 0.83$) (Fig. 2, Table 1). In some cases understory seedlings did not drop their leaves until more than five weeks after canopy abscission.

In general, regardless of canopy type, leaves of IES seedlings flushed earlier, abscised later, and began losing chlorophyll later than NS seedlings ($P < 0.001$ for each, Figs. S2 & S3). As such, IES foliage was photosynthetically active for more of the pre- and post-canopy periods and exhibited significantly greater temporal niche breadth than NS foliage ($t_{1162} = 16.5$, $P < 0.001$). This resulted in IES seedlings having the potential to utilize substantially more light over the growing season under all three canopy types ($F_{1,2} = 237.9$, $P < 0.001$, Table 1).

Principal components analysis of phenological niche variation produced three significant axes. Principal component 1, which explained 56% of the variance, scaled positively with the total amount of potentially utilizable light and leaf lifespan, representing a gradient from more to less utilizable light available (Fig. 3). Component 2 accounted for 18% of the variance in environmental data, and scaled positively with the number of days the niche extended into post-canopy periods. Component 3 represented extension into pre-canopy periods and RG, and explained 17% of the variance. The IES-NS dichotomy strongly followed the indirect environmental gradient represented by all three principal components: seedlings that had access to more light and a higher RG, due to greater extension into pre- and post-canopies, were mostly IES.

Subshrubs flushed, on average, 8-11 days earlier and abscised 6-13 days later than did shrubs ($t_{818} = -3.91$ and 3.43 , respectively, $P < 0.001$ for each), and respective phenophases of which the latter were 7-10 days earlier and 5-10 days later than vines ($t_{950} = -10.7$ and 7.33 respectively, $P < 0.001$ for each) (Table 1). Vine species flushed last and began chlorophyll loss and abscission first, resulting in significantly shorter niche breadth ($F_{2,1} = 24.2$, $P < 0.001$) and less access to total season light ($F_{2,1} = 29.5$, $P < 0.001$) (Fig. S3).

Relative Growth

Across all canopy types, the average annual RG of IES, as a group, was significantly higher than that of NS ($t_{1163} = 8.33$, $P < 0.001$; Table 2, Fig. 4). Across functional groups and canopies, subshrub RG exceeded vine RG ($F_{1,2} = 10.7$, $P < 0.001$), which, in turn, was greater than shrub RG ($F_{1,2} = 16.7$, P

<0.001). However, when comparing functional groups within canopies, there was no significant difference in RG between subshrubs and vines under sugar maple and red oak canopies, although in all cases subshrubs and vines grew faster than shrubs (Table 2). Within each functional group, annual RG of IES was greater than the corresponding NS for shrubs and vines, except for shrubs growing in the relatively deep shade created by the sugar maple canopies (Fig. 4). In contrast, IES and NS subshrubs were not significantly different except under the higher light environment afforded by the white ash canopies, where the IES subshrub had a significantly greater RG than the NS subshrub (Fig. 4).

Annual growth for each species was positively correlated with the total amount of utilizable light ($R = 0.38 - 0.70$ depending on the species, $P < 0.001$ for each). Across canopy types, relationships between RG and light availability were quadratic (Fig. 5). Regression lines were significantly steeper for NS growth under white ash compared to sugar maple ($P_{b1} = 0.04$) and for IES growth under white ash compared to sugar maple ($P_{b1} = 0.03$) and red oak ($P_{b2} = 0.01$) canopies (Fig. 5). After total light, extra post-canopy days, the date of canopy abscission, and the date of canopy flush explained the most growth variation in IES, though these relationships varied with canopy type (Table 3). Similarly, total light available explained the most variation in NS RG, followed by canopy dates of full flush and abscission. Overall, models were able to explain a greater amount of variation in IES growth ($R^2 = 0.26 - 0.52$) than NS growth ($R^2 = 0.25 - 0.30$), with the highest amount of growth variation for both groups explained under white ash canopies (Table 3). Species-specific models varied slightly and explained 34 – 67% of the variation in annual RG (Table S2). Among functional groups, annual growth variation of subshrubs was explained the least (shrub $R^2 = 0.58$; vine $R^2 = 0.69$; subshrub $R^2 = 0.34$, Table S3).

DISCUSSION

I analyzed the responses of IES and NS growth to understory light availability mediated by phenological interactions between overstory and understory vegetation. The results supported my first hypothesis that IES exhibiting greater temporal niche breadth achieve greater RG than do NS.

Furthermore, in support of my second hypothesis, this difference was greatest under white ash canopies, which allowed for higher light availability (*i.e.*, greater light transmission, later spring phenophases, and shorter leaf lifespans). This is the first study to incorporate a) direct measures of biomass production (*i.e.*, destructive harvests) and b) overstory phenology in an assessment of extended leaf lifespan as a mechanism for IES growth advantage over NS in temperate deciduous forest understories. In doing so, I emphasized the significance of canopy phenological structure and understory leaf lifespans in IES and NS growth differences. As such, inclusion of information regarding canopy composition may result in a greater understanding of invasion success in interior forest communities.

Light availability is a dynamic property of forest understories (Perkins, Johnson & Nowak 2011), as is evidenced by the differential canopy phenology and transmission among overstory canopies. Across the growing season, white ash understories received the greatest amount of light, due to higher light transmission when canopy leaves were present and relatively shorter leaf lifespans (*i.e.*, later spring and earlier fall phenophases). The positive effects of higher light transmission on plant growth and development are well documented, with plants often exhibiting greater photosynthetic capacity, RG, and biomass production with increasing light availability (Pattison *et al.* 1998; Baruch, Pattison & Goldstein 2000; Meekins & McCarthy 2000; Athanasiou *et al.* 2010). Seasonal dynamics of light as a result of different plant phenologies, however, are less studied. Windows of opportunity for access to high light during pre-canopy leaf flush and post-canopy abscission also differ among canopy species and may be exploited by understory species through several means including extended temporal niche breadth, (Richards *et al.* 2006; Wolkovich & Cleland 2011), and occupying a “vacant niche” to utilize resources not being used by resident species (Elton 1958; Mack *et al.* 2000). In this study, IES leaf lifespan was extended through earlier spring phenophases (*i.e.*, budbreak; Xu, Griyn & Schuster 2007; Mcewan *et al.* 2009, and leaf flush; Harrington, Brown & Reich 1989) and delayed autumnal abscission (Harrington, Brown & Reich 1989; Zotz *et al.* 2000; Fridley 2012), resulting in a broader temporal niche for carbon acquisition (Uemura 1994) and access to vacant niches in spring and autumn. All IES flushed leaves

earlier than the three canopy species, thereby gaining access to unused resources; a fundamental premise of many hypotheses characterizing IES success and plant community susceptibility (Elton 1958; Harrington, Brown & Reich 1989; Davis *et al.* 2000; Mack *et al.* 2000; Shea & Chesson 2002; Wolkovich & Cleland 2011). However, because of delayed leaf flush relative to IES, NS were generally not able to take advantage of shorter windows of high light availability under sugar maple canopies. Almost all IES and NS species extended leaf lifespan beyond that of white ash and sugar maple, but not red oak canopies. However, annual RG was still significantly greater under red oak than sugar maple canopies, suggesting that the later spring flush and higher light transmission in red oak canopies provided a greater opportunity for understory species to gain carbon than the autumn window of high light available to those growing under sugar maple. Across canopies, white ash, which provided larger windows of high light availability in both spring and autumn as well as greater canopy transmittance when the canopy was fully flushed compared to either sugar maple or red oak, resulted in greater carbon gain for all understory species.

IES exhibited greater RG than did NS regardless of canopy type or understory seasonal light availability. This is consistent with shade house studies that have found RG to increase with higher light availability regardless of species or growth form (Reich *et al.* 1998; Toledo-Aceves & Swaine 2008). Plant growth and carbon gain is the result of a combination of many physiological, morphological, and biochemical growth determinants (Blackman 1919; Lambers & Poorter 1992; Kruger & Volin 2006). Consequently, IES success may be attributed to a wide variety or combination of traits. Previous studies have investigated these traits in attempts to identify plant invasiveness (Daehler 2003; Pyšek and Richardson 2008; Pyšek *et al.* 2009; Soti & Volin 2010; Volin *et al.* 2010) and environmental impact (Ehrenfeld 2010; Pyšek *et al.* 2012). Although all indicate that no single trait or group of traits completely explain IES success, IES are often noted for having higher values than NS with respect to traits associated with high performance (Van Kleunen *et al.* 2010). Moreover, these differences are species-specific and depend on environmental factors (Pyšek *et al.* 1995; Alpert, Bone & Holzapfel 2000; Daehler 2003; Pyšek and Richardson 2008; Tecco *et al.* 2010). Relative growth rates, in particular, are used as a performance indicator, as higher RG is related to fitness and often contributes to a successful competitive

strategy: plants are able to establish faster and outcompete neighbors for resources (Leicht & Silander 2006; Zheng *et al.* 2009; Matzek 2011). For seedlings, a small statistical difference in RG can have profound fitness implications in the early period of establishment and development (Walters & Reich 2000). Previous studies have noted higher RG in IES compared to NS regardless of irradiance levels (Pattison *et al.* 1998; Zheng *et al.* 2009, 2012) and under higher-resource conditions (Forcella, Wood & Dillon 1986; Burns 2004, 2006; Wilson, Wilson & Albano 2004; Garcia-Serrano *et al.* 2005; Gurevitch *et al.* 2008). However, while IES have commonly been studied in resource-rich environments, such as disturbed areas or edge habitats, invasion into light-limited interior forests is also relatively common (Canham *et al.* 1990; Martin & Marks 2006; Funk & Vitousek 2007). Therefore, the notion that IES, which are often characterized as fast-growing, resource-demanding species, are less likely to persist in low-resource habitats has been challenged in recent years (see Funk 2013 review).

In resource poor environments, longer leaf lifespans and more efficient use of resources may be more successful strategies than fast growth (Funk & Vitousek 2007; Coste *et al.* 2011; Matzek 2011; Heberling & Fridley 2013, 2016). Leaf lifespans represent a balance between construction and maintenance costs of a leaf across its lifetime and the time required to compensate for those costs through carbon gain (Chabot & Hicks 1982). Under shaded conditions, leaf lifespan increases as retaining leaves for longer time periods maximizes photosynthetic gains per unit of resource invested in leaf construction (Givnish 1988; Poorter *et al.* 2006). As such, longer leaf lifespans are generally associated with resource conservation, large investments in non-photosynthetic leaf structures, and slower plant growth, potentially resulting in lower RG, but higher resource use efficiencies. Funk & Vitousek (2007) found evidence of greater light-use efficiency in IES, suggesting IES outperform NS in shaded environments. However, the significance of resource conservation to IES success may be magnified when integrating instantaneous measures of resource-use efficiency over leaf lifespans characteristic of the temperate deciduous species used in this study (Heberling and Fridley 2013). This study focused on traits related to carbon gain, including phenological traits and RG, all of which are related to IES performance (Harrington, Brown &

Reich 1989; Pattison *et al.* 1998; Smith & Knapp 2001a; Gandiaga *et al.* 2009; Volin *et al.* 2010). IES may benefit from traits attributed to successful competition in both high- and low-resource environments, as they overall had greater RG and longer leaf lifespans.

With the exception of subshrubs growing under sugar maple and red oak canopies, my third hypothesis, that trends between IES and NS under the three canopy types will remain consistent within and across plant functional groups, was supported. For vines and shrubs, IES exhibited greater leaf lifespans than did NS, resulting in greater RG under all canopies for vines and under canopies with later spring phenophases (*i.e.*, red oak and white ash) for shrubs. However, IES and NS subshrubs showed no significant differences in growth except under white ash canopies. Although specific data on leaf lifespans for functional groups is limited, previous studies note greater RG in IES over NS for both vines (Leicht-Young, Silander & Latimer 2007; Fridley 2012) and shrubs (Fogarty & Facelli 1999; Grotkopp & Rejmánek 2007; Zou, Rogers & Siemann 2007; Gurevitch *et al.* 2008; te Beest, Esler & Richardson 2015). In my study, subshrubs were represented by one IES and one NS, both within the Rosaceae family. These two species did not differ in leaf lifespan or RG, similar to a previous comparison of an IES and NS in the Rosaceae family (Gurevitch *et al.* 2008). However, IES advantages over NS may be intensified with relative increases in resource availability (Daehler 2003), as was exemplified in my study by a greater RG in IES than NS subshrub under the higher light conditions afforded by the white ash canopy. Data from Heberling & Fridley (2013) (calculated from their supplementary information) also support the connection between differences in leaf lifespan and, subsequently, growth as IES and NS vines from their study did not exhibit a significant difference in leaf lifespan or carbon gain, while IES of shrub, were significantly greater than NS of shrub in terms of both. Similar to this study, these data also showed that shrub leaf lifespans were greater than those of vines, but carbon gain was not, suggesting another mechanism in vine success in temperate forest understories. One possibility is greater photosynthetic rates as these tend to be negatively correlated with leaf lifespan within and across plant functional groups (Reich, Walters & Ellsworth 1992; Wright *et al.* 2004) and positively correlated with higher RG, which is often greater in vines than in shrubs (Cornelissen, Castro Diez & Hunt 1996). Although data on

chlorophyll loss suggest that shrubs may be photosynthetically active later in the autumn compared to the situation in vines, further study is needed to determine the physiological differences in leaf activity between IES and NS, especially under different canopy types. A study that includes several species within each functional group would help to elucidate possible intrinsic differences among functional groups in regard to IES and NS.

Cumulative access to light across the growing season was most significant in explaining variation in growth for all understory species. Although previous studies confirm that light transmission accounts for a significant amount of the variation in understory growth (Pacala *et al.* 1994; Kobe *et al.* 1995; Finzi & Canham 2000), fewer studies recognize the role of phenology in seasonal light capture and availability (Kloeppel & Abrams 1995; Maeno & Hiura 2000). In this study, both the number of “extra” spring days and “extra” fall days were indicative of greater RG and IES advantage. However, while pre- and post-canopy conditions provide ample understory light, these periods may not be equal in their contributions to annual carbon gain. The potential for phenological extension of photosynthetic activity into pre- and post-canopy periods to enhance carbon gain depends on the amount of irradiance and plant physiological capacity during these periods. Irradiance in spring and autumn is not equivalent (Hutchison & Matt 1977; Gill, Amthor & Bormann 1998), with higher solar elevation angles in the spring resulting in greater light transmission through the overstory (Baldocchi *et al.* 1984; Constabel & Lieffers 1996). Higher light environments are matched by larger leaf areas and higher chlorophyll activities in the spring although these may differ among species (Harrington, Brown & Reich 1989; Reich *et al.* 1992; Gill, Amthor & Bormann 1998; Königer, Harris & Kibler 2000; Morecroft, Stokes & Morison 2003). Later autumnal abscission may result in late season respiratory losses that exceed carbon gains (Piao *et al.* 2008) or negative effects on nutrient retranslocation and storage, and thus on future growth (Killingbeck, May & Nyman 1990; Niinemets & Tamm 2005; Weih 2009). Either might explain why some studies report no extension of temporal niche breadth of understory species after canopy abscission (DePhamphillis & Neufeld 1989; Gill, Amthor & Bormann 1998; Augspurger & Bartlett 2003; Augspurger, Cheeseman & Salk 2005). In contrast, recent work by Fridley (2012) suggests that while post-canopy activity may not

be the greatest contributor to annual carbon gain, it was disproportionately more common in IES, providing an advantage over NS in the understory. A companion study to my project explored the relative importance of pre-, during- and post-canopy periods on photosynthetic capacity and temperature response of IES and NS, and found that IES indeed gained more carbon than did NS under canopies that allowed greater understory light through later spring phenophases, shorter leaf lifespans and higher transmittance (see Chapter 3). Thus, the role of community-level phenology in IES growth advantage in temperate forest understories is a significant one driven by the ability of IES to take advantage of a greater niche breadth and a vacant niche (Wolkovich & Cleland 2011).

My study stresses the importance of canopy-understory phenological interactions in IES growth and access to light in temperate deciduous forest understories. IES exhibited longer leaf lifespans than did NS, allowing for significantly more access to light during the growing season and, subsequently, greater RG. This advantage was pronounced under canopies that had larger windows of high light availability in the spring or autumn or greater light transmission during periods when canopy leaves were present. Previous research emphasizes the importance of resource availability in plant invasions (*e.g.*, Burke & Grime 1996; Davis *et al.* 2000; Leishman, Thomson & Cooke 2010). However, this study demonstrates the importance of systematic differences in overstory phenology to IES growth success in resource-poor temperate deciduous forest understories. As growing evidence suggests that future climate trends will lead to changes in both temperature and phenology (Bradley *et al.* 1999; Walther *et al.* 2002; Menzel *et al.* 2006), the incorporation of key seasonal factors determining invasive growth advantage will be fundamental to understanding the ecology of a changing world. My results elucidate the role of complex community-level predictors such as canopy species composition, plant phenology, and environmental site characteristics in understory growth and IES success. IES exhibit greater niche breadth and RG than do NS under canopies with higher light transmission, later spring phenophases, and shorter leaf lifespans. This may help land managers to prioritize areas for future management activities. Given the apparent influence of overstory phenology on IES and the potential for future climate-driven phenological shifts,

further study should focus on IES and NS growth response to warming under varying phenological conditions.

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TABLES

Table 1. Average (\pm SE) phenological extension (in days) and total amount of utilizable light (mol m^{-2}) available to four invasive exotic species (IES) and four native species (NS) grown under three canopy types during the seasons of 2014 and 2015. Extra days refer to the number of days a seedling was active prior to canopy leaf flush (spring) and after canopy abscission (autumn). Different letters within a row denote significant differences among canopy types at $P < 0.05$. One-way ANOVAs compare variables across species, IES and NS groups and functional groups within a canopy type, where site was a random effect. All ANOVAs are significant at $P < 0.001$ (***).

		Sugar Maple (<i>Acer saccharum</i>)	Red Oak (<i>Quercus rubra</i>)	White Ash (<i>Fraxinus americana</i>)
		“Extra” Spring Days†		
Group	Species			
	IES			
Shrub	<i>Berberis thunbergii</i>	9.3 \pm 1.0 ^b	22.9 \pm 1.0 ^a	24.9 \pm 1.2 ^a
Shrub	<i>Euonymus alatus</i>	9.2 \pm 0.6 ^b	23.6 \pm 0.8 ^a	23.4 \pm 0.6 ^a
Subshrub	<i>Rosa multiflora</i>	10.7 \pm 1.3 ^b	24.7 \pm 1.4 ^a	26.5 \pm 1.3 ^a
Vine	<i>Celastrus orbiculatus</i>	0.5 \pm 0.7 ^b	13.7 \pm 0.9 ^a	13.6 \pm 0.7 ^a
	NS			
Shrub	<i>Lindera benzoin</i>	-1.4 \pm 1.1 ^b	11.1 \pm 1.2 ^a	10.4 \pm 1.0 ^a
Shrub	<i>Kalmia latifolia</i>	-0.5 \pm 2.3 ^b	13.7 \pm 2.0 ^a	15.9 \pm 1.9 ^a
Subshrub	<i>Rubus alleghiensis</i>	8.0 \pm 0.9 ^c	22.7 \pm 1.2 ^a	17.4 \pm 0.9 ^b
Vine	<i>Parthenocissus quinquefolia</i>	-6.4 \pm 1.0 ^b	5.6 \pm 1.3 ^a	7.4 \pm 0.9 ^a
IES		6.5 \pm 0.5 ^b	21.6 \pm 0.6 ^a	20.5 \pm 0.5 ^a
NS		-0.4 \pm 0.6 ^b	13.4 \pm 0.8 ^a	11.6 \pm 0.7 ^a
ANOVA		***	***	***
		IES>NS	IES>NS	IES>NS
Shrub		6.3 \pm 0.5 ^b	20.0 \pm 0.6 ^a	19.5 \pm 0.6 ^a
Subshrub		9.4 \pm 0.8 ^c	24.8 \pm 1.1 ^a	21.5 \pm 1.0 ^b
Vine		-1.6 \pm 0.6 ^b	11.0 \pm 0.9 ^a	11.6 \pm 0.8 ^a
ANOVA		***	***	***
		SS>S>V	SS>S>V	SS>S>V
		“Extra” Autumn Days††		
Group	Species			
	IES			
Shrub	<i>Berberis thunbergii</i>	31.1 \pm 1.5 ^a	5.6 \pm 1.9 ^b	30.5 \pm 1.4 ^a
Shrub	<i>Euonymus alatus</i>	37.8 \pm 1.2 ^a	9.7 \pm 1.6 ^b	39.5 \pm 1.3 ^a
Subshrub	<i>Rosa multiflora</i>	36.9 \pm 2.8 ^a	10.7 \pm 3.2 ^b	35.1 \pm 2.5 ^a
Vine	<i>Celastrus orbiculatus</i>	26.9 \pm 0.7 ^a	-1.8 \pm 1.0 ^b	25.2 \pm 0.7 ^a
	NS			
Shrub	<i>Lindera benzoin</i>	19.2 \pm 1.9 ^a	-10.2 \pm 2.3 ^b	15.7 \pm 1.8 ^a
Shrub	<i>Kalmia latifolia</i>	28.6 \pm 2.9 ^a	9.3 \pm 2.4 ^b	30.5 \pm 2.6 ^a
Subshrub	<i>Rubus alleghiensis</i>	41.3 \pm 1.6 ^a	12.4 \pm 1.8 ^c	35.8 \pm 1.6 ^b
Vine	<i>P. quinquefolia</i>	13.1 \pm 0.9 ^a	-17.6 \pm 1.2 ^c	9.9 \pm 1.0 ^b
IES		32.8 \pm 0.8 ^a	5.7 \pm 1.2 ^b	32.6 \pm 0.7 ^a
NS		23.9 \pm 1.2 ^a	-3.1 \pm 1.5 ^b	20.6 \pm 1.0 ^a
ANOVA		***	***	***
		IES>NS	IES>NS	IES>NS
Shrub		31.4 \pm 0.9 ^a	3.8 \pm 1.2 ^b	30.8 \pm 0.8 ^a
Subshrub		39.1 \pm 1.5 ^a	11.4 \pm 2.0 ^b	35.4 \pm 1.4 ^a
Vine		22.7 \pm 1.1 ^a	-7.0 \pm 1.7 ^b	20.3 \pm 1.1 ^a
ANOVA		***	***	***
		SS>S>V	SS>S>V	SS>S>V

		Total Available Light (mol m ⁻²)		
Group	Species			
Shrub	IES			
	<i>Berberis thunbergii</i>	1013±29 ^b	1196±26 ^a	1261±35 ^a
Shrub	<i>Euonymus alatus</i>	1288±17 ^b	1297±23 ^b	1417±16 ^a
Subshrub	<i>Rosa multiflora</i>	1298±32 ^b	1332±35 ^{ab}	1486±28 ^a
Vine	<i>Celastrus orbiculatus</i>	994±17 ^b	988±18 ^b	1209±25 ^a
	NS			
Shrub	<i>Lindera benzoin</i>	837±25 ^b	905±32 ^{ab}	918±27 ^a
Shrub	<i>Kalmia latifolia</i>	1047±58 ^a	1066±67 ^a	1115±57 ^a
Subshrub	<i>Rubus alleghiensis</i>	1114±27 ^b	1277±27 ^{ab}	1281±33 ^a
Vine	<i>P. quinquefolia</i>	694±22 ^b	761±30 ^{ab}	792±23 ^a
IES		1177±13 ^b	1196±15 ^b	1323±18 ^a
NS		933±19 ^b	981±21 ^a	997±24 ^a
ANOVA		***	***	***
		IES>NS	IES>NS	IES>NS
Shrub		1152±17 ^a	1173±14 ^a	1172±18 ^a
Subshrub		1284±28 ^b	1288±24 ^b	1340±30 ^a
Vine		894±22 ^a	931±18 ^a	928±26 ^a
ANOVA		***	***	***
		SS>S>V	SS>S>V	SS>S>V

† Calculated as [Julian Date Canopy Flush] – [Julian Date Seedling Flush]

†† Calculated as the [Julian Date Seedling Abscission] – [Julian Date Canopy Abscission]

Table 2. Average (\pm SE) relative growth ($\text{g g}^{-1} \text{yr}^{-1}$) measured for four invasive exotic species (IES) and four native species (NS) under three canopy types pooled by species group and functional group over two growing seasons. Different letters within a row denote significant differences among canopy types at $P < 0.05$. One-way ANOVAs compare variables across species groups within a canopy type, where site was a random effect. In comparing growth across all canopy types, interactions between canopy type and species group from mixed model, two-way ANOVAs are also included.

		Sugar Maple (<i>Acer saccharum</i>)	Red Oak (<i>Quercus rubra</i>)	White Ash (<i>Fraxinus americana</i>)	Average
	Species	Relative Growth ($\text{g g}^{-1} \text{yr}^{-1}$)			
	IES				
Shrub	<i>Berberis thunbergii</i>	0.35 \pm 0.13 ^b	0.69 \pm 0.15 ^b	1.23 \pm 0.14 ^a	0.91 \pm 0.08
Shrub	<i>Euonymus alatus</i>	0.58 \pm 0.06 ^b	0.80 \pm 0.08 ^b	1.11 \pm 0.06 ^a	0.84 \pm 0.06
Subshrub	<i>Rosa multiflora</i>	0.94 \pm 0.26 ^b	1.08 \pm 0.14 ^b	1.94 \pm 0.18 ^a	1.43 \pm 0.09
Vine	<i>Celastrus orbiculatus</i>	0.74 \pm 0.06 ^b	1.39 \pm 0.09 ^a	1.41 \pm 0.07 ^a	1.13 \pm 0.06
	NS				
Shrub	<i>Lindera benzoin</i>	0.36 \pm 0.1 ^a	0.47 \pm 0.13 ^a	0.79 \pm 0.09 ^a	0.54 \pm 0.08
Shrub	<i>Kalmia latifolia</i>	0.58 \pm 0.07 ^b	0.61 \pm 0.08 ^b	0.71 \pm 0.07 ^a	0.63 \pm 0.14
Subshrub	<i>Rubus alleghiensis</i>	0.71 \pm 0.22 ^b	0.89 \pm 0.26 ^{ab}	1.66 \pm 0.22 ^a	1.07 \pm 0.1
Vine	<i>Parthenocissus quinquefolia</i>	0.21 \pm 0.07 ^b	0.27 \pm 0.05 ^{ab}	0.43 \pm 0.05 ^a	0.32 \pm 0.09
Species Group					
Overall IES		0.89 \pm 0.07 ^b	1.11 \pm 0.04 ^a	1.16 \pm 0.09 ^a	1.03 \pm 0.04
Overall NS		0.39 \pm 0.1 ^a	0.57 \pm 0.06 ^a	0.61 \pm 0.12 ^a	0.51 \pm 0.05
Summary of ANOVA					
Canopy					**
Group		***	***	***	***
Canopy*Group					NS (0.94)
Direction		IES>NS	IES>NS	IES>NS	IES>NS
Functional Group					
Shrubs (S)		0.54 \pm 0.06 ^b	0.65 \pm 0.06 ^b	0.87 \pm 0.06 ^a	0.7 \pm 0.04
Subshrubs (SS)		0.81 \pm 0.17 ^b	1.03 \pm 0.13 ^b	1.79 \pm 0.12 ^a	1.27 \pm 0.07
Vines (V)		0.80 \pm 0.13 ^a	1.10 \pm 0.11 ^a	1.25 \pm 0.14 ^a	1.07 \pm 0.05
Summary of ANOVA					
Canopy					**
Group		*	***	***	***
Canopy*Group					***
Direction		SS=V>S	SS=V>S	SS>V>S	SS>V>S

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$

Table 3. Regression models using significant environmental and phenological site variables (as indicated in a stepwise regression) to explain the empirical variation in relative annual growth ($\text{g g}^{-1} \text{yr}^{-1}$) for invasive exotic species (IES) and native species (NS) grown under three different canopy types; sugar maple (*Acer saccharum*), red oak (*Quercus rubra*) and white ash (*Fraxinus americana*).

Variable	R ²	P for the factor	P for the model
Sugar Maple			
IES	0.26		<0.001
Total Available Light		<0.001	
Seedling 50% Abscission		<0.001	
NS	0.25		<0.001
Total Available Light		<0.001	
Seedling 50% Abscission		0.006	
Red Oak			
IES	0.31		<0.001
Total Available Light		<0.001	
Extra Fall Days		<0.001	
Canopy Flush Date		0.007	
Seedling 50% BudBreak		0.002	
Canopy Drop Date		0.01	
NS	0.24		<0.001
Total Available Light		<0.001	
Canopy Flush Date		0.05	
Canopy Drop Date		0.10	
White Ash			
IES	0.52		<0.001
Total Available Light		<0.001	
Canopy Flush Date		<0.001	
Seedling 50% Abscission		0.005	
NS	0.30		<0.001
Total Available Light		<0.001	
Extra Spring Days		<0.001	
Canopy Flush Date		<0.001	

FIGURE LEGENDS

Figure 1. Nine common garden sites located in Storrs, Connecticut, USA. Sites were constructed under canopies of white ash (*Fraxinus americana*, black circles), sugar maple (*Acer saccharum*, white circles), and red oak (*Quercus rubra*, grey circles).

Figure 2. Average (\pm SE) photosynthetically active radiation (PAR) available to the understory of white ash (*Fraxinus americana*, red line), sugar maple (*Acer saccharum*, blue line), and red oak (*Quercus rubra*, green line) stands across the 2014 and 2015 growing seasons ($n = 3$ for all three canopy species). Horizontal bars represent average leaf lifespan of four invasive exotic understory species (IES) and four native species (NS) and whiskers represent the dates of the first seedling flushed and the last seedling abscised for each species or group. Darker bars indicate IES and lighter bars indicate NS. Full species names are the same as in Table 1.

Figure 3. Principal component analysis of four invasive exotic species (IES, $n = 872$) and four native species (NS, $n = 793$) grown in common gardens under three canopy types varying in leaf phenology, using variables based on seedling and canopy leaf phenologies (see Table 1 for species names and canopy types). For each seedling these included its leaf lifespan, the number of pre- and post- canopy days incorporated in leaf lifespan (extra spring and fall days, respectively), the availability of utilizable light (Total Season Light), and annual relative growth (RG). Each point represents the average of 2014 and 2015 measurements taken on IES (black circles) and NS (grey circles) seedlings. Vectors represent the strength and direction of the relationship between seedling positions and phenological variables.

Figure 4. Averages (\pm SE) for annual relative growth ($\text{g g}^{-1} \text{yr}^{-1}$) measured for three functional groups under stands of white ash (*Fraxinus Americana*, red), sugar maple (*Acer saccharum*, blue), and red oak (*Quercus rubra*, green) during the growing seasons of 2014 and 2015. Labels on the x-axis also note the native status and functional group of each species. Different letters denote significant differences between invasive (IES) and native (NS) species for each combination of functional group and canopy type at $P <$

0.05. One-way ANOVAs compared variables across IES and NS groups and functional groups within a canopy type, where site was a random effect.

Figure 5. Quadratic regressions relating relative growth of seedlings with the total amount of utilizable light available to them given their leaf phenology and growing conditions. Each point represents the average of 2014 and 2015 measurements taken on each seedling by the canopy type under which they were grown (red circles = white ash, blue circles = sugar maple, and green circles = red oak). Regression lines represent relationships for invasive exotic species (IES, solid lines) and native species (NS, dashed lines) coded by canopy type.

Figure 1

FIGURES



Figure 2

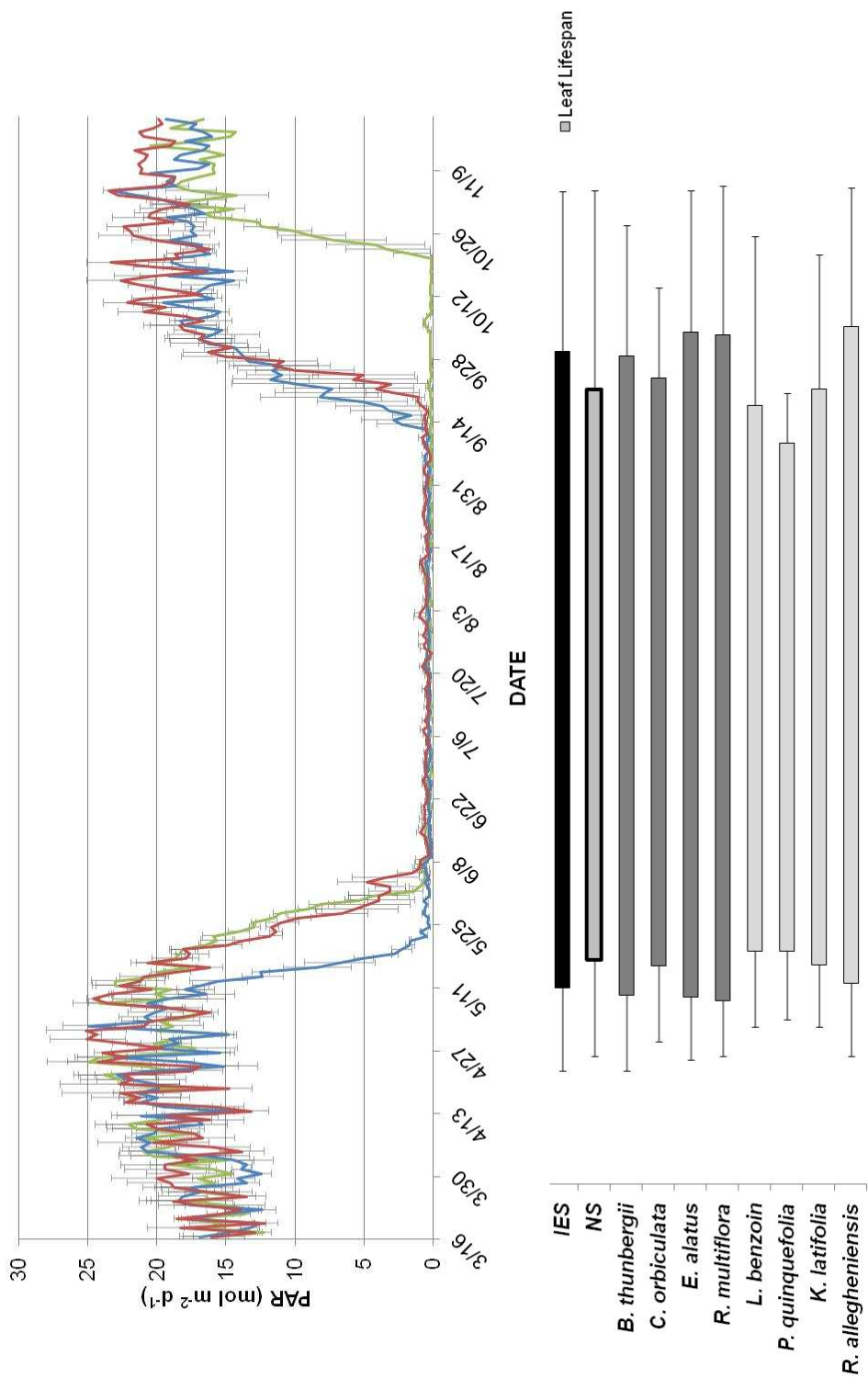


Figure 3

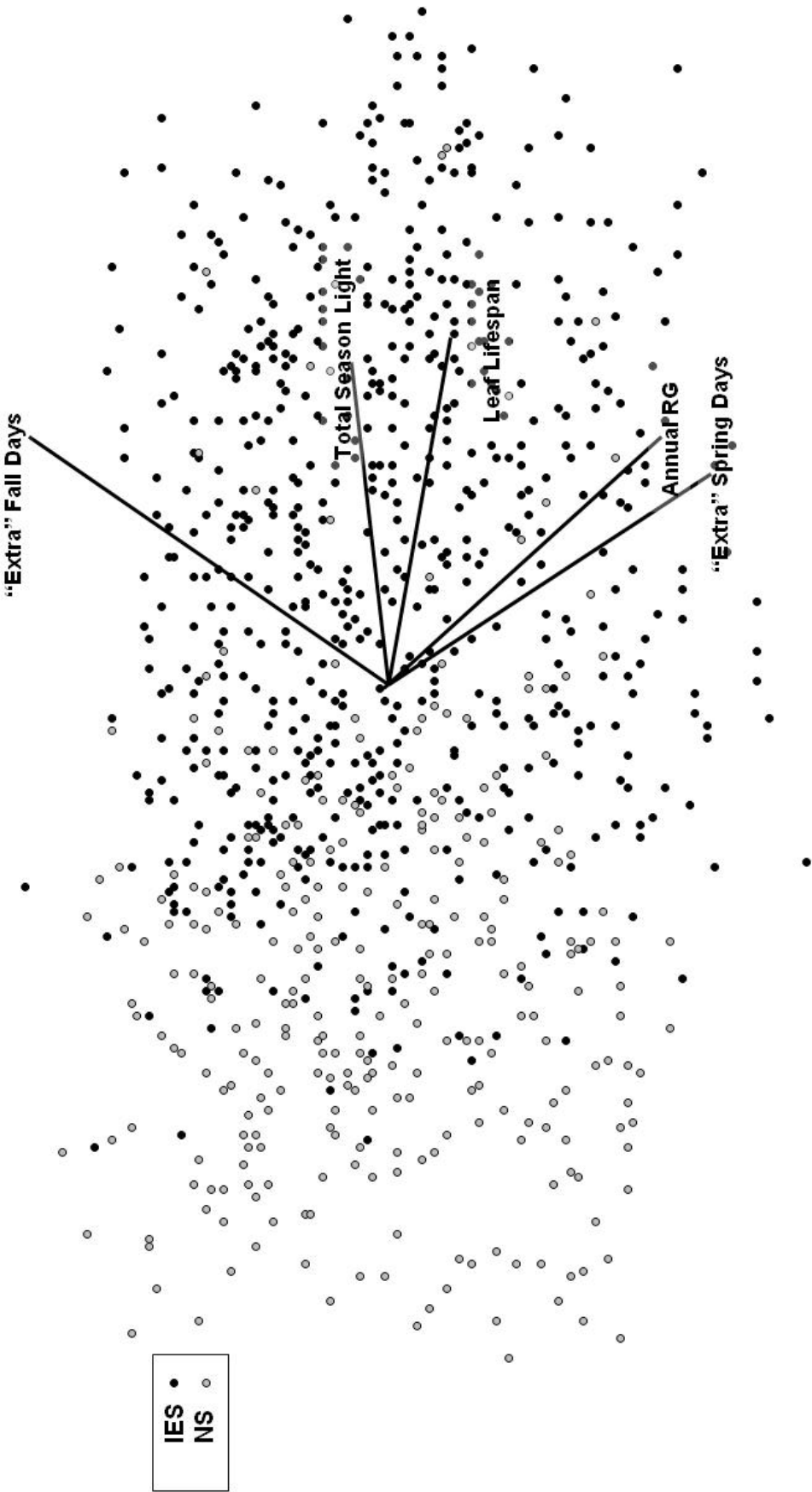
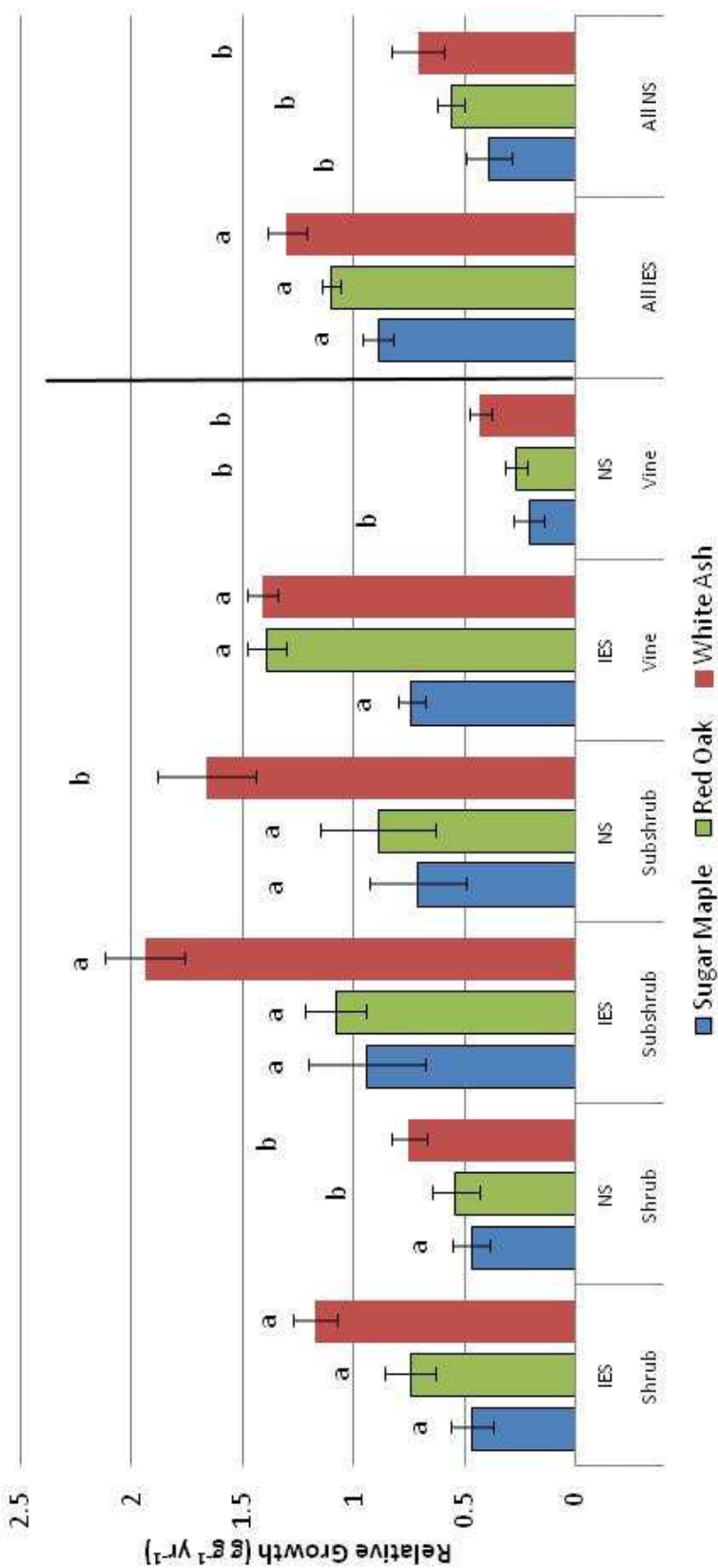


Figure 4



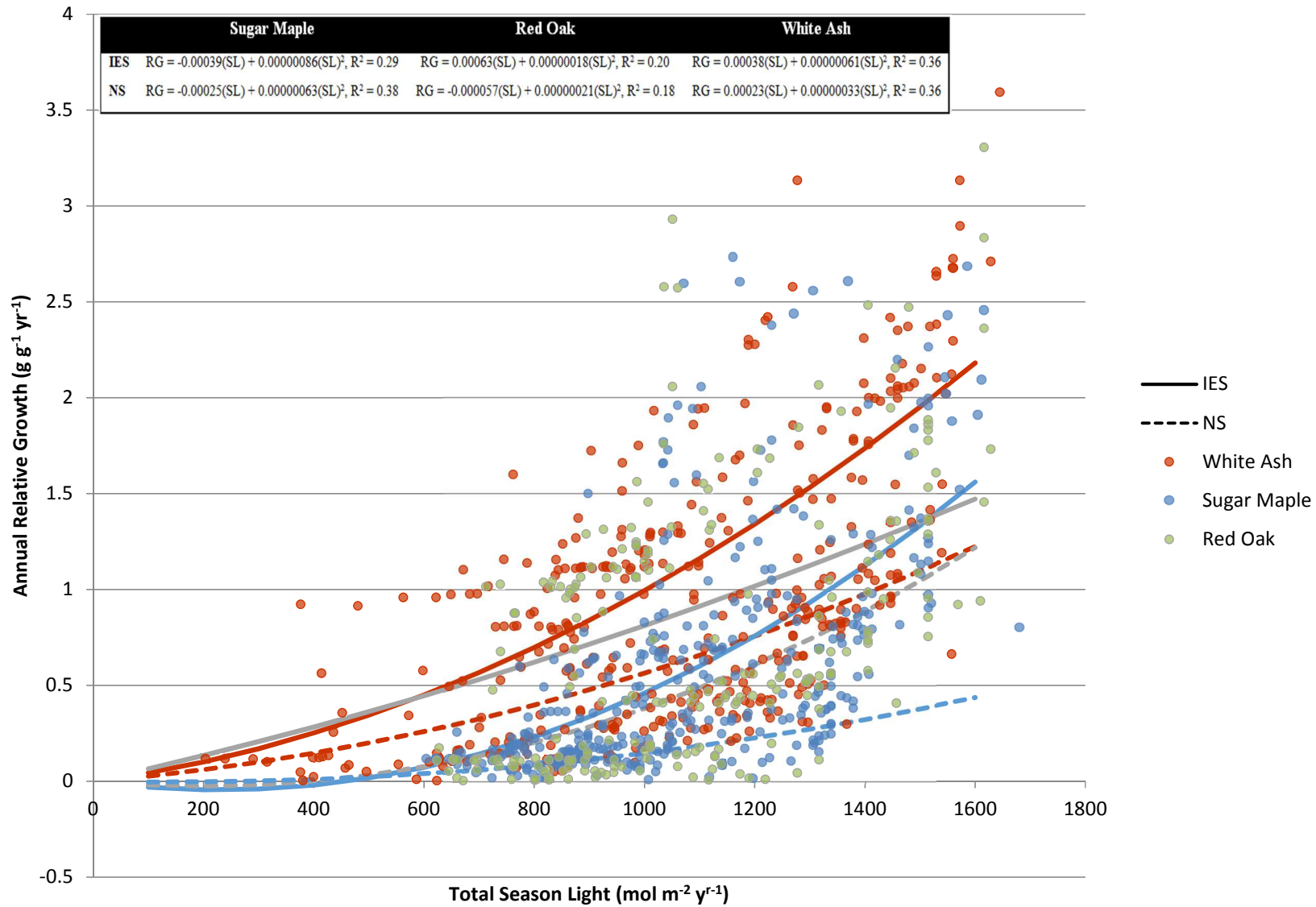


Figure 5

SUPPORTING INFORMATION

Table S1. Allometric growth equations and coefficients of determination for eight understory species based on initial harvests in March 2014 and 2015. Relationships were used to estimate initial plant mass of all seedlings *in situ* and for subsequent relative growth determinations. Diameter (D) and Height (H) were measured in mm.

Species	Allometric Regression
<i>Berberis thunbergii</i>	Initial Mass (g) = $0.0007(D^2H) + 0.003$, $R^2 = 0.79$
<i>Celastrus orbiculatus</i>	Initial Mass (g) = $0.0007(D^2H) + 0.005$, $R^2 = 0.77$
<i>Euonymus alatus</i>	Initial Mass (g) = $0.0006(D^2H) + 0.024$, $R^2 = 0.62$
<i>Kalmia latifolia</i>	Initial Mass (g) = $0.001(D^2H) + 0.024$, $R^2 = 0.68$
<i>Lindera benzoin</i>	Initial Mass (g) = $0.0006(D^2H) - 0.003$, $R^2 = 0.88$
<i>Parthenocissus quinquefolia</i>	Initial Mass (g) = $0.0007(D^2H) + 0.053$, $R^2 = 0.76$
<i>Rosa multiflora</i>	Initial Mass (g) = $0.0009(D^2H) + 0.051$, $R^2 = 0.79$
<i>Rubus allegheniensis</i>	Initial Mass (g) = $0.0004(D^2H) + 0.107$, $R^2 = 0.80$

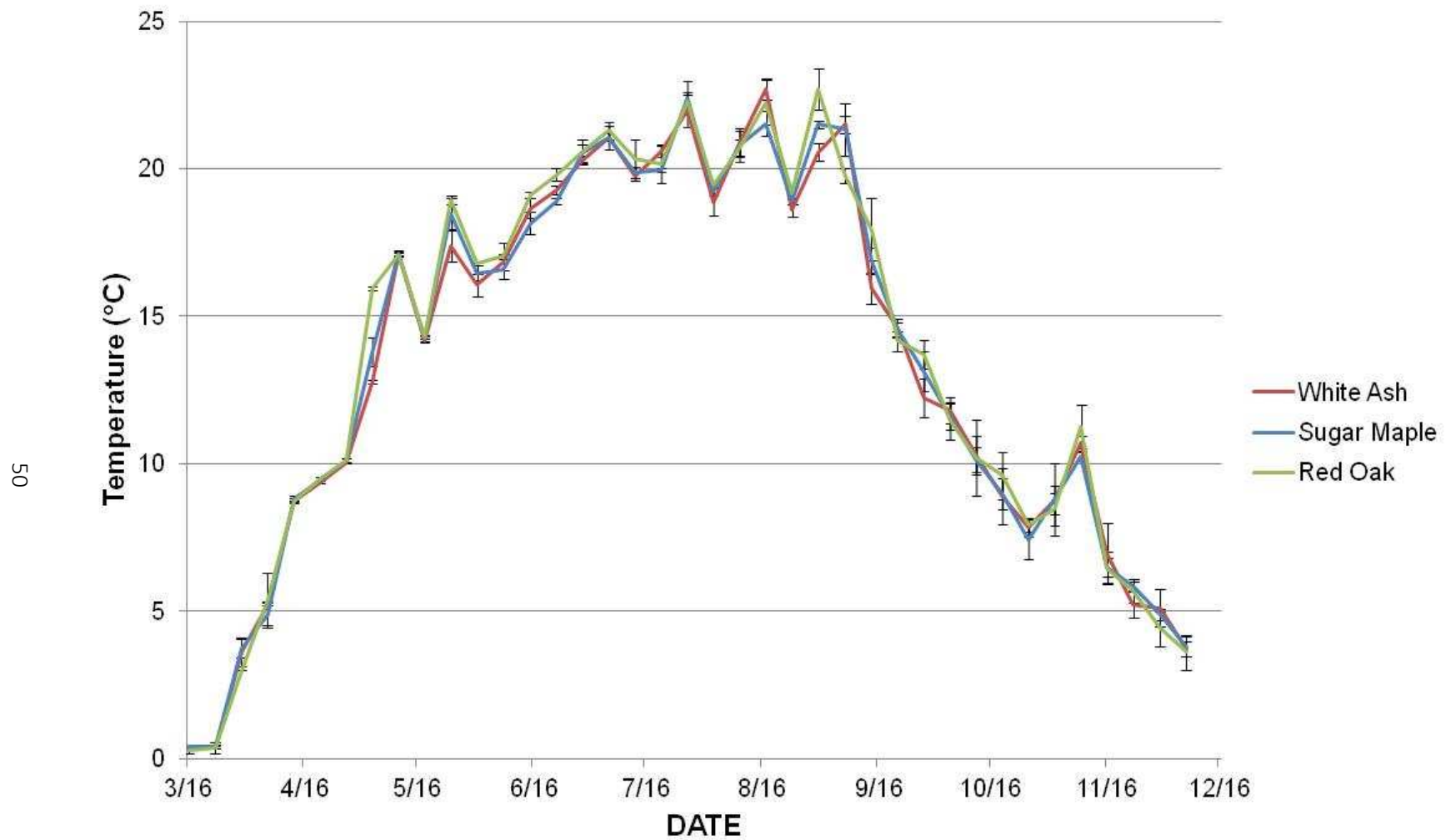


Figure S1. Weekly average (\pm SE) temperature under white ash (*Fraxinus americana*) (red line), sugar maple (*Acer saccharum*) (blue line), and red oak (*Quercus rubra*) (green line) stands across the 2014 and 2015 growing seasons ($n = 3$ for all three canopy species).

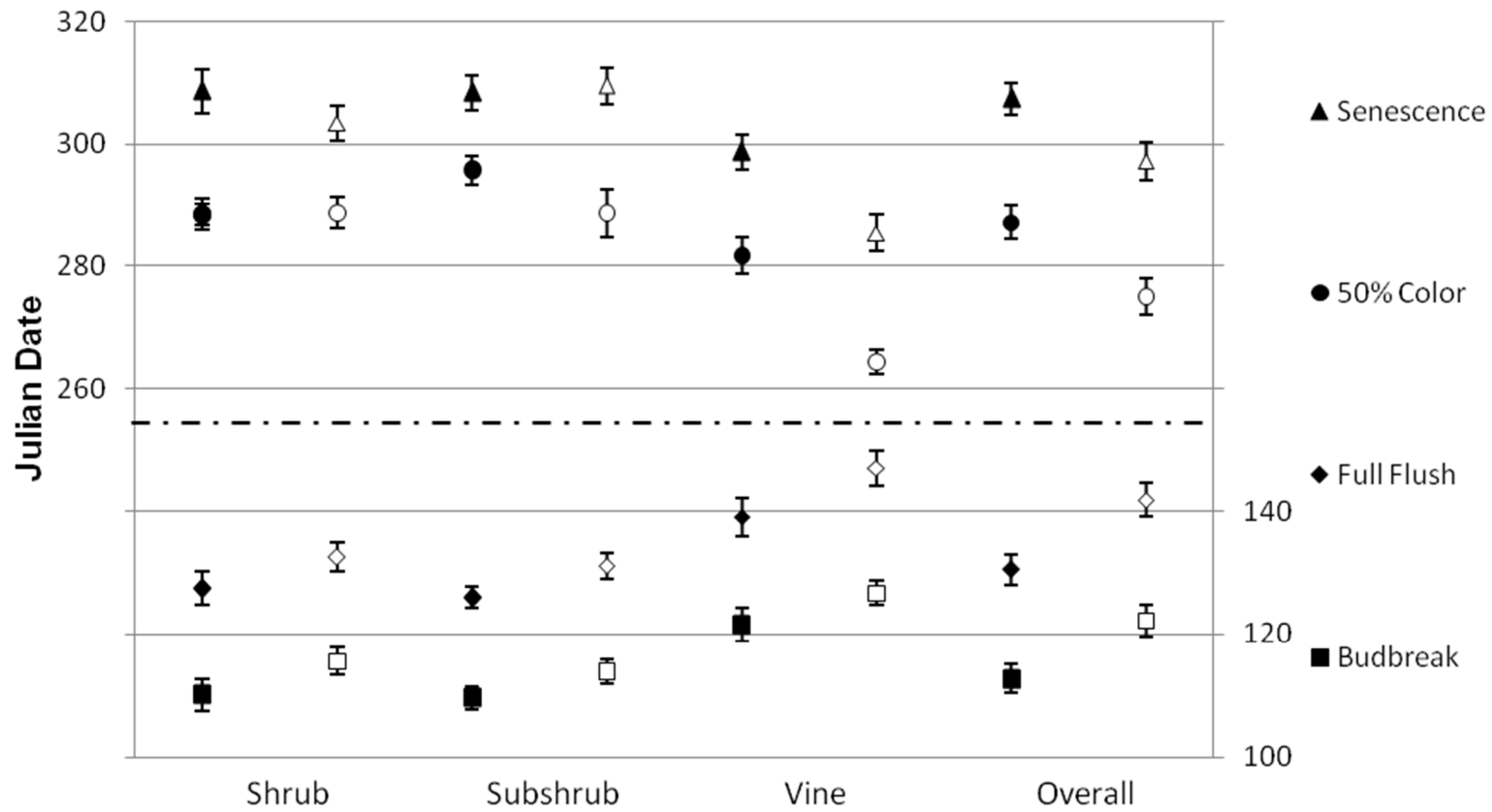


Figure S2. Average (\pm SE) dates of phenological events for invasive exotic species (IES; black) and native species (NS; white). Budbreak (square), full flush (diamond), 50% autumn color (circle), and abscission (triangle) are given for IES and NS within each functional group (*i.e.*, shrub, subshrub, and vine) and for overall pooled IES and NS.

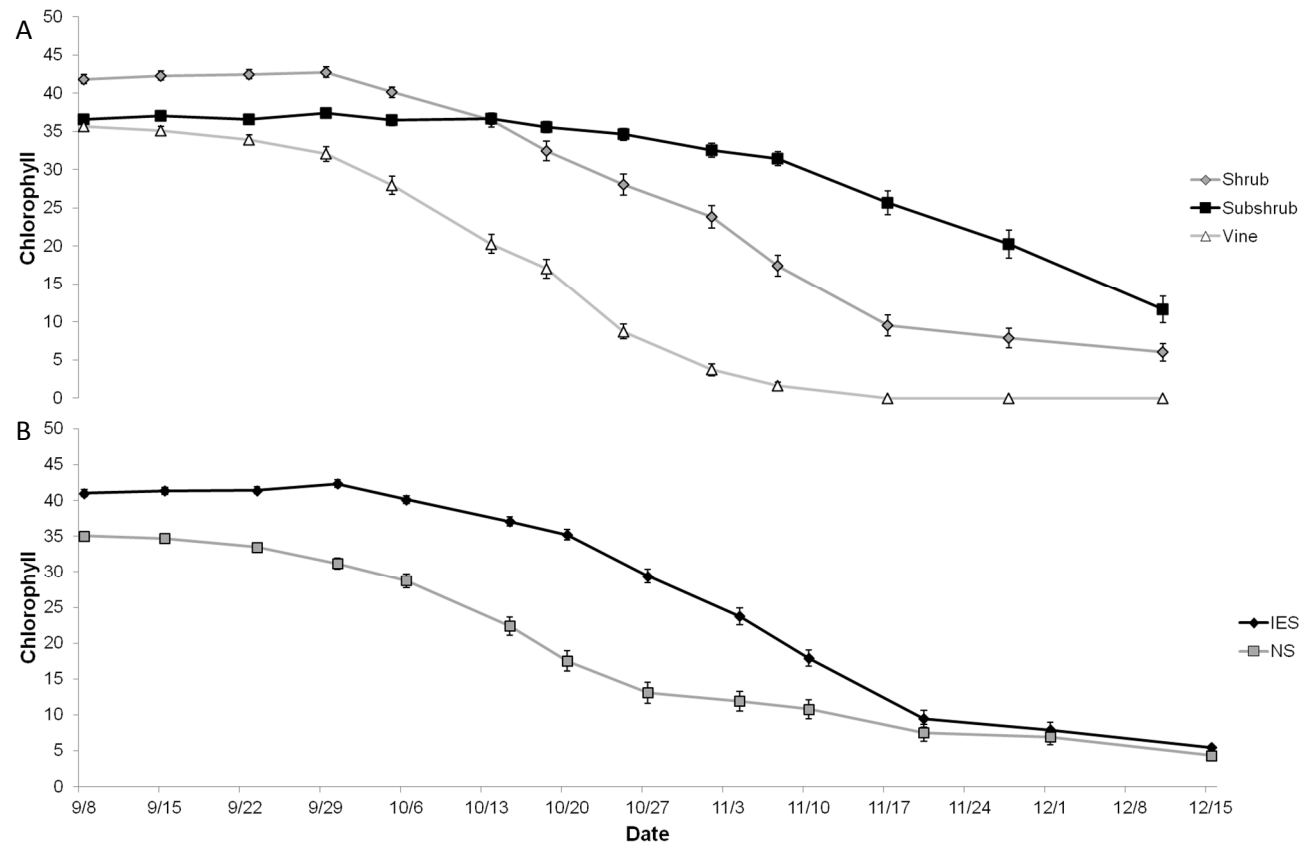


Figure S3. Average (\pm SE) autumn chlorophyll for 2014 and 2015 growing season. Species are grouped by functional group (A) and by native status (B) (*i.e.*, invasive exotic species (IES) or native species (NS)).

Table S2. Regression models using significant environmental and phenological site variables (as indicated in a stepwise regression) to explain the empirical variation in relative annual growth ($\text{g g}^{-1} \text{yr}^{-1}$) for seedlings of four invasive exotic species (IES) and four native species (NS).

Dependent Variables	R ²	P for the factor	P for the model	Dependent Variables	R ²	P for the factor	P for the model
Invasive Species	0.25		<0.001	Native Species	0.25		<0.001
<i>Berberis thunbergii</i>	0.65		<0.001	<i>Lindera benzoin</i>	0.52		<0.001
Total Available Light		<0.001		Total Available Light		<0.001	
Seedling Abscission		0.001		Canopy Flush Date		<0.001	
Seedling 50% Color		0.05		Canopy Drop Date		<0.001	
Canopy Drop Date		0.05					
Extra Spring Days		0.10					
<i>Celastrus orbiculatus</i>	0.64		<0.001	<i>Parthenocissus quinquefolia</i>	0.44		<0.001
Total Available Light		<0.001		Total Available Light		<0.001	
Canopy Flush Date		<0.001		Canopy Drop Date		<0.001	
Extra Fall Days		0.02		Extra Spring Days		<0.001	
Seedling Abscission		0.02		Seedling Full Flush		<0.001	
<i>Euonymus alatus</i>	0.62		<0.001	<i>Kalmia latifolia</i>	0.67		<0.001
Total Available Light		<0.001		Total Available Light		<0.001	
Canopy Flush Date		<0.001		Canopy Flush Date		<0.001	
Extra Fall Days		0.03		Canopy Drop Date		<0.001	
				Seedling Full Flush		0.03	
<i>Rosa multiflora</i>	0.39		<0.001	<i>Rubus allegheniensis</i>	0.34		<0.001
Total Available Light		<0.001		Total Available Light		<0.001	
Canopy Flush Date		0.004		Canopy Flush Date		0.01	
Seedling Budbreak		0.09					

Table S3. Regression models using significant environmental and phenological site variables (as indicated in a stepwise regression) to explain the empirical variation in relative annual growth ($\text{g g}^{-1} \text{yr}^{-1}$) for seedlings of three functional groups.

Dependent Variables	R ²	P for the factor	P for the model
Shrub	0.58		<0.001
Total Available Light	<0.001		
Canopy Flush Date	<0.001		
Canopy Drop Date	<0.001		
Seedling 50% Color	<0.001		
Subshrub	0.34		<0.001
Total Available Light	<0.001		
Extra Fall Days	0.05		
Seedling Budbreak	0.11		
Vine	0.69		<0.001
Total Available Light	<0.001		
Canopy Flush Date	<0.001		
Extra Fall Days	<0.001		

CHAPTER TWO

ELUCIDATING MECHANISMS UNDERLYING DIFFERENCES IN GROWTH BETWEEN NATIVE AND INVASIVE SEEDLINGS IN DECIDUOUS FOREST UNDERSTORIES

ABSTRACT

Invasive exotic plant species (IES) have been noted for their ability to achieve higher rates of biomass growth than native species (NS), yet the mechanisms underlying this difference remain unclear and less studied in resource-limited environments. I examined the mechanistic basis for differences in relative growth (RG) between co-occurring IES and NS in deciduous forest understories where light is limiting, but seasonally and spatially dynamic as a result of variation in overstory species composition. In these environments, extended leaf lifespan may contribute to IES growth advantage, especially if it results in net carbon gain when the overstory canopy is leafless. I hypothesized that IES RG exceeds that of NS and, after accounting for phenology, this contrast is related to differences in several intrinsic growth determinants. Four IES and four NS were grown in common gardens located under three canopy types - sugar maple (*Acer saccharum*), red oak (*Quercus rubra*), and white ash (*Fraxinus americana*) - which differed in the total amount of light afforded to the understory during the growing season. I assessed relationships between RG and its determinants, including seedling phenology, over two growing seasons. Mean RG ranged between 0.2 and 1.9 g g⁻¹ yr⁻¹, and was significantly explained by extension of understory leaf lifespan into periods when the canopy was leafless as well as by area-based, mass-based, and whole-plant photosynthesis. After accounting for phenology, leaf area ratio (LAR) was the most important explanatory variable for growth, with more influence from specific leaf area (SLA) than leaf mass ratio (LMR). Correspondingly, relative to NS, IES were able to achieve greater seasonal growth at similar photosynthetic capacities, via more efficient light capture as well as an extended duration of photosynthetic activity. Thus, IES exhibit traits that enhance resource capture (*i.e.*, higher RG) and resource conservation (*i.e.*, longer leaf lifespans) in low-resource environments.

ABBREVIATIONS

A_{area} – Area-based Photosynthesis;

A_{mass} – Mass-based Photosynthesis;

A_{max} – Maximum Photosynthetic Rate;

A_{plant} – Whole-plant Photosynthesis;

CUE – Carbon Use Efficiency;
GAR – Gross Assimilation Rate;
GRC – Growth Response Coefficient;
IES – Invasive Exotic Species;
LAR – Leaf Area Ratio;
LMR – Leaf Mass Ratio;
NAR – Net Assimilation Rate;
NS – Native Species;
PFD – Photosynthetic Flux Density;
RG(R) – Relative Growth (Rate);
RMR – Root Mass Ratio;
SLA – Specific Leaf Area;
SMR – Shoot Mass Ratio

INTRODUCTION

Invasive exotic plant species (IES) pose a serious risk to ecosystems worldwide, but the causes for success in invaded environments are often unclear. Invasion ecologists often seek mechanistic explanations for observed differences in plant growth between IES and native species (NS) as expressed in particular traits. Growth determinants are commonly used to identify plant invasiveness (Daehler 2003; Pyšek & Richardson 2007; Pyšek *et al.* 2009; Soti & Volin 2010; Volin *et al.* 2010) and environmental impact (Ehrenfeld 2010; Pyšek *et al.* 2012), as they may provide a valuable conceptual basis for describing variation in plant ecological strategies and differential responses of plant species to different environmental conditions (Weiher & Keddy 1999; Diaz & Cabido 2001; Lavorel & Garnier 2002; Suding *et al.* 2008). Although most studies indicate that no single trait or group of traits completely explains IES success, IES are often noted for having higher values than do NS with respect to traits associated with high performance (van Kleunen *et al.* 2010). In particular, relative growth rate (RGR) and its set of principal determinants are often used as they are directly related to fitness and strategies of carbon capture.

RGR is used in traditional analyses of growth to explain variations in growth, as it is a result of a combination of many physiological, morphological, and allocational characteristics (Blackman 1919; Lambers & Poorter 1992; Kruger & Volin 2006). RGR of plants reflects net assimilation rates (NAR, rate of dry matter production per unit leaf area) and leaf area ratio (LAR, leaf area per unit total plant mass), such that $RGR = NAR \times LAR$ (Evans 1972, Causton and Venus 1981). NAR is a physiological component, determined by photosynthetic carbon gain and respiration losses. LAR reflects the amount of leaf area of a plant and depends on biomass allocation to leaves relative to total plant mass (leaf mass ratio, LMR) and the amount of leaf area per unit leaf biomass (specific leaf area, SLA), such that $LAR = LMR \times SLA$. Variation in leaf traits is thought to align along a leaf economic spectrum representing carbon fixation strategies and trade-offs between resource capture and resource conservation (Reich, Walters & Ellsworth 1997; Westoby *et al.* 2002; Wright *et al.* 2004, 2005). RGR, in particular, can increase with increasing NAR, SLA, or LMR, but, the importance of particular components in explaining variation in RGR may differ with respect to species or growing condition. Some studies find SLA to be the primary determinant (Poorter & Remkes 1990; Cornelissen, Castro-Diez & Carnelli 1998) while others suggest that NAR is more influential (Veneklaas & Poorter 1998; Villar *et al.* 2005; Shipley 2006). The importance of particular determinants may change with environmental conditions (Walters, Kruger & Reich 1993; Shipley 2002, 2006). According to the carbon gain hypothesis, plants under low-light conditions generally enhance light interception by augmenting carbon allocation to leaves (LMR) and producing thinner leaves (higher SLA), leading to higher LAR (Givnish 1988), although not in all cases (Valladares & Niinemets 2008). In high light environments, higher irradiance should allow for greater RGR through higher carbon fixation and NAR due to greater photosynthetic capacity (Pattison, Goldstein & Ares 1998; Baruch, Pattison & Goldstein 2000; Kruger & Volin 2006). However, multiple mechanistic pathways link RGR with its various components, and these relationships are often species-specific and dependent on environmental factors. For example, physiological and morphological traits that influence RGR are thought to be high in rapidly growing and spreading IES (Pattison *et al.* 1998;

Baruch & Goldstein 1999; Grotkopp & Rejmánek 2007; James & Drenovsky 2007; Leishman *et al.* 2007; Van Kleunen *et al.* 2010).

Much research has centered on differences in RGR between IES and NS, as higher growth rates generally contribute to a successful competitive strategy: IES are able to establish faster and outcompete NS for resources (Walck, Baskin & Baskin 1999; Bellingham *et al.* 2004; Burns 2004). IES could achieve higher RGR than do NS by exhibiting higher rates of photosynthesis or lower rates of respiration (high NAR), thereby allocating more biomass to leaves (high LMR) or producing more leaf area per unit biomass (high SLA). SLA is generally considered to be a strong indicator of invasiveness and a robust predictor of RGR in IES (*e.g.*, Grotkopp & Rejmánek 2007; James & Drenovsky 2007), with IES exhibiting higher SLA (Leishman *et al.* 2007; Van Kleunen *et al.* 2010) and achieving a greater return on biomass invested in leaves than do NS (Lambers & Poorter 1992). However, for some species, NAR is a stronger predictor of RGR (Grotkopp, Erskine-Ogden & Rejmánek 2010). Ultimately, these and other traits position IES contribute to an ecological strategy that favors resource capture over resource conservation (Wright *et al.* 2004; Leishman *et al.* 2010). However, previous studies noting higher RGR in IES compared to NS are focused on growth under higher-resource conditions (Forcella *et al.* 1986; Burns 2004, 2006; Wilson *et al.* 2004; Garcia-Serrano *et al.* 2005; Gurevitch *et al.* 2008). Typically, traits expressed in resource-rich environments may be disadvantageous for plants invading resource-poor environments where slow growth and tissue retention are important (Berendse 1994). While traits enhancing conservation and efficient use of resources may be more advantageous in resource-poor systems, they also culminate in a lower RGR.

Though IES are common in resource-poor environments (Canham *et al.* 1990; Martin & Marks 2006), relatively few studies have evaluated the underlying causes of differences in RGR between IES and NS under these conditions. Increasing evidence supports IES success over NS in both high-and low-resource environments (Funk & Vitousek 2007; Heberling & Fridley 2013, 2016; Volin, Parent & Dreiss 2013). IES may still exhibit greater RGR than do NS, regardless of irradiance levels (Pattison *et al.* 1998;

Zheng *et al.* 2009, 2012), with differences in IES and NS increasing with increases in resource availability (Daehler 2003). Several studies have found that a greater RGR for IES was due to greater NAR or maximum photosynthesis (A_{\max}) in both high and low light, as well as greater LAR in low light (see Kruger & Volin 2006). As such, the importance of particular determinants in explaining growth differences between IES and NS may change with resource availability.

In deciduous forest understories in eastern North America, IES, compared to NS, often exhibit higher RGR, characteristic of fast-growing, resource-demanding growth strategies, and longer leaf lifespans, associated with resource conservation. This suggests that IES may possess traits that enhance competitive ability in both high- and low-resource environments (see Chapter 1; Funk & Vitousek 2007; Funk 2013; Heberling & Fridley 2013). In these environments, seasonal light availability is relatively low and a function of canopy structure (governing light transmission) and phenology (timing of leaf flush and abscission), both of which differ considerably among deciduous tree species. This results in variation in *in situ* understory light with space and time (Kato & Komiyama 2002). Success of IES has been attributed to extended leaf lifespan into pre- and post-canopy periods, when understory light availability is high and competition from NS is low (Harrington, Brown & Reich 1989; Xu, Griyn & Schuster 2007; Fridley 2012). However, the benefits of extended temporal niche breadth and, thus, the potential advantage of IES over NS, are mediated by overstory vegetation. For instance, in the northeastern United States, spring leaf flush in sugar maple (*Acer saccharum*) typically occurs 1-3 weeks earlier than in red oak (*Quercus rubra*) or white ash (*Fraxinus americana*) (Salisbury 1916, Lechowicz 1984, Dreiss and Volin 2013). In the autumn, canopies of white ash abscise at the same time as those of sugar maple, and up to four weeks before those of red oak. Previous studies note the influence of light transmission on growth strategies (Yamashita *et al.* 2000; Sanford *et al.* 2003; Gurevitch *et al.* 2008; Knight *et al.* 2009; Schulte *et al.* 2011), but fewer recognize the role of phenology in seasonal light capture and availability (Harrington, Brown & Reich 1989; Gill, Amthor & Bormann 1998; Routhier & Lapointe 2002; Jolly *et al.* 2005; Richardson & O 'Keefe 2009). Species grown under low-light conditions typically exhibit

slower growth and higher resource-use efficiency (Pacala *et al.* 1994), but longer leaf lifespans and extension of leaf activity into canopy-off periods may significantly enhance growth rates over an entire growing season (Heberling & Fridley 2013).

Plant biomass growth represents a set of relationships among intrinsic determinants that are specific to species and environmental conditions, begging the question of how IES are able to gain a growth advantage over NS in low-light, deciduous, forest understories. As such, the objective of this study was to determine the mechanistic basis for biomass growth differences between IES and NS in these environments. I assessed determinants of annual relative growth (RG) in four IES and four NS under three canopy types that differ in light transmission and phenology. Consequently, I assessed how RG corresponds with extended leaf lifespans into periods when the canopy is leafless. I hypothesized that extended leaf lifespans resulting in photosynthetic activity during periods prior to canopy leaf flush and after canopy abscission contribute to greater seasonal growth in IES compared to NS. I also hypothesized that, after accounting for phenology, differences in RGR of IES and NS are explained by several intrinsic determinants. In particular, on the basis of expected trade-offs between SLA and resource availability, I predicted that IES would demonstrate higher SLA and greater leaf biomass after controlling for differences in plant size, thus gaining an advantage over NS in understories with low and variable seasonal light availability.

METHODS

Study Sites

All sites were on tracts in the University of Connecticut Forest (41.80° N, 72.25° W; see Chapter 1 Fig. 1). Approximately 82 tree and shrub species are present in Connecticut, the most abundant canopy species are *Acer rubrum*, *Acer saccharum*, *Fagus grandifolia*, *Quercus alba*, and *Quercus rubra* (Wharton et al. 2004). In this region, the annual mean temperature is 8.89° C with mean January and July

temperature being -3.5° C and 21.3° C, respectively. Annual mean snowfall is 109.2 cm and the mean total annual precipitation is 116.8 cm (NOAA, 2010). I established three sites under each of three dominant canopy types: *A. saccharum*, *Q. rubra*, and *Fraxinus americana*. These three canopy species represent a range in phenological traits and light transmittance (Dreiss & Volin 2013). To be classified as a particular canopy cover type, percent canopy cover of the target species needed to exceed 70% of total overstory cover. Sites were even-aged forests greater than 75 years old (as determined from aerial photography between 1934 and 2010 from the University of Connecticut Map and Geographic Information Center: <http://magic.lib.uconn.edu/>).

Common Gardens

Common gardens containing seedlings of four IES and four NS were constructed under each of the nine sites. Gardens consisted of 4 x 4 m fenced enclosures in which 0.33 m of topsoil was excavated and replaced with a common experimental soil (5:1 volume mixture of sand and soil extracted and mixed from all forest sites). The eight understory species were chosen because they are common to the region and because they represent three functional groups (shrub, subshrub, and vine) as defined by the USDA Plant database (http://plants.usda.gov/growth_habits_def.html). The four IES included two shrubs, *Euonymus alatus* (burning bush) and *Berberis thunbergii* (Japanese barberry), a subshrub, *Rosa multiflora* (multiflora rose), and a vine, *Celastrus orbiculatus* (oriental bittersweet). Similarly, four commonly co-occurring NS included two shrubs, *Kalmia latifolia* (mountain laurel) and *Lindera benzoin* (spicebush), a subshrub, *Rubus allegheniensis* (blackberry), and a vine, *Parthenocissus quinquefolia* (Virginia creeper). Between twenty and thirty-five individuals of each species were transplanted into each site. Individuals were collected from the field during the summer of 2013, transplanted in a stratified random manner with regards to canopy type and site and labeled in each garden matrix (1,665 plants total). Initial plant sizes ranged from 0.02 – 0.48 g. All gardens were watered as needed to maintain field capacity and fertilized with a 15:9:12 slow-release fertilizer (The Scotts Company, Marysville, OH, USA) on a bi-monthly basis during the growing seasons.

Garden Characteristics

Critical phenophases in overstory and understory vegetation were tracked for each species with monitoring every other day in all gardens. These included dates of initial and full leaf flush in spring, and leaf color and abscission in fall (*sensu* Dreiss & Volin 2013). From these records, I calculated phenological extension, defined here as the number of days that understory leaves were present during canopy-off periods. Garden environments were characterized through monitoring of understory photosynthetically active radiation (PAR) and air temperature at 10-minute intervals using fixed-position *Hobo* H21-002 sensors and dataloggers (Onset, Inc, Cape Cod, MA, USA).

Growth Measurements

Comparisons of annual relative growth (RG) between IES and NS seedlings over two growing seasons were based on a combination of destructive harvests and nondestructive measurements to estimate plant biomass (*i.e.*, height and diameter, *sensu* Kaelke *et al.* 2001). At the beginning of the growing season in 2014, two leafless individuals per species were harvested in each garden, and all harvested as well as non-harvested plants were measured for stem basal diameter (D , 2 cm above the soil surface) and total height (H , from ground line to the base of the terminal bud). Nondestructive allometric measurements were taken again at the end of the 2014 growing season and at the beginning and end of the 2015 growing season.

Destructive harvests were conducted on 6-11 individuals of each species at each canopy site on July 15 in 2014 and in 2015. Roots and shoots of harvested plants were separated, and roots were rinsed free of soil. ImageJ software was used to calculate leaf area for each individual. Plant tissues were then oven-dried at 70°C to a constant mass and weighed. For each species, regression equations were developed based on allometric measurements (see Chapter 1 Table S1), using data from both years, in which the total dry mass of harvested plants was regressed against a stem volume index (D^2H , cm³) *sensu* Kaelke *et al.* (2001). Final harvest data were coupled with allometric estimates of initial mass for

individual seedlings in a particular year to calculate annual relative growth (RG) as $\ln(\text{final mass}) - \ln(\text{initial mass})$. Specific leaf area, SLA [$\text{m}^2 \text{ leaf area (kg leaf mass)}^{-1}$] was calculated for each harvested seedling. Seasonally averaged LMR was calculated based on two growth phases: an exponential phase from April to July harvest and a linear phase from July harvest to November. This approach is predicated on the assumption that production of new leaves was negligible after harvest (Xu, Griyn & Schuster 2007), which was true for all species except the subshrubs. As such, the LMR calculation was modified as a single exponential growth phase from leaf flush to abscission in the case of subshrubs.

Gas Exchange

Diagnostic gas exchange was generally measured *in situ* using a LI-6400 portable photosynthesis system (Li-Cor Biosciences) for 4-5 days per week from May to November 2015 on fully expanded leaves (30-50 gas exchange curves per species and canopy type) to determine species-specific photosynthetic responses to variation in leaf temperature and light intensity in environments exhibiting wide seasonal variation (Man & Lieffers 1997; Xu, Griyn & Schuster 2007). Photosynthetic light responses were assessed during morning hours (8:00-11:30AM), across a range of leaf temperatures throughout the growing season using five light (PAR) levels ranging from 25 to 1500 $\mu\text{mol m}^{-2} \text{ s}^{-1}$. Temperatures included ambient and ambient $\pm 5^\circ \text{C}$ to determine photosynthetic responses to warming and cooling.

The photosynthetic light response model of Hanson *et al.* (1987) was used in a nonlinear least squares analysis to compute maximum photosynthetic rate (A_{max}), dark respiration (R_d), and light compensation point (LCP) for each *in situ* light-response curve:

$$A = A_{\text{max}} (1 - [1 - R_d/A_{\text{max}}]^{1 - \text{PAR/LCP}}) \quad (\text{eqn 1})$$

Daily integrals of photosynthesis were estimated using a stochastic model sensitive to variations in temperature and light. The temperature dependence of photosynthetic parameters (A_{\max} , R_d , and LCP) was then modeled using the Arrhenius function:

$$P = P_n * \exp(E_v/0.008314*(1/293-1/(273+T))) \quad (\text{eqn 2})$$

where P is the parameter, P_n is the parameter scaled to reference temperature n , E_v is the activation energy, and T is the air temperature of the garden, which was assumed to equal leaf temperature.

Activation energies, the minimum energy necessary for particular reactions to take place, provide a quantitative description of plant processes based on thermodynamic considerations and are often used to characterize changes in plant photosynthetic characteristics with temperature variation (Hikosaka *et al.* 2006). For each parameter, temperature-normalized values and activation energies were calculated at the leaf-level given data for each combination of species, canopy type, and month the measurement was taken. The temperature at which parameters were normalized was determined by the average mid-day temperature of that month. Average and standard error were determined for temperature-normalized values and activation energies across leaves of a species in a given canopy type and month of measurement. Photosynthesis (A) was calculated for each 10-minute interval by substituting the Arrhenius equation (eqn 2) into the Hanson *et al.* (1987) model of light response (eqn 1) for each corresponding photosynthetic parameter. Each temperature-normalized value and activation energy was sampled from empirical Gaussian distributions for leaves within a species, given the canopy type and month being modeled. PAR and T were taken from the garden environment dataset. Photosynthesis for each 10-minute interval was added up across each day for daily integrals (A_{area} , $\text{mmol m}^{-2} \text{d}^{-1}$).

Data Analysis

Prior to hypothesis testing, a regression analysis was conducted to examine the influence of initial plant mass on RG and its determinants (McConnaughay & Coleman 1999; Volin *et al.* 2002; Kruger & Volin 2006; Soti *et al.* 2015). Regression analysis indicated a negative relationship between RG and the

natural log of initial plant mass ($RG = -0.58 \cdot \ln(\text{initial mass}) - 0.64$, $P < 0.001$ for data pooled across all species and sites). Moreover, there was no significant variation in the slope of this relationship across species and sites ($P = 0.32$). Additionally, LMR was significantly related to plant mass at harvest ($P < 0.001$). Given these relationships, predicted values of RG and LMR and associated residuals (observed – predicted) were calculated for each seedling. RG and LMR were then adjusted based on the average initial mass of all seedlings and residuals of individual seedlings. Relationships between RG and LMR and other variables were analyzed using adjusted RG and LMR values, respectively.

Statistical analyses were performed using JMP v. 5.0 and SAS v. 9.3 (The SAS Institute). Dates of observed understory and overstory phenophases were used to calculate, for each seedling, leaf lifespan and extension of temporal niche (in days) into pre- and post-canopy periods - calculated as canopy flush date minus seedling flush date and seedling abscission date minus canopy abscission date, respectively. Estimates of mass-based photosynthesis [A_{mass} , $\text{mmol CO}_2 \text{ g}^{-1} \text{ d}^{-1}$] were calculated as the product of SLA and the daily integral for leaf net photosynthesis (A_{area} , $\text{mmol CO}_2 \text{ m}^{-2} \text{ d}^{-1}$). Estimates of net photosynthesis per unit plant mass [A_{plant} , $\text{mmol CO}_2 (\text{g plant})^{-1} \text{ d}^{-1}$] were calculated as the product of seasonal average LAR and A_{area} . Average A_{plant} was determined for the growing season by combining 15-d means for A_{area} with corresponding harvest data. These components were compared with a daily rate of growth ($RGR \text{ mg g}^{-1} \text{ d}^{-1}$), which was calculated as the average amount of growth each day given the RG and the photosynthetic season (*i.e.*, leaf lifespan) of each seedling. Relationships between RGR and growth determinants were analyzed for the entire dataset as well as by pooled IES and NS groups and by seedlings grown under each canopy type.

To determine differences in foliar phenophases and plant growth traits among species ($n = 24$), IES and NS groups ($n = 6$), and functional groups ($n = 9$), foliar phenophases were compared across canopy types and years using mixed-effects, two-way ANOVAs. Statistically, values across years did not differ significantly and therefore an average across both years is reported in the results. Across species, treatment main effects and interactions were tested using analysis of variance techniques appropriate for a 3x8 factorial split-plot completely randomized design. Within species and functional groups, treatments

were tested using a randomized complete-block design. Similarly, to test for differences in growth response, RG on a seasonal basis and RGRs on a daily basis were compared between species, IES and NS groups, and functional groups using ANOVAs. Relationships between plant growth and intrinsic determinants were also examined with Spearman's rank correlation coefficients.

After accounting for phenology, RGRs on a daily basis were used to describe growth variation. Relationships among RGR and its determinants were examined with linear regression. To further explore differences in growth response of IES and NS groups and growth across canopy types, differences in slopes between RGR and growth determinants were tested using Student's t-test. The importance of particular growth determinants as explanatory variables for IES and NS within and across canopy types was also examined with growth response coefficients (GRCs, *sensu* Poorter & van der Werf 1998; Kruger & Volin 2006). To ensure that a given set of complementary GRCs summed to unity, I used [GAR, (g biomass gain) $\text{m}^{-2} \text{d}^{-1}$] to represent A_{area} , which was calculated as the quotient of A_{area} [converted from ($\text{mmol C}) \text{m}^{-2} \text{d}^{-1}$ to ($\text{mg C}) \text{m}^{-2} \text{d}^{-1}$] and plant carbon concentration ([C], fraction in dry tissue). A tissue [C] of 50% dry mass was assumed (Penuelas & Estiarte 1997; Thomas & Martin 2012). Carbon-use efficiency (CUE) was calculated as the quotient of RGR and the product of GAR and LAR (*i.e.*, the potential rate of plant biomass gain). Using linear regression, the natural logs of LAR, GAR, and CUE were each regressed against the natural log of RGR, and the respective GRCs were taken to be the slopes of these relationships. GRCs were calculated for each species grown under each canopy type as represented by their respective understory photoperiod average (photosynthetic flux density, PFD).

RESULTS

Garden Measurements

In both years, the period of favorable conditions for photosynthesis (*i.e.*, air temperatures $> 5^{\circ}\text{C}$) was approximately March 28 – November 15. During this period, understory vegetation had more access to light beneath white ash ($2,229 \pm 57 \text{ mol m}^{-2}$) than it did beneath red oak ($1,926 \pm 54 \text{ mol m}^{-2}$) or sugar

maple ($1,593 \pm 61 \text{ mol m}^{-2}$) ($F_{2,8} = 30.6$, $P < 0.001$; see Chapter 1 Fig. 2). This was a result of greater light transmitted during canopy-on periods for white ash compared to those of the other canopy species ($F_{2,8} = 25.8$, $P = 0.001$) as well as larger opportunities for pre-canopy light compared to sugar maple ($F_{1,5} = 9.8$, $P < 0.01$) and post-canopy light compared to red oak ($F_{1,5} = 19.2$, $P = 0.002$). Understory air temperature did not differ significantly across canopy types (see Chapter 1 Fig. S1).

In general, leaf flush occurred earlier and abscission significantly later in IES than in NS (see Chapter 1 Fig. 2). The earlier leaf flush and later abscission of IES resulted in significantly longer presence of leaves during canopy-off periods than NS ($t_{238} = 8.67$, $P < 0.001$).

Relative Growth and its Determinants

Annual RG ($\text{g g}^{-1} \text{ yr}^{-1}$) of IES pooled was significantly greater than pooled NS ($t_{235} = 5.48$, $P < 0.001$; Table 1). Significant differences between IES and NS were manifested in under all canopy types ($t_{81} = 4.31$, $t_{84} = 2.79$, and $t_{66} = 2.18$, $P < 0.001$, $P = 0.007$, and $P = 0.006$, for white ash, red oak, and sugar maple, respectively; Fig. 1). And between these, the differences in RG between IES and NS were greatest under white ash canopies (Fig. 1).

When plotted against phenological differences, annual growth was positively related to phenological extension ($R^2 = 0.18$, $P < 0.001$, Fig. 2A, Table 2). IES and NS differed significantly in the relationship between RG and phenological extension, with IES exhibiting significantly greater phenological extension ($t_{235} = 8.67$, $P < 0.001$) and RG ($t_{235} = 5.48$, $P < 0.001$), and a more pronounced response of the latter to variation in the former (Fig. 2B, Table 3). A similar response was found when examined by canopy types, but in this case, points representing plants under white ash canopies were shifted toward greater growth and phenological extension as compared to the situation under sugar maple and red oak canopies (Fig. 2C, Table 4). However, the slopes of the three relationships were not significantly different. Phenological extension was positively correlated with several growth

determinants, including area-based, mass-based, and whole-plant photosynthesis as well as SLA (Table 2).

After accounting for differences in phenology, RGR ($\text{mg g}^{-1} \text{d}^{-1}$) was significantly and positively related to the daily integral of photosynthesis expressed per unit leaf area (A_{area} , $R^2 = 0.30$), leaf mass (A_{mass} , $R^2 = 0.53$) and plant mass (A_{plant} , $R^2 = 0.08$) ($P < 0.001$ in all cases, Fig. 3A-C). Similar responses were found when RGR was analyzed by group (*i.e.*, IES vs. NS) (Fig. 3D-F) as well as by canopy types (Fig. 3G-I). In all cases, A_{plant} , which incorporates physiological (A_{area}), morphological (SLA) and allocational (LMR) determinants of growth, explained the most variation in growth for all seedlings (Fig. 3G), for IES and NS groups (Fig. 3F), and for growth under different canopy types (Fig. 3I).

Like their physiological counterparts, examination of morphological (*i.e.*, SLA) and allocational (*i.e.*, LMR) determinants of growth revealed a significant correlation with RGR (Table 2). However, variation in growth was only significantly explained by SLA, but not by LMR when analyzed across seedlings (Table 1, Fig. 4A&B), groups (Fig. 4C&D), and canopies (Fig. 4E&F). Similarly, SLA, but not LMR differed significantly between IES and NS groups, with IES exhibiting greater SLA (Table 3).

Growth response coefficients (GRCs) were calculated to compare the relative influences of the principal growth determinants on RGR. Among the GRCs, LAR was greater than GAR, which, in turn, was greater than CUE for both IES and NS (Fig. 5). LAR GRCs were mostly influenced by SLA as the role of LMR was negligible. LAR and CUE GRCs did not differ significantly between groups or across light environments. In IES, GAR GRCs increased with increasing light and were significantly greater than NS under the white ash canopies, which had the highest overall understory light levels.

DISCUSSION

I explored the mechanistic basis for RGR differences between IES and NS seedlings grown in low-light deciduous forest understories over two growing seasons. In general, RGR and leaf trait relationships represent a set of economic trade-offs among resource capture by fast-growing, light-demanding species and resource conservation (Reich *et al.* 1997; Westoby *et al.* 2002; Wright *et al.* 2004, 2005). While IES are often considered the former, there is evidence that they are more successful than NS in both high- and low-resource environments (Funk & Vitousek 2007; Volin, Parent & Dreiss 2013; Heberling & Fridley 2013, 2016). This has led to recent interest in growth strategies of IES and NS as the extent to which the relationships for IES and NS growth determinants align may help to identify different mechanisms for IES success in different plant communities. My findings support my first hypothesis that extension of leaf lifespan into canopy-off periods results in greater overall photosynthetic activity and, thus, seasonal growth for IES compared to NS, as the former generally exhibited greater leaf lifespans that allowed them a greater advantage in carbon gain during canopy leaf-off periods. The greater RG of IES compared to NS is most closely and positively related to differences in phenology.

In deciduous forest understories, extended leaf lifespan may contribute to understory growth advantage, especially if it results in photosynthesis when the canopy is leafless (Iwasa & Cohen 1989; Kikuzawa & Kikuzawa 2003; Xu, Griyn & Schuster 2007). During the height of the growing season, understories are heavily shaded (< 5% of full sunlight) by fully flushed overstory canopy trees, which can restrain carbon gain and subsequent growth (Pacala *et al.* 1994). However, as a result of the deciduous nature of many canopy species, light availability is seasonally and spatially dynamic (Kato & Komiyama 2002; Perkins *et al.* 2011). This was evident in the differential phenology and light transmission observed among the three canopy types that I studied. White ash understories received the greatest amount of light due to higher light transmission when canopy leaves were present and relatively short canopy leaf lifespans. Although the positive effects of higher light transmission on understory growth rates are well

documented (Baruch & Goldstein 1999; Baruch *et al.* 2000; Meekins & McCarthy 2000; Athanasiou *et al.* 2010), the seasonal dynamics of understory light as a result of phenological variation is not often taken into account. Here, later spring phenophases and shorter leaf lifespans, as exhibited by white ash canopies, may make it easier for understory plants to extend their photosynthetic activity into periods prior to canopy leaf flush or after canopy leaf abscission as understory lifespans would not need to be long to extend past the lifespan of the white ash canopy. Greater phenological extension into pre- and post-canopy periods would afford understory plants more time (or days) to assimilate resources during periods of high light availability and low competition (Davis *et al.* 2000; Wolkovich & Cleland 2011). The ability to take advantage of “extra” days beyond the lifespan of canopy foliage is fairly common in vegetation growing in temperate forest understories including seedlings (Seiwa 1998), saplings (Gill, Amthor & Bormann 1998; Seiwa 1999), understory trees (DePhamphillis & Neufeld 1989), and shrubs (Gill, Amthor & Bormann 1998), but my study shows that the cumulative number of “extra” spring and fall days is positively related to greater seasonal growth. Differences among canopy types manifest as shifts along the common slope describing relationships in understory leaf lifespans and phenological extension into canopy-off periods. Additionally, the most seasonal growth occurred under white ash canopies with greater spring and autumn windows of high light and the least under sugar maple canopies which allowed the shortest spring windows. Although larger windows of high light in both spring and autumn contributed to greater seasonal light availability and growth under white ash canopies, phenological extension was also a function of understory leaf lifespans, which differed significantly between IES and NS.

IES exhibited greater seasonal growth than NS, which was in part due to greater phenological extension and was most pronounced under white ash canopies. As in previous studies, IES leaf lifespans were extended through both earlier spring phenophases (*i.e.*, budbreak; Xu, Griyn & Schuster 2007; Mcewan *et al.* 2009, and leaf flush; Harrington, Brown & Reich 1989) and delayed autumnal abscission (Harrington, Brown & Reich 1989; Zotz *et al.* 2000; Fridley 2012), resulting in a broader temporal niche

for carbon gain (Uemura 1994). As a result, IES foliage was photosynthetically active for more canopy-off days compared the situation for NS, which was positively related to greater seasonal growth. Although this relationship was positive for both groups, the slope was steeper for IES suggests that IES are able to take better advantage of each day of extended leaf activity in terms of biomass gain. This supports previous research suggesting that IES persist over NS in low-resource understories due to greater resource-use efficiencies (see Funk 2013 review). Furthermore, seasonal growth advantages of IES were significant under canopies allowing more understory light (*i.e.*, red oak and white ash). These findings are supported by previous literature which suggest that IES may exhibit greater RGR than NS regardless of irradiance levels (Pattison *et al.* 1998; Zheng *et al.* 2009, 2012), with differences between IES and NS intensifying with increases in resource availability (Daehler 2003). By extending leaf lifespans further into pre- and post-canopy periods than NS, IES are able to benefit by gaining access to vacant niches in spring and autumn (Elton 1958, Mack *et al.* 2000) and by occupying a greater niche space (Richards *et al.* 2006; Wolkovich & Cleland 2011), which ultimately allows for greater access to resources and seasonal assimilation of those resources, respectively.

After accounting for phenology, seedling RGR was significantly and positively related to photosynthesis on a leaf area-, leaf mass-, and plant mass-basis, but IES growth advantage over NS was most attributed to differences in whole plant photosynthesis. Relationships were strongest on a whole-plant basis regardless of species group (*i.e.*, IES or NS) or canopy type. Previous literature supports stronger correlations between RGR and photosynthesis expressed in mass (Poorter & Remkes 1990; Garnier 1991; Reich *et al.* 1992; Walters *et al.* 1993). Kruger and Volin (2006) also found that RGR was most highly correlated with photosynthesis expressed per unit plant mass because estimates of whole-plant photosynthesis incorporate multiple determinants of growth (*i.e.*, A_{area} , SLA, and LMR), making it a more holistic representation of plant growth. Variation in RGR was therefore a result of variation in assimilation rates (A_{area}) and variation in leaf area produced per unit total plant mass (LAR). IES generally exhibited greater A_{mass} , A_{plant} , and SLA than did NS. However, for A_{mass} and SLA, slopes of

relationships between RGR and its determinants did not significantly differ between IES and NS groups. This is similar to previous findings which suggest that there is no difference between IES and NS in the functional relationships underpinning their carbon capture strategies: that they fall along the same carbon economic spectrum, but IES leaf traits are at a point along the spectrum favoring faster growth (Leishman *et al.* 2010; Shen *et al.* 2011; Ordonez & Olff 2013; Hou *et al.* 2015). However, in the case of A_{area} and A_{plant} , IES and NS both scale positively with RGR, but the slopes of those relationships differ: slopes are steeper for IES than for NS. These differences suggest that IES are more efficient in carbon assimilation (Funk & Vitousek 2007; Shen *et al.* 2011). Thus, my findings support my second hypothesis that overall growth and growth differences between IES and NS were explained by a number of intrinsic growth determinants after accounting for phenology, such as whole-plant photosynthesis and SLA.

Similar to many other studies, SLA was significantly greater in IES than NS (Smith & Knapp 2001; Deng *et al.* 2004; Burns 2006; Grotkopp & Rejmánek 2007; Leishman *et al.* 2007; Schumacher *et al.* 2009). On the other hand, it appears that SLA was not the primary determinant explaining differences in growth between IES and NS in my study. All of these studies that report SLA as an indicator of IES success were conducted under irradiances greater than 35% full sunlight. Far fewer studies focus on such comparisons at low light levels. McDowell (2002) studied IES and NS species of the Rosaceae family grown in forest sites dominated by Douglas-fir and found IES had lower SLA than did NS. At 10% irradiance, Zheng *et al.* (2009) found no differences between IES and NS in LAR, LMR or SLA, but IES did have a higher A_{max} . In my study, understory light levels averaged less than 5% of full sunlight, and I found that, while SLA was an important explanatory variable in growth, different assimilation efficiencies appeared to be a main determinant explaining the differences in RGR variation between IES and NS. Similar to this study, Baruch & Goldstein (1999) also found higher SLA and net photosynthesis in IES over NS, finding greater resource-use efficiency and lower leaf construction costs were the key to IES advantage. Hou *et al.* (2015) also found no differences in SLA between species groups grown at 5-10% sunlight, but found that SLA differed with irradiance treatment possibly suggesting that trait differences

between IES and NS species may actually reflect the different environmental conditions of the sites where they occur rather than invasiveness. In resource-poor environments, longer leaf lifespans, greater plasticity, and more efficient resource use may be more successful strategies compared to fast growth (Funk & Vitousek 2007; Coste *et al.* 2011; Matzek 2011; Heberling & Fridley 2013, 2016). Funk and Vitousek (2007) found evidence of greater light use efficiency in IES, suggesting that IES outperform NS in shaded environments. The significance of resource conservation to IES success may be magnified when integrating instantaneous measures of resource-use efficiency over the longer leaf lifespans and phenological extension exhibited by IES (Heberling & Fridley 2013). As such, the findings of this study suggest that IES may benefit from traits attributed to successful competitors in both high- and low-resource environments as they overall had greater RGR and longer leaf lifespans.

Although SLA was only a secondary determinant in explaining IES growth advantage, growth response coefficients (GRCs) indicate that LAR had the highest relative influence on RGR across canopy types and groups. LAR had the highest GRCs, then did GAR, while the role of CUE was negligible, which was consistent with results of Kruger & Volin (2006) in lower light environments: LAR was more important in explaining growth variation, while GAR became more important with increasing light intensity (also see Shipley 2002, 2006). Similar to this study, Kruger and Volin (2006) found that SLA was more influential than LMR. Along with Kruger & Volin (2006), this study is contrary to others examining RGR variation among plants grown in differing light environments. These previous studies often suggest that RGR is influenced more by LAR than by NAR or photosynthetic rates in low light (Poorter & Remkes 1990; Walters *et al.* 1993). However, discrepancies in such patterns may be related to the degree of correlation between NAR and LAR obscuring relationships between RGR and NAR (Poorter & van der Werf 1998; Kruger & Volin 2006; James & Drenovsky 2007), which did not occur in my study.

The relative influence of LAR, GAR, and CUE were similar in IES and NS groups. However, across canopy types, IES GAR GRCs suggested an increasing trend, and became significantly greater

than NS GAR GRCs under white ash understory light conditions. More responsive IES GAR GRCs may reflect the importance of differences in photosynthetic rates in IES growth advantage over NS. This may also suggest greater photosynthetic plasticity in IES even with small changes in seasonal light availability (Pattison *et al.* 1998; Durand & Goldstein 2001; Wang, Feng & Li 2002; Feng *et al.* 2007; Hou *et al.* 2015).

My study illuminates the importance of extended leaf lifespans and multiple growth determinants in enhancing the relative growth success of IES over NS in low-light deciduous forest understories. IES exhibited greater phenological extension than NS as well as greater seasonal growth for each day of leaf photosynthetic activity, suggesting IES were more efficient in biomass gain over the growing season. Furthermore, growth advantages of IES were most pronounced under canopies with shorter leaf lifespans, as this contributed to the potential for understory phenological extension. My results also demonstrate the importance of SLA and whole-plant photosynthesis for growth in low-light environments, and for IES in particular. Though SLA was not the most influential variable in explaining growth in low-light environments, relationships between growth and A_{plant} were steeper in IES than NS, suggesting greater assimilation efficiencies at the whole-plant level. Together, the potential for greater resource-use efficiency and longer periods of resource assimilation contributed to IES seasonal growth advantage over NS. Such leaf traits would be most advantageous when resource availabilities are low, but seasonally variable, as they promote both greater resource capture and resource conservation. Further study should focus on seasonal variability in determinants conferring IES advantage over NS as IES may also benefit from greater plasticity in traits that would allow them to change from “sun” individuals prior to canopy leaf flush to “shade” individuals during the rest of the growing season. Such information would also contribute to a more advanced understanding of how IES growth advantage will adapt with global warming and climate-driven shifts in phenology.

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TABLES

Table 1. Average annual relative growth (RG), and its determinants: area-based photosynthesis (A_{area}), mass-based photosynthesis (A_{mass}), whole-plant photosynthesis (A_{plant}), leaf area ratio (LAR), specific leaf area (SLA), leaf mass ratio (LMR), root mass ratio (RMR), and stem mass ratio (SMR) (\pm SE) for four invasive exotic species (IES) and four native species (NS) grown for two years under three different canopy types: sugar maple (*A. saccharum*), red oak (*Q. rubra*), and white ash (*F. americana*). Mixed model, two-way ANOVAs compare variables across species ($n = 3$), IES and NS groups ($n = 6$) and interactions, where site was a random effect. P – values are reported, with significant effects denoted with an asterisk: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Species	Canopy Type	RG (g g ⁻¹ yr ⁻¹)	A_{area} (mmol m ⁻² d ⁻¹)	A_{mass} (mmol g ⁻¹ d ⁻¹)	A_{plant} (mmol g ⁻¹ d ⁻¹)	LAR (m ² kg ⁻¹)	SLA (m ² kg ⁻¹)	LMR (kg kg ⁻¹)	RMR (kg kg ⁻¹)	SMR (kg kg ⁻¹)
IES										
<i>B. thunbergii</i>	Sugar Maple	0.35 \pm 0.13	338 \pm 24	11.3 \pm 1.4	7.08 \pm 1.1	24.1 \pm 2.5	29.4 \pm 3.5	0.61 \pm 0.04	0.14 \pm 0.03	0.27 \pm 0.03
	Red Oak	0.69 \pm 0.15	280 \pm 34	7.88 \pm 2.0	4.52 \pm 1.3	15.5 \pm 2.1	27.5 \pm 4.0	0.56 \pm 0.04	0.25 \pm 0.05	0.27 \pm 0.04
	White Ash	1.23 \pm 0.14	299 \pm 27	9.64 \pm 1.6	6.75 \pm 1.0	21.1 \pm 2.5	32.2 \pm 3.8	0.65 \pm 0.03	0.16 \pm 0.04	0.24 \pm 0.03
<i>E. alatus</i>	Sugar Maple	0.58 \pm 0.06	217 \pm 17	5.67 \pm 1.0	4.62 \pm 0.8	14.2 \pm 1.6	22.9 \pm 2.7	0.56 \pm 0.03	0.18 \pm 0.02	0.25 \pm 0.02
	Red Oak	0.80 \pm 0.08	298 \pm 24	14.2 \pm 1.4	7.99 \pm 1.0	29.7 \pm 2.7	44.5 \pm 4.7	0.64 \pm 0.03	0.10 \pm 0.03	0.27 \pm 0.03
	White Ash	1.11 \pm 0.06	290 \pm 23	12.8 \pm 1.4	7.63 \pm 0.9	25.5 \pm 2.1	35.7 \pm 3.4	0.61 \pm 0.03	0.15 \pm 0.04	0.30 \pm 0.03
<i>C. orbiculatus</i>	Sugar Maple	0.74 \pm 0.06	251 \pm 23	9.43 \pm 1.4	6.75 \pm 1.1	21.2 \pm 2.3	33.2 \pm 3.4	0.61 \pm 0.04	0.18 \pm 0.03	0.20 \pm 0.03
	Red Oak	1.39 \pm 0.09	364 \pm 29	15.8 \pm 1.7	10.4 \pm 1.3	25.8 \pm 3.1	37.7 \pm 5.3	0.61 \pm 0.04	0.16 \pm 0.04	0.24 \pm 0.03
	White Ash	1.41 \pm 0.07	488 \pm 28	16.5 \pm 1.6	10.2 \pm 1.0	20.9 \pm 2.2	28.9 \pm 3.9	0.57 \pm 0.04	0.12 \pm 0.04	0.33 \pm 0.03
<i>R. multiflora</i>	Sugar Maple	0.94 \pm 0.26	267 \pm 32	9.59 \pm 1.8	6.21 \pm 1.7	18.6 \pm 2.6	31.7 \pm 4.7	0.53 \pm 0.05	0.14 \pm 0.06	0.31 \pm 0.07
	Red Oak	1.08 \pm 0.14	283 \pm 34	13.8 \pm 2.0	7.57 \pm 1.5	22.4 \pm 2.8	44.6 \pm 4.8	0.55 \pm 0.05	0.18 \pm 0.05	0.27 \pm 0.06

85	NS	White Ash	1.94 ± 0.18	298 ± 39	14.9 ± 2.3	8.10 ± 1.4	23.5 ± 3.4	38.8 ± 5.0	0.47 ± 0.05	0.23 ± 0.07	0.33 ± 0.06
		<i>L. benzoin</i>									
		Sugar Maple	0.36 ± 0.10	335 ± 30	9.31 ± 1.7	5.43 ± 1.3	14.3 ± 2.1	23.9 ± 4.2	0.48 ± 0.05	0.19 ± 0.03	0.36 ± 0.03
		Red Oak	0.47 ± 0.13	259 ± 32	7.52 ± 1.9	5.53 ± 1.2	15.5 ± 2.0	25.0 ± 4.6	0.54 ± 0.04	0.14 ± 0.03	0.34 ± 0.03
		White Ash	0.79 ± 0.09	534 ± 37	13.2 ± 2.1	8.17 ± 1.3	17.1 ± 2.1	22.4 ± 3.8	0.60 ± 0.05	0.12 ± 0.04	0.25 ± 0.04
	<i>K. latifolia</i>	Sugar Maple	0.58 ± 0.07	240 ± 52	4.25 ± 1.0	3.28 ± 1.7	8.61 ± 2.7	14.6 ± 5.5	0.61 ± 0.08	0.15 ± 0.05	0.28 ± 0.05
		Red Oak	0.61 ± 0.08	172 ± 37	5.58 ± 1.7	3.90 ± 1.1	8.20 ± 3.1	17.1 ± 7.2	0.54 ± 0.09	0.21 ± 0.07	0.25 ± 0.06
		White Ash	0.71 ± 0.07	193 ± 63	6.96 ± 3.7	4.49 ± 1.5	19.6 ± 3.1	19.9 ± 8.5	0.57 ± 0.07	0.12 ± 0.07	0.36 ± 0.07
	<i>P. quinquefolia</i>	Sugar Maple	0.21 ± 0.07	324 ± 30	10.7 ± 1.7	5.33 ± 1.8	17.8 ± 2.2	25.5 ± 4.2	0.53 ± 0.05	0.20 ± 0.03	0.22 ± 0.03
		Red Oak	0.27 ± 0.05	224 ± 35	6.45 ± 2.1	4.51 ± 2.0	20.2 ± 2.4	28.3 ± 4.8	0.67 ± 0.05	0.23 ± 0.04	0.11 ± 0.03
		White Ash	0.43 ± 0.05	451 ± 49	10.4 ± 2.9	4.96 ± 1.4	10.8 ± 2.6	18.7 ± 6.0	0.51 ± 0.06	0.30 ± 0.06	0.15 ± 0.05
	<i>R. allegheniensis</i>	Sugar Maple	0.71 ± 0.22	303 ± 45	8.97 ± 2.1	6.31 ± 1.4	19.9 ± 3.2	30.2 ± 4.8	0.65 ± 0.07	0.15 ± 0.05	0.20 ± 0.05
		Red Oak	0.89 ± 0.26	217 ± 45	11.1 ± 2.5	7.58 ± 1.9	33.7 ± 6.3	49.2 ± 7.1	0.68 ± 0.06	0.12 ± 0.07	0.24 ± 0.06
		White Ash	1.66 ± 0.22	272 ± 49	6.68 ± 2.8	4.40 ± 1.3	15.1 ± 2.1	25.2 ± 6.0	0.57 ± 0.06	0.14 ± 0.07	0.24 ± 0.06
	ANOVA										
	Canopy		***(< 0.001)	***(< 0.001)	*(0.03)	** (0.005)	*(0.05)	(0.11)	(0.19)	(0.17)	*(0.05)
	Group		***(< 0.001)	(0.37)	** (0.004)	** (0.002)	** (0.008)	** (0.004)	(0.31)	(0.78)	(0.34)
	Canopy*Group		(0.34)	** (0.001)	*(0.03)	(0.19)	(0.53)	(0.34)	(0.61)	(0.47)	(0.45)

Table 2. Correlation matrix for relative growth rate (RGR), and its determinants: area-based photosynthesis (A_{area}), mass-based photosynthesis (A_{mass}), whole-plant photosynthesis (A_{plant}), leaf area ratio (LAR), specific leaf area (SLA), leaf mass ratio (LMR), root mass ratio (RMR), and stem mass ratio (SMR) as well as leaf lifespan and phenological extension (defined as number of days understory leaves existed prior to and after canopy leaves) for all species grown under three canopy types. Correlations significant at $P < 0.05$ are shown in bold.

Variable	RGR ($\text{mg g}^{-1} \text{d}^{-1}$)	A_{area} ($\text{mmol m}^{-2} \text{d}^{-1}$)	A_{mass} ($\text{mmol g}^{-1} \text{d}^{-1}$)	A_{plant} ($\text{mmol g}^{-1} \text{d}^{-1}$)	SLA ($\text{m}^2 \text{kg}^{-1}$)	LMR (kg kg^{-1})	RMR (kg kg^{-1})	SMR (kg kg^{-1})	LL (days)
RGR									
A_{area}	0.55								
A_{mass}	0.73	0.61							
A_{plant}	0.89	0.58	0.80						
SLA	0.40	0.08	0.55	0.47					
LMR	0.20	0.06	0.02	0.29	0.12				
RMR	-0.09	-0.04	-0.08	-0.10	0.03	0.09			
SMR	-0.02	0.06	0.08	0.01	-0.04	-0.12	-0.55		
LL	0.19	0.13	0.09	0.07	0.22	0.01	-0.10	0.08	
Extension	0.50	0.22	0.35	0.40	0.23	0.06	-0.06	0.06	0.60

Table 3. Summary of relationships between leaf structural, physiological, and phenological characteristics for invasive (IES) and native (NS) seedlings. Relationships include relative growth rate (RGR) in $\text{mg g}^{-1} \text{d}^{-1}$ versus: area-based photosynthesis (A_{area}), mass-based photosynthesis (A_{mass}), whole-plant photosynthesis (A_{plant}), leaf area ratio (LAR), specific leaf area (SLA), and leaf mass ratio (LMR) for all seedlings grown under three canopy types (*A. saccharum*, *Q. rubra* and *F. americana*). Relationships are also given for annual relative growth (RG) in $\text{g g}^{-1} \text{yr}^{-1}$ versus phenological extension (PE; defined as number of days understory leaves existed prior to and after canopy leaves). Regression equations and coefficients of determinations are given. Contrasts of regressions lines are also indicated.

Relationship	IES	NS	ANOVA (IES vs NS)	Slopes
<i>RGR vs</i>				
A_{area}	$= -0.25 + 0.02(A_{\text{area}}), 0.37^{***}$	$= 0.81 + 0.01(A_{\text{area}}), 0.22^{***}$	$F = 0.59, P = 0.44$	$***, \text{IES} > \text{NS}$
A_{mass}	$= 0.89 + 0.23(A_{\text{mass}}), 0.52^{***}$	$= 0.45 + 0.22(A_{\text{mass}}), 0.46^{***}$	$F = 8.41, P = 0.004$	(0.76)
A_{plant}	$= 0.43 + 0.40(A_{\text{plant}}), 0.79^{***}$	$= 0.42 + 0.35(A_{\text{plant}}), 0.78^{***}$	$F = 9.92, P = 0.002$	$*, \text{IES} > \text{NS}$
SLA^{\dagger}	$= -0.12 + 0.50(\ln \text{SLA}), 0.31^{***}$	$= -0.22 + 0.53(\ln \text{SLA}), 0.37^{***}$	$F = 9.23, P = 0.002$	(0.75)
LMR^{\dagger}	$= 1.51 + 0.06(\ln \text{LMR}), (0.66)$	$= 1.53 + 0.32(\ln \text{RGR}), (0.36)$	$F = 1.04, P = 0.31$	(0.52)
<i>RG vs</i>				
Extension	$= 0.22 + 0.007(\text{PE}), 0.11^{***}$	$= 0.14 + 0.003(\text{PE}), 0.16^{***}$	$F = 75.2, P < 0.001$	$*, \text{IES} > \text{NS}$

† Relationships were analyzed between the natural log of variables

$*, P < 0.05; **, P < 0.01; ***, P < 0.001$

Table 4. Summary of relationships between leaf structural, physiological, and phenological characteristics for seedlings grown under three canopy types. Parameters are as defined in Table 3. Regression equations and coefficients of determinations are given. Contrasts of regressions lines are also indicated.

Relationship	Sugar Maple (<i>Acer saccharum</i>)	Red Oak (<i>Quercus rubra</i>)	White Ash (<i>Fraxinus americana</i>)	ANOVA	Slopes
<i>RGR</i> vs					
A_{area}	$= -0.31 + 0.01(A_{area}), 0.32^{***}$	$= 0.54 + 0.01(A_{area}), 0.24^{***}$	$= 1.48 + 0.007(A_{area}), 0.23^{***}$	$F = 12.8, P < 0.001$	(0.41)
A_{mass}	$= 0.29 + 0.23(A_{mass}), 0.59^{***}$	$= 0.93 + 0.21(A_{mass}), 0.47^{***}$	$= 1.31 + 0.22(A_{mass}), 0.46^{***}$	$F = 7.06, P = 0.002$	(0.61)
A_{plant}	$= 0.37 + 0.38(A_{plant}), 0.78^{***}$	$= 0.56 + 0.36(A_{plant}), 0.69^{***}$	$= 0.51 + 0.42(A_{plant}), 0.84^{***}$	$F = 9.75, P < 0.001$	(0.17)
SLA^{\dagger}	$= -0.12 + 0.49(\ln SLA), 0.31^{***}$	$= -0.30 + 0.53(\ln SLA), 0.38^{***}$	$= -0.02 + 0.51(\ln SLA), 0.31^{***}$	$F = 6.52, P = 0.002$	(0.72)
LMR^{\dagger}	$= 1.44 + 0.21(\ln LMR), (0.31)$	$= 1.45 - 0.69(\ln LMR), 0.08^{*}$	$= 2.04 + 0.73(\ln LMR), (0.09)^{**}$	$F = 1.36, P = 0.32$	$^{*}, A > M > O$
<i>RG</i> vs					
Extension	$= 0.19 + 0.006(PE), 0.06^{*}$	$= 0.13 + 0.013(PE), 0.15^{***}$	$= 0.18 + 0.007(PE), 0.10^{***}$	$F = 70.8, P < 0.001$	(0.33)

† Relationships were analyzed between the natural log of variables

$^{*}, P < 0.05; ^{**}, P < 0.01; ^{***}, P < 0.001$

FIGURE LEGENDS

Figure 1. Boxplots showing annual relative growth for invasive (IES; dark) and native (NS; light) species grown under each of three different canopy types: sugar maple (*A. saccharum*; blue), red oak (*Q. rubra*; green), and white ash (*F. americana*; red). Boxes represent 25-75% of the data with the whiskers extending from minimum to maximum values. Within boxes, solid lines indicate medians. The asterisks identify significant differences between IES and NS within a canopy type at $P < 0.01$ (**) levels.

Figure 2. Relative growth ($\text{mg g}^{-1} \text{ yr}^{-1}$) over two growing seasons in relation to extended plant lifespan beyond canopy-on periods (in days) for A) all seedlings, B) invasive (IES; black circles and line) and native (NS; grey circles and line) species groups, and C) seedlings grown under three different canopy types; white ash (*F. americana*, black circles, solid line), sugar maple (*A. saccharum*, white circles, dotted line), and red oak (*Q. rubra*, grey circles, solid line). Regression equations are given in Tables 3 & 4.

Figure 3. General relationships between RGR and estimated daily integrals of photosynthesis per unit (A) leaf area (A_{area}), (B) leaf mass (A_{mass}), and (C) plant mass (A_{plant}), where $n = 256$. $P < 0.0001$ for all regressions. Relationships are given for all seedlings, invasive (IES; black) and native (NS; grey) species groups (D-F), and seedlings grown under three different canopy types (G-I): white ash (*F. americana*) (black points, solid line), sugar maple (*A. saccharum*) (white points, dotted line), and red oak (*Q. rubra*) (grey points, solid line). Regression equations are given in Tables 3&4.

Figure 4. General relationships of \ln relative growth rates (RGR) versus its morphological (specific leaf area, SLA) and allocational (leaf mass ratio, LMR) determinants. Where (A) is the average \ln SLA for all seedlings, (B) \ln LMR for all seedlings, $P < 0.001$ and 0.36, respectively. Relationships are given for all seedlings, invasive (IES; black) and native (NS; grey) species groups (C&D), and seedlings grown under three different canopy types (E&F); white ash (black points, solid line), sugar maple (white points, dotted line), and red oak (grey points, solid line). Regression equations are given in Tables 3&4. Trend lines and R^2 s are only shown for significant (at $P < 0.05$) relationships.

Figure 5. Variation in average (\pm SE) growth response coefficients (GRCs) of LAR (squares), GAR (diamonds), and CUE (triangles) along a gradient in photoperiod average photon flux density (PPFD) for invasive exotic species (IES) (black) and native species (NS) (white). Note that the lowest light level corresponds to seedlings grown under sugar maple (*A. saccharum*), followed by red oak (*Q. rubra*) followed by white ash (*F. americana*) canopies. * identifies significant differences between IES and NS within a treatment at $P < 0.05$. Full species names are in Table 1.

FIGURES

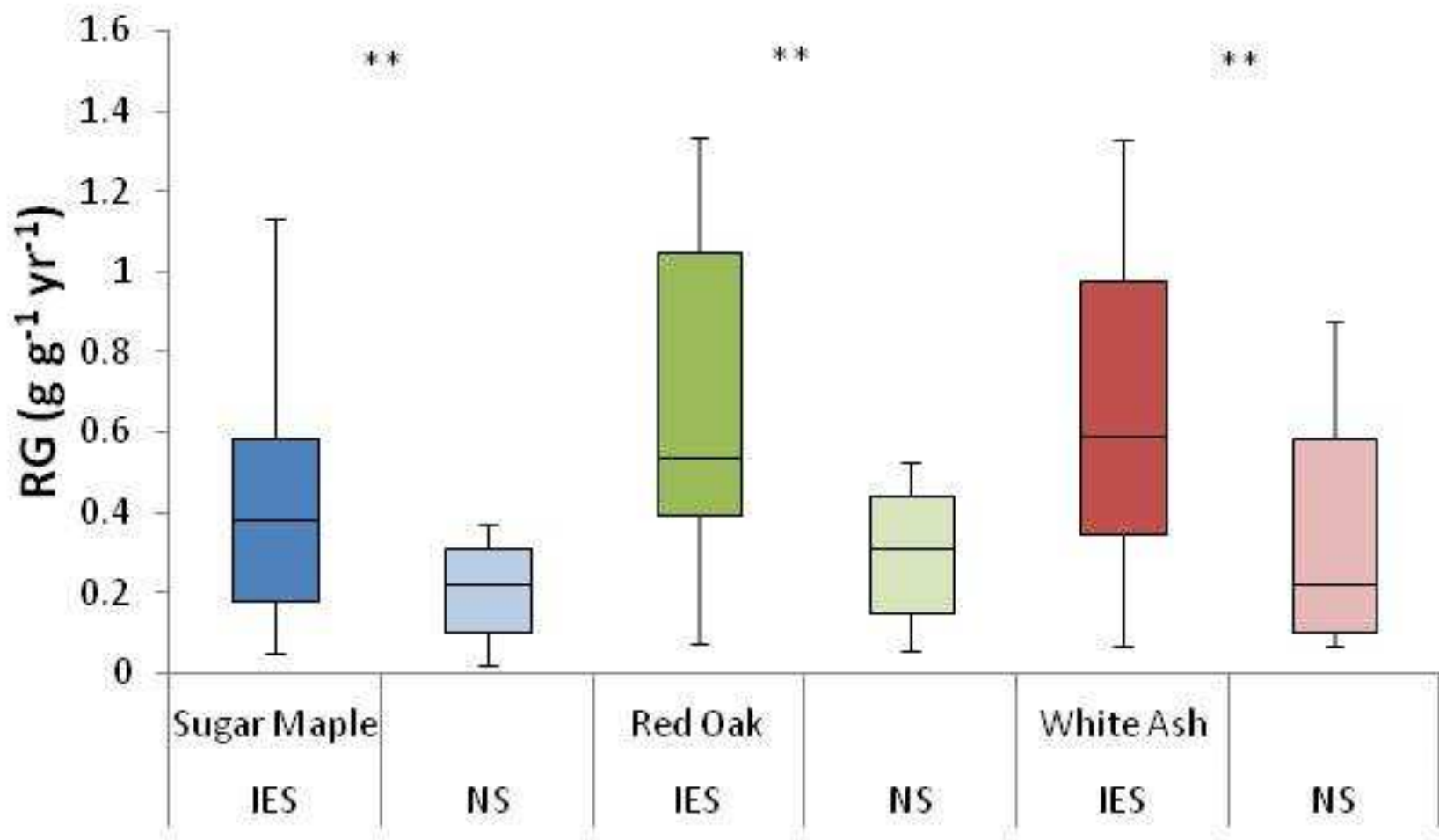


Figure 2

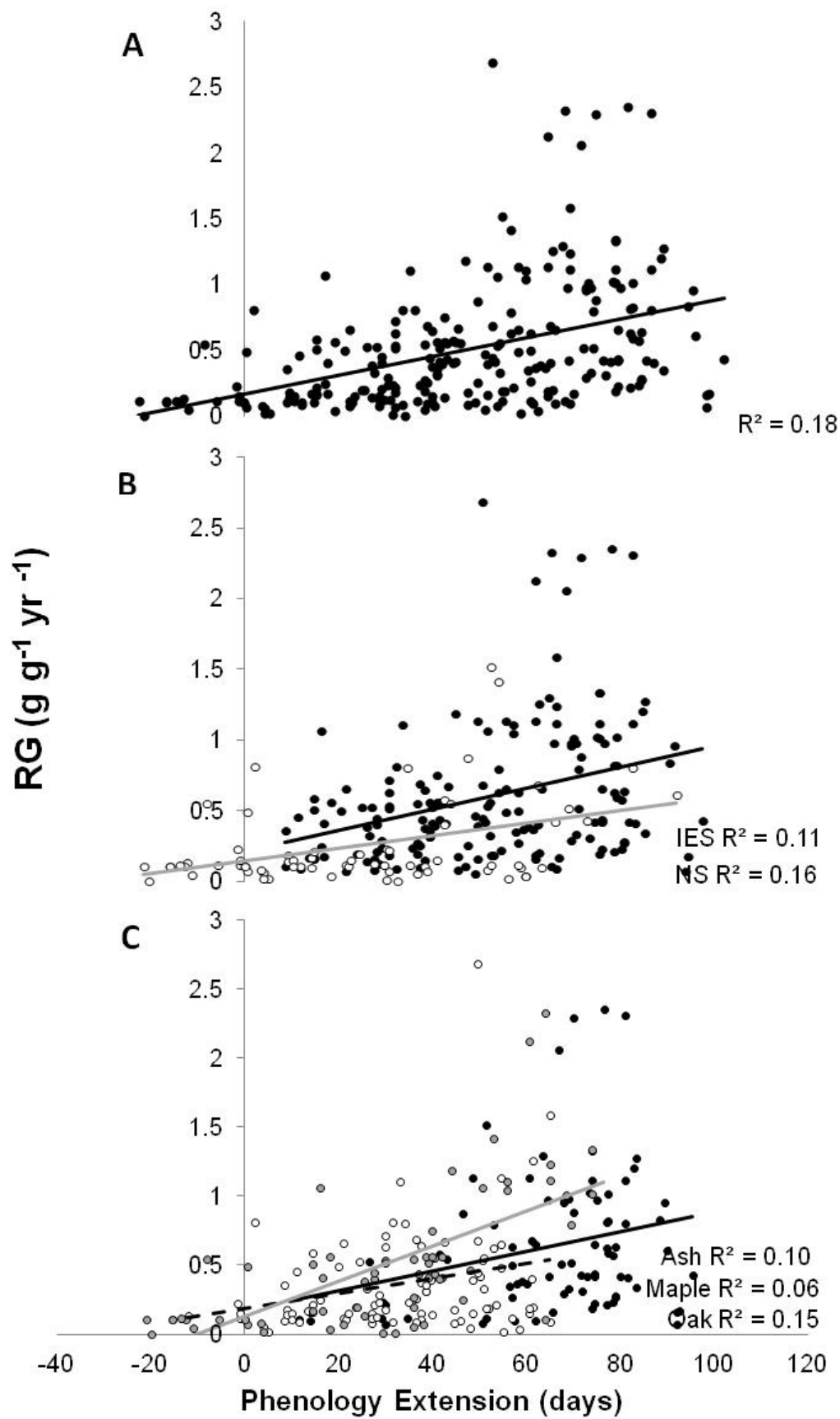


Figure 3

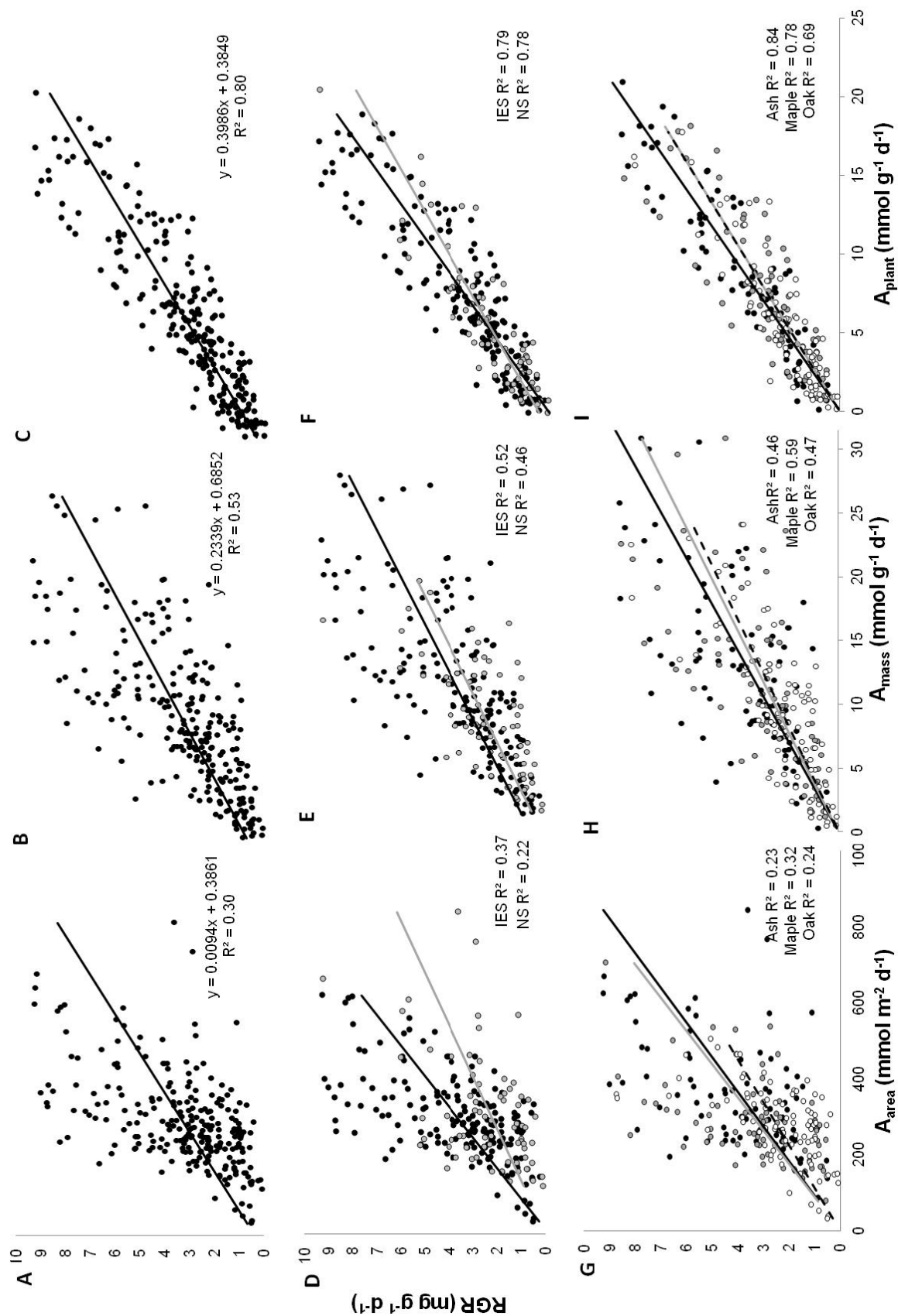


Figure 4

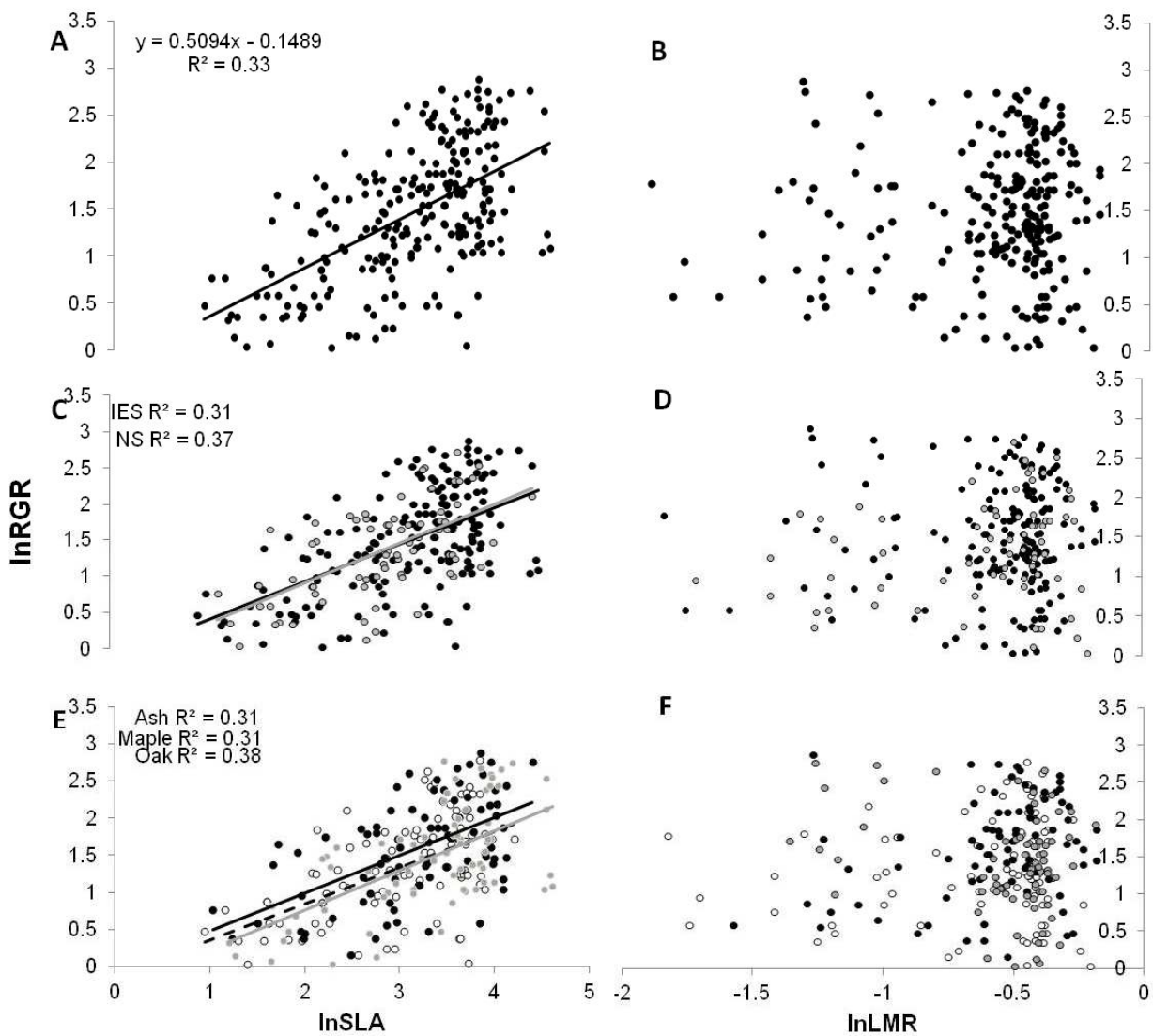
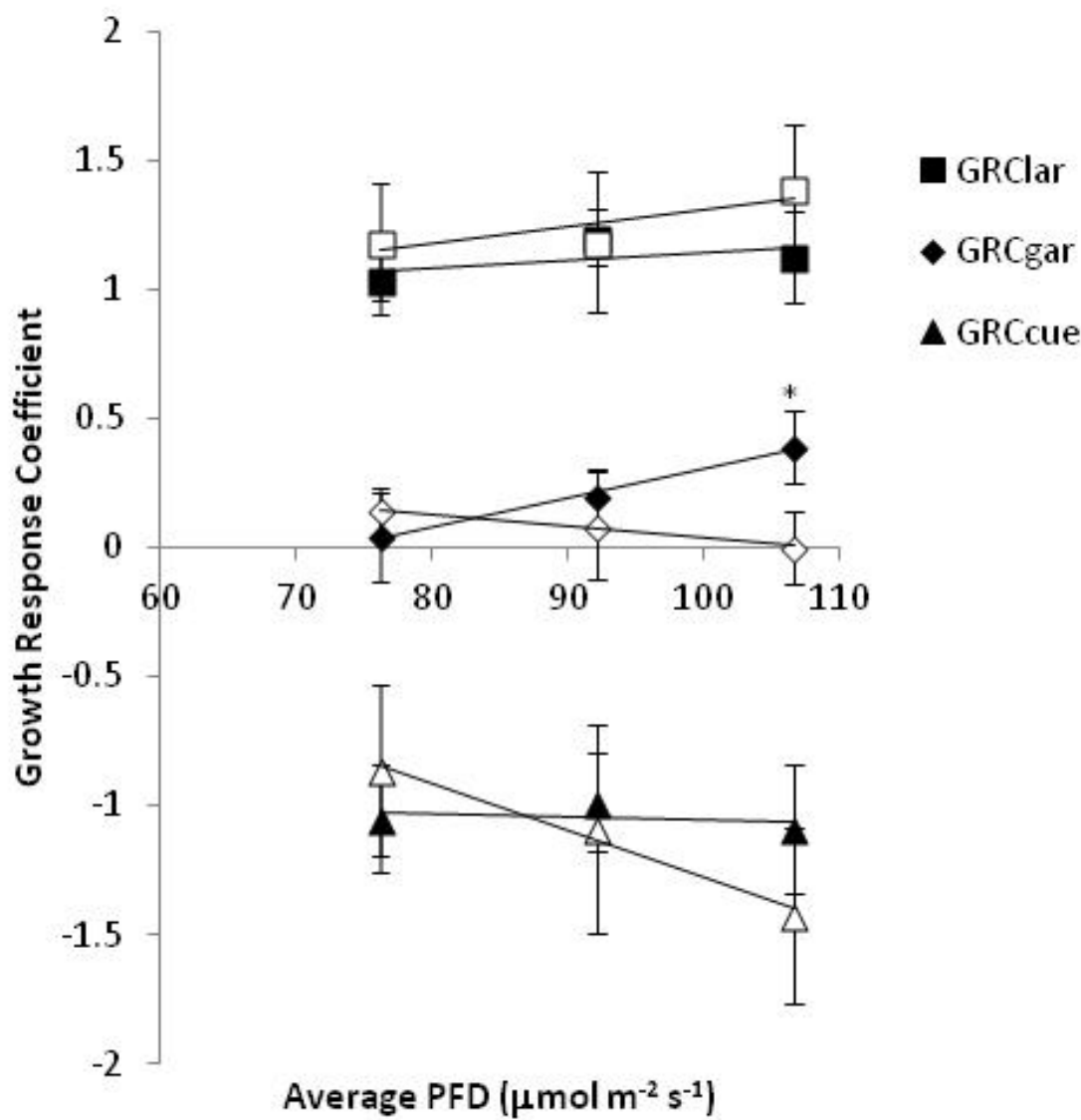


Figure 5



	LAR	GAR	CUE
IES	$= 0.003(\text{PFD}) + 0.839, R^2 = 0.32$	$= 0.012(\text{PFD}) - 0.843, R^2 = 0.99$	$= -0.034(\text{PFD}) + 2.36, R^2 = 0.83$
NS	$= 0.0067(\text{PFD}) + 0.638, R^2 = 0.73$	$= -0.005(\text{PFD}) + 0.498, R^2 = 0.98$	$= -0.018(\text{PFD}) + 0.545, R^2 = 0.98$

CHAPTER THREE

CLARIFYING THE IMPLICATIONS OF OVERSTORY PHENOLOGY FOR LEAF- LEVEL CARBON GAIN BY NATIVE AND INVASIVE EXOTIC SPECIES IN DECIDUOUS FOREST UNDERSTORIES

ABSTRACT

Invasive exotic plant species (IES) may gain an advantage over native species (NS) in temperate forest understories by extending annual photosynthetic activity into pre- and post-canopy periods of high resource availability and low competition. However, the potential advantage of extended leaf activity is mediated by seasonal climate dynamics and overstory phenology. I developed a stochastic model of leaf photosynthesis based on its responses to seasonal trends in air temperature and light availability to examine leaf-level carbon gain under canopy species with different phenologies. Results supported my hypotheses in that IES gained more carbon than did NS, especially under canopies that provided greater understory light availability (*i.e.*, later spring phenophases, shorter leaf lifespans, and higher transmittance). Also supported was my hypothesis positing that pre-canopy photosynthetic activity would be more significant than post-canopy activity in contributing to annual carbon gain. Advantage of IES may be attributed to greater temporal niche breadth, greater temperature response, and enhanced photosynthetic capacity during spring and summer. This highlights the importance of community-level phenological interactions and seasonal physiological responses that affect growth of IES in temperate forest understories.

ABBREVIATIONS

A – Photosynthetic Rate;
 A_{\max} – Maximum Photosynthetic Rate;
AQY - Apparent Quantum Yield;
 E_v – Activation Energy
IES – Invasive Exotic Species;
LCP – Light Compensation Point;
NA – Net Assimilation;
NS – Native Species;
PAR – Photosynthetically Active Radiation;
 R_d – Dark Respiration Rate

INTRODUCTION

The ability of invasive exotic plant species (IES) to rapidly colonize and dominate deciduous forest understories in eastern North America has been attributed to myriad factors (*e.g.*, Martin *et al.* 2009). One of the more recently investigated contributors is an extended duration of annual photosynthetic activity in IES foliage, often as a result of different and more plastic phenologies compared to those of native species (NS) (Davidson, Jennions & Nicotra 2011; Wolkovich & Cleland 2011). Leaf lifespan may be extended via earlier spring budbreak (Xu, Griyn & Schuster 2007; McEwan *et al.* 2009) and leaf flush (Harrington, Brown & Reich 1989) or delayed autumnal abscission (Harrington, Brown & Reich 1989; Zotz *et al.* 2000; Fridley 2012), resulting in a broader temporal niche and enhanced carbon gain (Uemura 1994). Extended leaf lifespan commonly occurs in temperate forest seedlings (Seiwa 1998), saplings (Gill, Amthor & Bormann 1998; Seiwa 1999), understory trees (DePhamphillis & Neufeld 1989), and shrubs (Gill, Amthor & Bormann 1998), and is particularly beneficial if it results in photosynthetic activity when the canopy is leafless. Given favorable conditions for photosynthesis (*i.e.*, air and soil temperatures $> 5^{\circ}\text{C}$), pre- and post-canopy periods of high light exposure and low competition may result in a significant amount of carbon gain for growth and survival in otherwise heavily shaded understories (Gill, Amthor & Bormann 1998; Davis *et al.* 2000; Augspurger 2008). Nonetheless, the benefits of extended temporal niche breadth and, thus, the potential competitive advantage of IES over NS, are mediated by two environmental factors, overstory canopies that drive understory light availability via transmittance and phenology, and air temperature.

Light is a limiting resource for understory growth, and is a function of transmission (quantity and quality) and seasonality (timing of availability). Although light transmission accounts for a significant amount of the variation in understory growth (Pacala *et al.* 1994; Kobe *et al.* 1995; Finzi & Canham 2000), few recognize the role of phenology in seasonal light capture and availability (Harrington, Brown & Reich 1989; Gill, Amthor & Bormann 1998; Kawamura *et al.* 2001; Routhier & Lapointe 2002; Jolly *et al.* 2005; Richardson & O'Keefe 2009). Both light transmission and phenology can differ considerably

among deciduous tree species. Consequently, *in situ* availability of understory light is regulated by overstory species composition and varies in space and time (Kato & Komiyama 2002). For example, in the northeastern United States, spring leaf flush in sugar maple (*Acer saccharum*) typically occurs 1-3 weeks earlier than in red oak (*Quercus rubra*) and white ash (*Fraxinus americana*) (Salisbury 1916; Lechowicz 1984; Dreiss & Volin 2013). In the autumn, white ash canopies abscise with sugar maple, and up to four weeks before red oak. All else being equal, a species with extended temporal niche breadth will acquire a greater annual carbon subsidy if located under white ash due to a short canopy leaf lifespan and large windows of high light exposure in spring and autumn. Furthermore, if IES exhibit longer leaf lifespans, IES advantage may also be greater under white ash canopies compared to canopies with earlier spring phenophases and longer leaf lifespans. Dreiss & Volin (2013) found higher IES presence in temperate deciduous forests dominated by white ash as a result of both later spring phenophases and higher light transmission through the canopy. However, relatively little is known regarding overstory phenological influences on understory carbon gain and its potential role in IES growth success.

An important step toward understanding responses of IES and NS to canopy phenology lies in investigation of critical periods for carbon acquisition. Daily carbon gain in the understory is correlated with total daily light availability, which is greatest during pre-and post-canopy periods (Kuppers 1984; Ellsworth & Reich 1993). Mathematical models predict that alteration of phenology to match these periods of high light availability results in maximum carbon gain (Iwasa & Cohen 1989; Kikuzawa 1991). Although pre- and post-canopy conditions provide ample understory light, these periods may not be equal in their contributions to annual carbon gain. The potential for phenological adjustment by understory plants to enhance carbon gain depends on the amount of irradiance and plant physiological capacity during these periods. Irradiance in spring and autumn is not equivalent (Hutchison & Matt 1977; Gill, Amthor & Bormann 1998) because higher solar elevation angles in the spring result in greater light transmission through the overstory (Baldocchi *et al.* 1984; Constabel & Lieffers 1996). Higher light environments are matched by greater leaf areas and chlorophyll activities in the spring, but these may differ among understory species (Harrington, Brown & Reich 1989; Seiwa 1998; Königer *et al.* 2000;

Morecroft *et al.* 2003). Later autumnal abscission may result in late season respiratory losses that exceed carbon gains (Piao *et al.* 2008) or negative effects on nutrient retranslocation and storage (Killingbeck *et al.* 1990; Niinemets & Tamm 2005; Weih 2009). Either of which might explain why some studies report little-to-no extension of temporal niche breadth by understory species after canopy abscission (DePhamphillis & Neufeld 1989; Gill, Amthor & Bormann 1998; Augspurger & Bartlett 2003; Augspurger *et al.* 2005). Conversely, recent work suggests that while post-canopy activity may not be the greatest contributor to annual carbon gain, it may be more common in IES, potentially providing an advantage over NS in the understory (Fridley 2012). In either case, the role of phenology in providing a growth advantage to IES in temperate forest understories is two-fold; extended understory leaf lifespan may allow IES to take advantage of a vacant niche (Wolkovich & Cleland 2011) and canopy phenology may control the amount and fluctuation of unused resources during that niche (Davis *et al.* 2000). As such, a community-level assessment of phenology and its role on physiological responses of IES and NS may help elucidate the apparent success of IES in the temperate forest understory.

Temperature is another important determinant of growing season length and plant photosynthetic activity. Growth initiation of understory plants is influenced by snowmelt and temperature of air and soil (Fitter *et al.* 1995), while the timing of canopy closure is related to the air temperature of the previous month (Menzel 2003; Gordo & Sanz 2005). In autumn, deciduous plants shed their leaves to avoid colder temperatures that are unfavorable for photosynthesis (Estrella & Menzel 2006). Based on ecological attributes (*e.g.*, greater plasticity, rapid evolutionary change, broader environmental tolerances, greater phenological tracking), IES may disproportionately benefit from an increase in temperature. Nonetheless, comparative temperature tolerances and responses of IES and NS are not well documented (Dukes *et al.* 2009). Temperature responses of understory species likely vary because the temperature response of photosynthesis itself varies with genotype, environmental conditions, and growth temperature (Slayter & Morrow 1977; Berry & Björkman 1980; Lewis, Olszyk & Tingey 1999). For example, the relationship between photosynthesis and leaf temperature differs with light intensity, leading to seasonal variation in physiological activity (Ludlow & Wilson 1971). Moreover, photosynthesis can be more sensitive to leaf

temperature in certain times of the season (Schwarz, Fahey & Dawson 1997; Bassow & Bazzaz 1998); understory individuals may act as "sun" plants in the spring prior to moving into summer shade (Augspurger 2008). As such, understanding the responses of leaf photosynthesis to variation in leaf temperature is fundamental for predicting seasonal variations in plant carbon gain. A more comprehensive understanding of the effects of temperature response of *in situ* productivity requires information about light responses at multiple temperatures (Berry & Björkman 1980). Consequently, models predicting carbon gain, growth, or survival may need to be modified to include seasonal variations in light and temperature.

The influence of different overstory phenologies on understory growth, the growth sensitivities of IES and NS to pre- and post-canopy periods, and the seasonal variation in photosynthetic temperature response is not well understood. The objective of this study was to examine growth responses of understory IES and NS to differences in seasonal phenology and temperature under different overstory species. I developed a stochastic model of photosynthesis to predict effective carbon gain as a function of understory photosynthetically active radiation and temperature. I hypothesized that carbon gain of IES would exceed that of NS under all environmental conditions due to extended temporal niche breadth and that this advantage would be most pronounced under canopies that have higher transmittance, later spring phenophases, and shorter leaf lifespans. I also hypothesized that the growth advantage of IES over NS would be influenced most by pre-canopy periods due to greater plant photosynthetic capacities in the spring versus autumn.

METHODS

Common Gardens

The hypotheses were tested using a set of common gardens located at the University of Connecticut (41.80° N, 72.25° W). Study sites were selected based on the dominant overstory canopy

species (*i.e.*, sugar maple, white ash or red oak), which are of ecological importance to the region and represent a range of phenological traits and understory light transmittance (Dreiss & Volin 2013; see Chapter 1 Fig. 1). Gardens were constructed under three stands of each canopy type resulting in nine planted gardens. Gardens consisted of 4 x 4 m fenced enclosures in which at least the enclosures in which 0.33 m of topsoil was excavated and replaced with a common experimental soil (5:1 volume mixture of sand and soil extracted and mixed from all forest sites). Slow release fertilizer was added to all gardens every other month (Osmocote 15:9:12, The Scotts Company, Marysville, OH, USA). Eight species, four IES and four NS, representing three functional groups (shrub, subshrub, and vine), were used. The four IES included two shrubs, *Euonymus alatus* (burning bush) and *Berberis thunbergii* (Japanese barberry), a subshrub, *Rosa multiflora* (multiflora rose), and a vine, *Celastrus orbiculatus* (oriental bittersweet). Similarly, four commonly co-occurring NS included two shrubs, *Kalmia latifolia* (mountain laurel) and *Lindera benzoin* (spicebush), a subshrub, *Rubus allegheniensis* (blackberry), and a vine, *Pathenocissus quinquefolia* (Virginia creeper). Between twenty and thirty-five individuals of each species were transplanted into each site. Individuals were collected from the field during the summer of 2013, transplanted in a stratified random manner with regards to canopy type and site and labeled in each garden matrix (1,665 plants total). Initial plant sizes ranged from 0.02 – 0.48 g. Plants were watered weekly to maintain field capacity and were allowed to acclimate for a full growing season (*i.e.*, 2014) before diagnostic gas exchange measurements were conducted.

Field Measurements

Critical phenophases in overstory and understory vegetation were tracked for all species in all gardens every other day during February – May and August – January (see Dreiss & Volin 2013). Julian dates of initial and full leaf flush in spring and leaf color and leaf abscission in the fall (Komiya, Kato & Teranishi 2001). Garden environments were characterized by understory PAR and temperature in 10-

minute intervals using fixed-position *Hobo H21-002* sensors and dataloggers (Onset, Inc, Cape Cod, MA, USA) at understory plant height.

Diagnostic gas exchange was measured *in situ* using a LI-6400 portable photosynthesis system (Li-Cor Biosciences) for 4-5 days per week from May to November 2015 on fully expanded leaves (30-50 gas exchange curves per species and canopy type, *i.e.*, ~1,030 photosynthetic temperature light response curves were conducted over the course of the season) to determine species-specific photosynthetic responses to seasonal variation (Man & Lieffers 1997; Xu, Griyn & Schuster 2007). Photosynthetic light responses were assessed during morning hours (8:00-11:30AM), across a range of leaf temperatures, throughout the growing season using five light (photosynthetically active radiation; PAR) levels ranging from 25 to 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Temperatures included ambient and $\pm 5^\circ \text{C}$ to determine photosynthetic responses to warming and cooling.

The photosynthetic light response model of Hanson *et al.* (1987) was used in a nonlinear least squares analysis to compute maximum photosynthetic rate (A_{max}), dark respiration (R_d), light compensation point (LCP), and apparent quantum yield (AQY):

$$A = A_{\text{max}} (1 - [1 - R_d/A_{\text{max}}]^{1 - \text{PAR/LCP}}) \quad (\text{eqn 1})$$

Comparisons of annual net assimilation (NA) between IES and NS in the various canopy types were based on a combination of destructive measures and nondestructive, allometric estimates of plant biomass (*sensu* Kaelke *et al.* 2001). At the beginning of the growing season in 2015, two leafless individuals per species were harvested in each garden, and all harvested as well as non-harvested plants were measured for stem basal diameter (D , 2 cm above the soil surface) and total height (H , from ground line to the base of the terminal bud). Diameter and height were measured again for all seedlings in July and November. Species-specific linear regressions were developed, in which the total dry mass of harvested plants is regressed against a stem volume index (D^2H , cm^3) *sensu* Kaelke *et al.* (2001) (see Chapter 1 Table S1). In July of 2014 and 2015, 6-11 individuals per species were harvested from each

garden. Roots, stems and leaves of harvested plants were separated and leaf area was measured. ImageJ software was used to calculate leaf area for each individual and species-specific regressions between leaf area and seedling mass were used to estimate leaf area at the start of the growing season in April. Net assimilation in $\text{g m}^{-2} \text{yr}^{-1}$ was calculated based on two growth phases: an exponential phase from April to July harvest and a linear phase from July harvest to November.

$$\text{NA (g)} = \{[(M_2 - M_1)] * [(\ln L_2 - \ln L_1)/(L_2 - L_1)] * LL_1\} + \{[(M_3 - M_2)]/L_2 * LL_2\} \quad (\text{eqn 2})$$

where, M is mass in grams and L is leaf area in April (1), July (2), and November (3), respectively and LL is the leaf lifespan in days from leaf flush to harvest (1) and harvest to leaf abscission (2). This approach is predicated on the assumption that production of new leaf area was negligible after harvest (Xu, Griyn & Schuster 2007), which was true for all species except the subshrubs. As such, the NA calculation was modified as a single exponential growth phase from leaf flush to abscission for these species.

Model

A mechanistic temperature-dependent carbon balance model was created to facilitate evaluation of the role of variation in temporal niche breadth (Wolkovich & Cleland 2011) in the performances of IES and NS under sugar maple, white ash, and red oak canopies. The model projected carbon gain for each of the eight understory species given empirical physiological attributes, phenological observations, leaf area estimates, and garden environment (PAR and temperature).

For each species, the average date of full flush and abscission defined the bounds of the simulated growing season. The model stochastically estimated daily whole-plant carbon gain per unit plant area for the growing season by treating photosynthetic parameters as random variables sampled from empirical Gaussian distributions. Temperature dependence of photosynthetic parameters A_{max} , R_d , and LCP, along with AQY and stomatal conductance (g_s), were modeled using the Arrhenius function:

$$P = P_n * \exp(E_v/0.008314*(1/293-1/(273+T))) \quad (\text{eqn 3})$$

where P is the parameter, P_n is the parameter normalized at leaf temperature n , E_v is the activation energy, and T is the air temperature of the garden, which was assumed equal to leaf temperature. Activation energies, the minimum energy necessary for particular reactions to take place, provide a quantitative description of plant processes based on thermodynamic considerations and are often used to characterize changes in plant photosynthetic characteristics with temperature variation (Hikosaka *et al.* 2006). For each parameter, temperature-normalized values and activation energies were calculated at the leaf-level given data for each combination of species, canopy type, and month. The temperature at which parameters were normalized was determined by the average mid-day temperature of that month. Average and standard error were determined for temperature-normalized values and activation energies across leaves of a species given the canopy type and month of measurement.

Photosynthesis (A) was calculated for each 10-minute interval by substituting the Arrhenius equation (eqn 3) into the Hanson *et al.* (1987) model of light response (eqn 1) for each corresponding photosynthetic parameter. Each temperature-normalized value and activation energy was sampled from empirical Gaussian distributions for leaves within a species, given the canopy type, and month being modeled. PAR and T were taken from the garden environment dataset.

For each day a plant had leaves, it assimilated carbon according to the function:

$$\text{C gain (g)} = \Sigma[A \times 600 \times (12 \times 10^{-6})] \quad (\text{eqn 4})$$

where A is stochastic photosynthesis as described above and the constants convert seconds to 10-minute intervals and μmol to grams. Carbon gain per unit leaf area accounted for responses to fluctuating light and air temperature and was calculated for each 10-minute interval that garden conditions were recorded. Carbon gain at 10-minute intervals was added up for each day across the entire growing season. The simulation included 1,000 permutations of annual trajectories of carbon gain per unit leaf area over a

growing season (approximately late March through November). The model was run for each understory species (8) under each canopy type (3), resulting in a total of 24 models.

Statistical Analyses

Statistical analyses were performed using JMP v. 5.0 and SAS v. 9.3 (The SAS Institute). Model inputs (*i.e.*, activation energies and temperature-normalized values) for all photosynthetic parameters were compared across species, canopy types, and months using mixed-effects, two-way ANOVAs and validated with observed leaf-level field measurements. Due to lower sample size compared to other months, July measurements were grouped with August values for model parameterization. To ensure that input parameters were valid representations of typical leaf behavior, leaf-level observations were compared to predicted values, estimated via a minimization of sums of squares for error (SSE) resulting from the comparison of observed and predicted parameter values (Excel Solver, Microsoft Corp., Redmond, WA, USA).

Validation graphs and regressions were used to assess the performance of the model comparing observed NA with predicted values of biomass gain per unit leaf area estimated from model outputs. For this comparison, a tissue [C] concentration of 50% dry mass was assumed (Penuelas & Estiarte 1997; Thomas & Martin 2012). Model outputs were compared among understory species and across canopy type using two-way ANOVAs. Simulated carbon gain was also pooled to test general differences between IES and NS ($n = 6$). Carbon gain during pre-, during-, and post-canopy periods was calculated as a raw total and percent of the entire growing season and standardized by day for each species. Significant mean differences among species and canopy type were determined at $P < 0.05$.

RESULTS

Garden Measurements

The period of favorable conditions for photosynthesis (*e.g.*, when air temperatures $> 5^{\circ}\text{C}$) was March 28 – November 15. During this period, understory vegetation had more access to light beneath white ash ($2,229 \pm 57 \text{ mol m}^{-2}$) understories received more total seasonal light than did canopies of red oak ($1,926 \pm 54 \text{ mol m}^{-2}$) or sugar maple ($1,593 \pm 61 \text{ mol m}^{-2}$) ($F_{2,8} = 30.6$, $P < 0.001$; see Chapter 1 Fig. 2). This was due to greater light transmitted during canopy-on periods for white ash compared to each of the other canopy species ($F_{2,8} = 25.8$, $P = 0.001$) as well as greater opportunities for pre-canopy light than sugar maple ($F_{1,5} = 9.8$, $P < 0.01$) and post-canopy light than red oak ($F_{1,5} = 19.2$, $P = 0.002$). Understory air temperature did not differ significantly among canopy types (see Chapter 1, Fig. S1).

In the understory, leaf flush occurred significantly earlier and abscission significantly later in IES than in NS ($t_{1149} = 4.59$ and 3.66 , respectively, $P < 0.001$ for each; Fig. 1). Temporal niche breadths were significantly different between IES and NS within each functional group, except for subshrubs (subshrubs, $P = 0.2$; shrubs and vines, $P < 0.001$ for each, see Chapter 1).

Gas Exchange Parameters

In a comparison of model inputs, activation energies were significantly lower for A_{max} than for other gas exchange parameters (*i.e.*, R_d , LCP, AQY and g_s), while others varied significantly across the growing season, quickly declining in the autumn (Table 1 & S1). IES exhibited significantly greater activation energies than in NS for R_d , LCP, and g_s ($P < 0.001$, $P = 0.007$, and $P = 0.002$, respectively), though this varied by month and canopy type (Table 1). In particular, temperature response was greater in IES than NS for LCP in May, June, and August (canopies pooled, $P = 0.05$, $P < 0.001$, and $P < 0.001$, respectively), for R_d in June and August ($P < 0.01$ and $P = 0.01$, respectively), and for g_s in May, September and October ($P = 0.03$, $P = 0.04$ and $P = 0.02$, respectively).

Like activation energies, all temperature-normalized gas exchange parameters exhibited similar seasonal variation to temperature response, with significantly lower values in the fall (Table 1). Values of A_{\max} were significantly higher in IES than NS in June both when analyzed by canopy ($P < 0.01$ for each) as well as when canopies were pooled ($P < 0.001$). IES also exhibited greater photosynthetic capacity than did NS under sugar maple canopies with higher g_s in May, June, and August ($P = 0.04$, $P = 0.002$, and $P = 0.03$, respectively) and lower LCP in May and June ($P = 0.03$ and $P = 0.001$, respectively) (Table 1).

Model Validation

Simulations of plant carbon gain were conducted for eight understory species (four IES and four NS) and three canopy types (sugar maple, white ash and red oak) with corresponding environmental conditions (PAR and temperature). Comparison between predicted and observed values for stochastic parameters (A_{\max} , R_d , and LCP), stomatal conductance (g_s), and apparent quantum yield (AQY) were assessed for model validation. Simulation errors were generally small as indicated by the linearity and slopes near unity for the comparison of simulated and observed values (Fig. 1). Model predictions of seasonal carbon gain slightly overestimated observed net assimilation ($R^2 = 0.73$, Fig. 2).

Simulated Growth

Overall, simulated carbon gain was significantly greater under white ash than under red oak or sugar maple canopies ($F = 3.93$, $P = 0.02$) (Fig. 3A). For each understory species, carbon gain was significantly greater under white ash and red oak than sugar maple with the exception of the native vine Virginia creeper (*P. quinquefolia*) (Table 2). IES gained significantly more carbon than did NS across all canopy types ($t = 8.46$, $P < 0.001$; Fig. 2, Table 2) and IES advantages were significantly greater under white ash and red oak than under sugar maple canopies ($F = 4.23$, $P = 0.017$). On average, IES gained

17.3 \pm 2.1 % of their annual carbon prior to co-occurring NS becoming photosynthetically active, and 3.0 \pm 1.0 % of carbon after NS abscission. The amount of simulated carbon gain was significantly different among species ($F = 6.91$, $P < 0.001$; Table 2) and greater for subshrubs than shrubs or vines ($F = 7.0$, $P = 0.001$). Within functional groups, there was no significant difference between IES and NS in subshrubs ($P = 0.39$; Table 2, Fig. 3B).

For all species and canopy types, canopy-on periods contributed significantly more to annual carbon gain ($P < 0.001$; Table 2). When standardized on a daily basis, however, pre-canopy days contributed significantly more carbon than did other seasons (1.9, 0.4, and 0.4 % per day for pre-, during-, and post-canopy, respectively; $P < 0.001$, Table S2). Within each canopy type, pre-canopy carbon gain was significantly greater in IES compared to NS, while carbon gain during canopy-on periods was significantly less in IES than NS (Table 2). Post-canopy carbon gain was not significantly different between IES and NS. When pooled across canopies, however, significant differences in carbon gain existed between IES and NS during pre-canopy and canopy-on periods, but not post-canopy.

DISCUSSION

I used *in situ* leaf-level, diagnostic, photosynthetic temperature light response measurements throughout the growing season to model the complex physiological responses of IES and NS to environmental variation under different deciduous canopy species. The output was a prediction of carbon gain based on the species-specific sensitivity to interactions of light and temperature. Temperature-normalized physiological measurements and simulation results supported my hypothesis that IES, occupying a broader temporal niche gain an advantage over NS under canopies with shorter leaf lifespans. This suggests that interactions between canopy and understory phenologies influence annual carbon gain in the understory. In addition, IES exhibited greater temperature response and photosynthetic capacities than did NS in spring and summer, potentially amplifying the contributions of pre-canopy photosynthetic activity to annual carbon gain and IES advantages. To my knowledge, no other study has 1) sampled this

extensively across a growing season, 2) incorporated a community-level approach to temporal phenological niche breadth, and 3) modeled temperature-dependence from light response curves to investigate IES growth success over NS. This approach was effective in incorporating the variability of environmental conditions for an *in situ* growth analysis of different co-occurring understory species. As such, it allowed me to elucidate the importance of canopy phenology on understory resource availability and differentiate the contributions of temporal niche breadth to annual carbon gain.

Overstory species had a significant influence on light availability and effective annual carbon gain in the understory. Among those studied, white ash understories experienced the greatest amount of light over the growing season, due to both higher light transmission when canopy leaves were present and shorter leaf lifespans (*i.e.*, later spring and earlier fall phenophases). The positive effects of higher light transmission on plant growth and development are well documented, with plants often exhibiting greater photosynthetic capacity, relative growth rate, and biomass production with increasing light availability (Pattison *et al.* 1998; Baruch *et al.* 2000; Meekins & McCarthy 2000; Athanasiou *et al.* 2010). In my study, maximum photosynthetic rates were higher under white ash canopies in June, but only significantly so for IES species. However, greater seasonal light availability in white ash understories was also attributed to relatively later spring flush and earlier leaf abscission, which provided greater windows of high light to the understory and higher carbon gain in spring and autumn compared to those growing under other canopies. Consequently, carbon gain was greater for almost all understory species growing under white ash. The exception was the native vine (*P. quinquefolia*), which had the shortest temporal niche breadth of the studied understory species. This was a result of being the latest to flush its leaves in the spring and the earliest to abscise in the late summer, failing to take full advantage of either pre- or post-canopy high light conditions. Data from Fridley (2012) also suggest that autumn is a critical period for carbon assimilation in IES vines of the *Lonicera* genus, which gained more carbon during post-canopy conditions than related NS.

Under all canopy types, IES were able to achieve greater annual carbon gain than did NS (see Fig. 3). IES may compete more successfully for irradiance through several mechanisms including greater

photosynthetic capacity. Greater photosynthetic capacity can be achieved through many physiological traits including higher A_{\max} , AQY, and stomatal conductance or lower R_d or LCP (Pattison *et al.* 1998; Kruger & Volin 2006). In particular, stomatal conductance can impose a large resistance to diffusion of CO_2 and rates of leaf gas exchange (Wong, Cowan & Farquhar 1979; Farquhar & Sharkey 1982). Like previous studies, my results suggest higher conductance for IES in pre-canopy periods (Carter & Teramura 1988; McDowell 2002; Deng *et al.* 2004; Xu, Schuster & Griffin 2007). However, contrary to Xu, Griyn & Schuster (2007), my study did not find higher photosynthetic rates in IES than NS prior to canopy closure. This suggests greater importance of pre-canopy extension of temporal niche breadth in IES advantage; the relative advantage increased each extra day IES were photosynthetically active prior to NS leaf flush. As such, when species exhibited similar phenologies (*e.g.*, subshrubs) there were no significant differences in annual carbon gain. A_{\max} , however, was significantly greater in all IES compared to NS when overstory canopies flushed leaves in June. Notably this response was even found under sugar maple canopies, which had the lowest light transmittance. This is consistent with studies that found greater ability of IES to photosynthetically acclimate to changes from high light conditions in spring to deep summer shade (Taylor & Percy 1976; Yamashita *et al.* 2000; Yamashita, Koike & Ishida 2002; Rothstein & Zak 2001; Tani & Kudo 2006; Feng *et al.* 2007). In the summer, IES also exhibited higher g_s and lower LCP than did NS, contributing to greater photosynthetic efficiency in low-light environments (Björkman 1981; Walters & Reich 2000; Givnish *et al.* 2004; Wyka *et al.* 2008; Funk 2013) and potentially explaining greater carbon gain in IES during canopy-on periods and under heavily shaded sugar maple understories. In autumn, lower rates of decline in photosynthetic capacity may aid IES, as this is characteristic of species with extended leaf lifespans (Field & Mooney 1983; Kitajima, Mulkey & Wright 1997). However, in this study, gas exchange parameters dropped significantly in the fall for both IES and NS, suggesting decreased photosynthetic capacity and IES advantage late in the growing season (Gill, Amthor & Bormann 1998).

IES advantages may also be due to a faster and more plastic response to changes in temperature. Plasticities in photosynthetic characteristics associated with variation in leaf temperature are often

characterized in terms of activation energies (Hikosaka *et al.* 2006) and can vary across climatic gradients and among species (Berry & Björkman 1980; Badger & Andrews 1982; Ferrar, Slatyer & Vranjic 1989; Hikosaka, Murakami & Hirose 1999; Hikosaka, Nabeshima & Hiura 2007). However, modeling studies often ignore intra- and inter-specific differences in photosynthetic responses to temperature due, in part, to the insufficient information on temperature response parameterization (Bernacchi *et al.* 2001; Leuning 2002; Medlyn *et al.* 2002). My results indicate significant temperature responses for all gas exchange parameters except A_{\max} , an exception which has been reported in previous studies (Oechel & Collins 1976b; Mooney, Björkman & Collatz 1978; Ow *et al.* 2008). Previous studies also note seasonal changes in gas exchange temperature dependence (Neilson, Ludlow & Jarvis 1972; DePuit & Caldwell 1973; Lange *et al.* 1974; Oechel & Collins 1976a; Slatyer & Morrow 1977), which in my study resulted in significant declines in autumn. Growth responses were greater in IES than NS, particularly in spring and summer. This may suggest greater capacities for IES to physiologically track climate earlier in the growing season, giving them an advantage over NS prior to and during canopy leaf flush. In particular, greater temperature response of IES LCP matched with lower normalized LCP values in May and June, suggest greater acclimation to changes in light and temperature by IES during this period (Song *et al.* 2010). Seasonal differences in temperature responses may relate to differences in phenological sensitivity to temperature variation across the growing season. Previous studies report strong relations between temperature and timing of events in spring, but weaker relationships with autumn events (Walther *et al.* 2002; Menzel *et al.* 2006; Vitasse *et al.* 2009). Fridley (2012) reported sensitivities of leaf flush with variation in spring temperatures, but no significant differences between IES and NS in phenological tracking. In contrast, my findings based on species-specific physiological temperature responses, suggest IES advantage may arise from a combination of systematic differences in phenology (Wolkovich & Cleland 2011) and being more responsive to temperature (Willis *et al.* 2010), both of which were apparent in spring and summer.

Due to a combination of differential phenology and seasonal variation in temperature response and photosynthetic capacity, daily physiological activity during pre-canopy periods contributed most to

annual carbon gain in all species under all canopy types (see Fig. 3A). Lower photosynthetic capacity among understory species may occur when canopy leaves are present and light quantity and quality are diminished (Shirley 1929; Björkman 1981; Kwesiga & Grace 1986). This may also occur post-canopy leaf abscission as a result of lower sun angles (Anderson 1964; Baldocchi *et al.* 1984) or leaf ontogeny (Jurik *et al.* 1979). Pre-canopy activity contributed to 16-37% of total annual carbon gain in NS and 23-44% in IES which falls within the range of previous studies. For example, two invasive shrubs with extended temporal niche breadth, *Rhamnus cathartica* and *Lonicera X bella*, gained 29% and 35% of their annual carbon, respectively, prior to leaf flush of the indigenous shrub, *Cornus racemosa* (Harrington, Brown & Reich 1989). Similarly, *Alliaria petiolata* is active during the spring window of opportunity, with little or no competition from developing native plants (Myers & Anderson 2003). In this study, each day of pre-canopy photosynthetic activity contributed 1.0-2.2% of annual carbon relative to 0-0.9% for each post-canopy day across all understory species (see Table S2). While IES were still able to gain a relatively large amount of carbon after canopy leaf abscission under white ash and sugar maple canopies, differences between IES and NS carbon gain were not significant when measurements from all canopy types were combined. These results are in contrast to those of Fridley (2012), who found that most IES capture a significant proportion of their annual carbon after canopy leaf fall. My study did not have the large number of species studied by Fridley, but as a consequence I was able to robustly capture the physiological status of fewer IES and NS under multiple natural understory environments. My comparison of growth under different canopy species is significant in understanding IES success in temperate forest understories as I found that whether IES gained significantly more post-canopy carbon than did NS depended on overstory species while pre-canopy advantages for IES were consistent regardless of overstory species.

My study stresses the importance of community-level interactions mediated by the phenological structure of overstory and understory vegetation and the seasonal variation of environmental conditions for IES growth in temperate forest understories. Results were consistent with previous studies of understory phenology and gas exchange demonstrating carbon gain during pre-and post-canopy periods of

the growing season. However, carbon gain in spring before canopy closure was more important to acquiring an annual carbon subsidy, suggesting earlier leaf flush is an important mechanism of IES establishment and growth. This was consistent with higher photosynthetic capacity and temperature light responses in spring and early summer, supporting the hypothesis that IES have an advantage during these periods, especially under canopies with late spring phenophases (see Dreiss & Volin 2013). Growing evidence suggests that future climate trends will lead to changes in temperature and phenology, the incorporation of key seasonal and physiological factors determining invasive growth advantage will be fundamental to understanding the ecology of a changing world. This model elucidates the role of community-level predictors such as canopy species composition, plant phenology, and environmental site characteristics under different growing conditions, and emphasizes their importance in understanding understory growth and development. Further exploration and development of this model should focus on IES and NS growth response to warming trends projected under future climate scenarios.

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Activation Energy (KJ mol ⁻¹)						Temperature-Normalized Value				
Parameter	May	June	August	September	October	May (20)	June (23)	August (25)	September (25)	October (20)
Amax										
IES										
White Ash	6.88 ± 1.3a	5.87 ± 1.5a	6.84 ± 1.2a	6.49 ± 1.3a	5.69 ± 1.4a	5.4 ± 0.4b	6.9 ± 0.2a	5.0 ± 0.3bc	4.1 ± 0.2cd	3.2 ± 0.4d
Sugar Maple	7.63 ± 1.4a	7.23 ± 1.1a	7.47 ± 1.3a	6.48 ± 1.1a	5.47 ± 1.2a	5.4 ± 0.2a	5.9 ± 0.3a	4.9 ± 0.3a	3.8 ± 0.2b	3.2 ± 0.2b
Red Oak	7.1 ± 1.5a	7.59 ± 1.2a	7.2 ± 1.1a	6.09 ± 1.2a	5.73 ± 1.3a	5.2 ± 0.3ab	6.2 ± 0.2a	5.2 ± 0.4ab	4.1 ± 0.3b	3.4 ± 0.2b
NS										
White Ash	11.9 ± 1.4a	7.75 ± 1.2ab	6.08 ± 1.1ab	6.82 ± 1.3b	4.67 ± 1.1b	5.5 ± 0.3a	4.5 ± 0.3a	4.8 ± 0.3a	4.2 ± 0.3a	2.7 ± 0.5b
Sugar Maple	7.73 ± 1.3a	7.75 ± 1.1a	6.02 ± 1.3a	6.32 ± 1.2a	4.2 ± 1.0a	4.7 ± 0.2a	4.6 ± 0.3a	5.3 ± 0.2a	3.3 ± 0.3b	2.7 ± 0.4b
Red Oak	6.77 ± 1.2a	7.87 ± 1.5a	6.47 ± 1.2a	6.3 ± 1.1a	4.55 ± 1.4a	4.9 ± 0.4a	4.8 ± 0.4a	4.7 ± 0.2a	3.4 ± 0.2ab	2.8 ± 0.6b
Summary of ANOVA										
Canopy	(0.18)	(0.27)	(0.75)	(0.64)	(0.96)	(0.72)	(0.80)	(0.97)	(0.76)	(0.98)
Group	(0.15)	(0.07)	(0.04)*	(0.74)	(0.25)	(0.52)	(0.02)*	(0.91)	(0.42)	(0.46)
Canopy*Group	(0.10)	(0.34)	(0.75)	(0.86)	(0.98)	(0.79)	(0.83)	(0.79)	(0.47)	(0.98)
Direction of Difference	IES>NS					IES>NS				
Rd										
IES										
White Ash	84.8 ± 3.2a	86.5 ± 2.7a	84.8 ± 3.1a	72.6 ± 2.6ab	65.9 ± 6.5b	0.92 ± 0.14a	0.69 ± 0.12a	0.60 ± 0.11a	0.77 ± 0.13a	0.56 ± 0.13a
Sugar Maple	83.0 ± 3.4ab	86.9 ± 3.4a	70.6 ± 3.5b	56.2 ± 3.1b	64.2 ± 5.4b	0.77 ± 0.16a	0.91 ± 0.14a	0.82 ± 0.10a	0.62 ± 0.12a	0.52 ± 0.15a
Red Oak	83.7 ± 2.1a	82.5 ± 2.8a	85.6 ± 3.3a	72.5 ± 3.4ab	63.8 ± 4.9b	0.93 ± 0.13a	0.74 ± 0.11a	0.85 ± 0.13a	0.64 ± 0.11a	0.56 ± 0.14a
NS										
White Ash	80.2 ± 4.1a	78.8 ± 3.3a	68.5 ± 3.0a	68.9 ± 3.7a	40.4 ± 9.5b	1.19 ± 0.11a	0.97 ± 0.1ab	0.76 ± 0.12ab	0.53 ± 0.14bc	0.45 ± 0.11c
Sugar Maple	72.8 ± 3.6a	67.3 ± 3.2a	67.9 ± 2.4a	53.2 ± 3.2b	38.9 ± 13.1b	1.01 ± 0.13a	1.00 ± 0.14a	0.98 ± 0.14a	0.70 ± 0.10ab	0.48 ± 0.13b
Red Oak	79.8 ± 4.4a	73.1 ± 4.0a	67.9 ± 3.5a	61.4 ± 2.4a	30.9 ± 11.6b	1.04 ± 0.12a	0.91 ± 0.13ab	0.96 ± 0.12ab	0.77 ± 0.11ab	0.51 ± 0.14b
Summary of ANOVA										
Canopy	(0.64)	(0.54)	(0.30)	(0.25)	(0.88)	(0.45)	(0.29)	(0.09)	(0.77)	(0.97)
Group	(0.16)	(<0.01)**	(0.01)*	(0.39)	(<0.01)**	(0.05)*	(0.02)*	(0.11)	(0.88)	(0.56)
Canopy*Group	(0.79)	(0.49)	(0.33)	(0.89)	(0.94)	(0.78)	(0.59)	(0.97)	(0.05)*	(0.95)
Direction of Difference	IES>NS					IES<NS				
LCP										
IES										
White Ash	96.6 ± 3.4a	98.2 ± 3.2a	96.8 ± 3.6a	63.5 ± 4.2b	37.7 ± 4.1c	64.5 ± 3.2a	64.1 ± 2.7a	67.6 ± 2.4a	52.7 ± 2.1b	33.3 ± 3.6c
Sugar Maple	81.4 ± 2.7a	90.7 ± 3.0a	90.2 ± 2.6a	58.1 ± 3.3b	43.1 ± 5.2c	58.7 ± 2.1a	62.1 ± 2.4a	62.5 ± 3.1a	51.8 ± 2.6a	39.5 ± 3.3b
Red Oak	96.0 ± 3.3a	93.9 ± 2.9ab	92.2 ± 3.4ab	80.9 ± 3.8b	60.7 ± 4.3c	52.4 ± 2.2a	57.5 ± 3.3a	54.4 ± 2.6a	60.5 ± 3.1a	32.9 ± 4.1b
NS										

Summary of ANOVA	White Ash	70.7 ± 3.1a	81.2 ± 3.5a	76.8 ± 4.1a	54.7 ± 3.0b	32.9 ± 5.1c	63.9 ± 2.7bc	81.9 ± 3.2a	69.7 ± 3.2c	63.0 ± 2.5c	24.9 ± 5.2d
	Sugar Maple	69.7 ± 2.8a	74.3 ± 3.3a	72.2 ± 3.2a	66.7 ± 3.2a	45.7 ± 4.4b	66.4 ± 2.4a	76.1 ± 3.0a	62.9 ± 2.6a	63.1 ± 3.2a	25.4 ± 5.5b
	Red Oak	89.5 ± 4.0a	77.4 ± 3.7ab	80.7 ± 3.5ab	73.9 ± 3.7b	46.1 ± 4.7c	52.4 ± 3.1a	57.5 ± 2.2a	54.3 ± 3.3a	60.5 ± 2.8a	32.9 ± 4.8b
	Canopy	(0.16)	(0.38)	(0.30)	(0.04)*	(0.32)	(0.64)	(0.35)	(0.28)	(0.97)	(0.84)
	Group	(0.04)*	(<0.001)***	(<0.001)***	(0.70)	(0.56)	(0.63)	(0.02)*	(0.43)	(0.23)	(0.10)
	Canopy*Group	(0.51)	(0.98)	(0.52)	(0.42)	(0.76)	(0.92)	(0.88)	(0.74)	(0.45)	(0.93)
Direction of Difference		IES>NS					IES<NS				
AQY											
IES											
NS	White Ash	42.6 ± 3.2ab	50.9 ± 3.0ab	53.3 ± 3.3a	39.8 ± 2.9bc	28.9 ± 3.5c	0.040 ± 0.003ab	0.048 ± 0.004ab	0.052 ± 0.002a	0.044 ± 0.003ab	0.037 ± 0.003b
	Sugar Maple	35.4 ± 3.4a	43.4 ± 2.6a	42.7 ± 2.8a	34.4 ± 2.4a	21.3 ± 3.2b	0.033 ± 0.002ab	0.040 ± 0.001a	0.041 ± 0.003a	0.034 ± 0.003ab	0.026 ± 0.004b
	Red Oak	41.1 ± 4.1a	48.7 ± 3.2a	50.1 ± 3.0a	41.2 ± 3.1a	24.4 ± 3.3b	0.037 ± 0.004a	0.043 ± 0.002a	0.046 ± 0.002a	0.038 ± 0.002a	0.032 ± 0.004a
	White Ash	39.8 ± 3.3a	46.2 ± 2.7a	47.3 ± 3.0a	41.4 ± 2.8a	21.6 ± 4.1b	0.031 ± 0.004b	0.039 ± 0.003ab	0.046 ± 0.002a	0.036 ± 0.003ab	0.029 ± 0.005b
	Sugar Maple	28.9 ± 3.0a	34.4 ± 3.1a	35.2 ± 2.6a	31.3 ± 3.3a	24.8 ± 4.9a	0.026 ± 0.004ab	0.035 ± 0.002a	0.037 ± 0.002a	0.032 ± 0.002ab	0.021 ± 0.005b
	Red Oak	30.4 ± 3.4b	42.1 ± 3.2ab	46.1 ± 3.1a	42.2 ± 2.9b	22.4 ± 4.6c	0.032 ± 0.004ab	0.038 ± 0.003a	0.042 ± 0.003a	0.034 ± 0.002ab	0.022 ± 0.006b
Summary of ANOVA											
	Canopy	(0.35)	(0.28)	(0.14)	(0.02)*	(0.80)	(0.52)	(0.52)	(0.12)	(0.31)	(0.36)
	Group	(0.17)	(0.17)	(0.31)	(0.96)	(0.47)	(0.05)*	(0.05)*	(0.32)	(0.21)	(0.13)
	Canopy*Group	(0.42)	(0.67)	(0.48)	(0.69)	(0.88)	(0.43)	(0.46)	(0.55)	(0.76)	(0.69)
Direction of Difference		IES>NS					IES>NS				
gs											
IES											
NS	White Ash	74.4 ± 4.2a	75.9 ± 3.0a	71.0 ± 3.3ab	60.7 ± 2.7bc	50.6 ± 3.4c	0.31 ± 0.02ab	0.37 ± 0.03a	0.29 ± 0.02ab	0.28 ± 0.02b	0.24 ± 0.02b
	Sugar Maple	63.5 ± 2.5ab	66.6 ± 3.4a	58.8 ± 2.9ab	55.0 ± 2.5b	58.4 ± 2.2ab	0.30 ± 0.01ab	0.34 ± 0.02ab	0.36 ± 0.03a	0.28 ± 0.03ab	0.25 ± 0.03b
	Red Oak	69.4 ± 3.3a	72.5 ± 2.4a	61.1 ± 3.6ab	55.8 ± 3.4bc	47.7 ± 2.9c	0.32 ± 0.02ab	0.37 ± 0.02a	0.32 ± 0.03ab	0.35 ± 0.02a	0.23 ± 0.03b
	White Ash	61.9 ± 3.5a	66.5 ± 3.2a	63.3 ± 2.3a	55.1 ± 3.2a	32.6 ± 6.1b	0.31 ± 0.02ab	0.36 ± 0.02a	0.33 ± 0.02ab	0.27 ± 0.01bc	0.19 ± 0.03c
	Sugar Maple	59.0 ± 3.2a	66.1 ± 2.7a	56.4 ± 3.0a	51.0 ± 2.6a	32.9 ± 8.4b	0.25 ± 0.02ab	0.27 ± 0.01a	0.29 ± 0.01a	0.25 ± 0.02ab	0.17 ± 0.04b
	Red Oak	62.3 ± 3.8ab	68.7 ± 3.1a	55.5 ± 2.8ab	48.4 ± 3.3b	30.7 ± 7.6c	0.27 ± 0.03ab	0.33 ± 0.02a	0.27 ± 0.01ab	0.21 ± 0.02bc	0.16 ± 0.04c
Summary of ANOVA											
	Canopy	(0.25)	(0.36)	(0.05)*	(0.19)	(0.95)	(0.49)	(0.27)	(0.52)	(0.31)	(0.90)
	Group	(0.03)*	(0.13)	(0.14)	(0.04)*	(0.02)*	(0.16)	(0.22)	(0.28)	(0.41)	(0.11)
	Canopy*Group	(0.62)	(0.48)	(0.82)	(0.86)	(0.98)	(0.56)	(0.82)	(0.15)	(0.90)	(0.92)
Direction of Difference		IES>NS					IES>NS				

Abbreviations and units: A_{\max} = area-based maximum photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); R_d = dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$); LCP = light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$); AQY = apparent quantum yield ($\mu\text{mol mol}^{-1}$); g_s = stomatal conductance ($\mu\text{mol m}^{-2} \text{s}^{-1}$)

Table 2. Simulated annual carbon gain per unit leaf area ($\text{g C m}^{-2} \text{ yr}^{-1}$) and the percentage (%) of that gain occurring in pre-, during-, and post-canopy periods to annual carbon for four invasive exotic species (IES) (*Berberis thunbergii*, *Euonymus alatus*, *Celastrus orbiculatus*, and *Rosa multiflora*) and four native species (NS) (*Lindera benzoin*, *Kalmia latifolia*, *Parthenocissus quinquefolia*, and *Rubus allegheniensis*) grown under three different overstory canopy types. Canopy species included sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), and red oak (*Quercus rubra*). Values are also pooled by invasive (IES) and native groups (NS) as well as functional groups. Invasive exotic species are highlighted in gray cells and NS in white. Two-way ANOVAs compare variables across species ($n = 3$), IES and NS groups ($n = 6$) and interactions, where site was a random effect and month was a fixed effect. Canopy types followed by the same lowercase letter within a variable are not significantly different at $P < 0.05$. P values are reported, with significant effects denoted with an asterisk: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Additionally, bolded values indicate significant differences ($p < 0.05$) between IES and NS within a column.

	SUGAR MAPLE				WHITE ASH				RED OAK			
	Total ($\text{g m}^{-2} \text{ yr}^{-1}$)	%Pre	%During	%Post	Total ($\text{g m}^{-2} \text{ yr}^{-1}$)	%Pre	%During	%Post	Total ($\text{g m}^{-2} \text{ yr}^{-1}$)	%Pre	%During	%Post
<i>B. thunbergii</i>	194 ± 13b	23.0 ± 1.7b	55.1 ± 1.4a	21.9 ± 0.3a	256 ± 11a	34.2 ± 0.7a	53.8 ± 0.8a	11.2 ± 0.3b	204 ± 10b	35.0 ± 0.5a	52.8 ± 1.6b	8.1 ± 0.2c
<i>L. benzoin</i>	116 ± 17b	16.0 ± 1.1bc	68.6 ± 1.5a	15.4 ± 1.4a	208 ± 15a	20.9 ± 1.2ab	71.0 ± 0.9a	8.2 ± 1.2b	189 ± 16a	24.5 ± 1.3a	71.2 ± 1.2a	4.3 ± 1.1b
<i>E. alatus</i>	219 ± 14b	30.5 ± 1.3b	48.3 ± 1.3a	20.2 ± 1.2a	272 ± 11a	39.5 ± 1.3a	50.3 ± 1.4a	12.2 ± 1.4b	242 ± 12ab	44.3 ± 1.4a	48.6 ± 0.7a	7.1 ± 1.1b
<i>K. latifolia</i>	195 ± 6.9b	20.0 ± 1.8b	62.7 ± 1.4ab	17.3 ± 1.3a	229 ± 10a	27.8 ± 1.4a	59.6 ± 0.7b	11.6 ± 1.5a	207 ± 11ab	31.1 ± 1.2a	65.1 ± 0.9a	4.8 ± 1.3b
<i>C. orbiculatus</i>	208 ± 11b	26.1 ± 1.5b	62.3 ± 1.5a	11.6 ± 1.2a	244 ± 7.9a	33.4 ± 1.0b	58.2 ± 1.6b	7.4 ± 1.3a	213 ± 12ab	39.0 ± 1.0a	58.3 ± 1.6ab	2.7 ± 1.2b
<i>P. quinquefolia</i>	139 ± 11a	19.5 ± 1.3b	72.8 ± 0.7a	7.7 ± 0.03a	152 ± 9.2a	28.5 ± 1.1a	71.4 ± 1.0b	1.1 ± 0.2b	136 ± 10a	26.6 ± 0.8a	74.4 ± 1.2a	0.0 ± 0.1b
<i>R. multiflora</i>	231 ± 19b	28.8 ± 1.3b	54.2 ± 1.3a	17.0 ± 1.4a	389 ± 37a	35.9 ± 1.2a	43.5 ± 1.4c	20.6 ± 1.2a	275 ± 26b	39.4 ± 1.4a	48.9 ± 0.6b	11.7 ± 1.1b
<i>R. allegheniensis</i>	206 ± 19b	32.1 ± 0.8b	52.9 ± 1.3a	14.5 ± 1.5a	295 ± 16a	32.4 ± 0.7b	46.8 ± 0.5b	20.8 ± 1.2a	257 ± 11a	37.5 ± 0.8a	53.3 ± 0.7a	10.3 ± 1.1b
IES	211 ± 17b	28.4 ± 1.4b	51.3 ± 4.0a	20.6 ± 1.2a	292 ± 18a	35.4 ± 2.3a	49.1 ± 2.1a	16.5 ± 1.2b	231 ± 16ab	37.3 ± 1.8a	54.0 ± 2.8a	8.7 ± 0.4c
NS	168 ± 19a	20.9 ± 1.9b	62.3 ± 3.1a	18.1 ± 0.9a	225 ± 16a	27.7 ± 1.8a	57.8 ± 3.5b	13.9 ± 1.4a	199 ± 18a	29.5 ± 1.5a	63.3 ± 3.4a	7.7 ± 0.5b
<i>Summary of ANOVA</i>												
Canopy												
Group	(0.11)	(<0.01)**	(0.03)*	(0.09)	(0.01)*	(<0.01)**	(0.02)*	(0.13)	(0.18)	(<0.01)**	(0.04)*	(0.12)
Canopy*Group												
Direction		IES>NS	IES<NS		IES>NS	IES>NS	IES<NS			IES>NS	IES<NS	
Shrub	181 ± 15b	22.8 ± 0.6b	60.7 ± 1.4a	16.4 ± 1.3a	232 ± 13a	31.2 ± 0.6a	58.6 ± 0.6b	14.2 ± 1.3a	202 ± 14ab	33.2 ± 1.6a	60.2 ± 0.8a	6.5 ± 1.1b
Subshrub	226 ± 25b	29.0 ± 1.5c	53.7 ± 1.3a	23.3 ± 1.4a	331 ± 22a	34.2 ± 1.4b	45.2 ± 1.4b	20.6 ± 1.5a	253 ± 19ab	37.6 ± 1.5a	51.3 ± 1.6a	11.1 ± 1.1b
Vine	173 ± 16a	23.4 ± 1.2b	66.0 ± 0.5a	10.6 ± 1.2a	207 ± 12a	29.2 ± 0.9a	65.4 ± 0.7a	4.3 ± 3.2b	206 ± 15a	32.0 ± 0.9a	66.3 ± 0.8a	1.7 ± 1.1c

Table 2 continued.

Total (g m ⁻² yr ⁻¹)	ALL		
	%Pre	%During	%Post
217 ± 10	35.4 ± 2.0	54.7 ± 0.6	9.9 ± 0.4
179 ± 14	20.1 ± 0.5	70.8 ± 0.6	9.1 ± 0.2
239 ± 13	40.8 ± 1.3	49.4 ± 0.3	9.8 ± 0.6
208 ± 11	25.1 ± 0.5	62.7 ± 0.3	12.3 ± 0.3
220 ± 10	33.6 ± 0.3	59.7 ± 0.4	6.7 ± 0.2
143 ± 11	24.4 ± 0.1	73.6 ± 0.3	2.0 ± 1.1
290 ± 22	32.8 ± 1.5	50.1 ± 1.0	17.2 ± 1.0
246 ± 18	33.7 ± 1.5	50.0 ± 0.8	16.3 ± 0.9
238 ± 12	32.6 ± 1.5	51.4 ± 3.4	16.1 ± 1.5
196 ± 15	24.1 ± 1.3	63.3 ± 2.3	12.6 ± 1.4
(0.04)*	(0.01)*	(0.49)	(<0.01)**
(0.01)*	(<0.001)***	(0.01)*	(0.09)
(0.72)	(0.90)	(0.89)	(0.79)
IES>NS	IES>NS	IES<NS	
206 ± 12	30.1 ± 1.0	58.5 ± 0.2	11.4 ± 0.2
268 ± 15	32.4 ± 0.6	50.6 ± 0.2	17.0 ± 0.2
190 ± 13	27.9 ± 1.5	65.4 ± 0.6	5.7 ± 0.6

FIGURE LEGENDS

Figure 1. Validation plots and coefficients of determination for model parameters, including maximum photosynthetic rate (A_{\max}), dark respiration (R_d), light compensation point (LCP), apparent quantum yield (AQY), and stomatal conductance (g_s), used in simulating annual carbon gain for four invasive exotic species and four native understory species grown under three canopy types. Solid lines represent 1:1 relationships.

Figure 2. Validation plot and coefficient of determination for predicted carbon gain per unit leaf area across the model-simulated growing season and observed net assimilation calculated from empirical seedling mass (M) and leaf area (L) measured from destructive harvests and allometric estimates. The solid line represents a 1:1 relationship and the dashed line represents linear regression between predicted and observed values, where $\text{Observed NA} = -25.4 + 0.93(\text{Predicted NA})$

Figure 3. (A) Simulated daily carbon gain per unit leaf area pooled for invasive exotic (IES) (black) and native (NS) (light gray) species, and (B) by IES and NS functional groups (shrubs, vines, and subshrubs), all grown in understory conditions with different phenological and light transmittance resulting from different overstory canopies of either sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), or red oak (*Quercus rubra*) (n=3 for all canopies) Annual carbon gain is represented by the total area under each curve. Dotted lines represent average dates of flush and abscission for each canopy species.

Figure 1

FIGURES

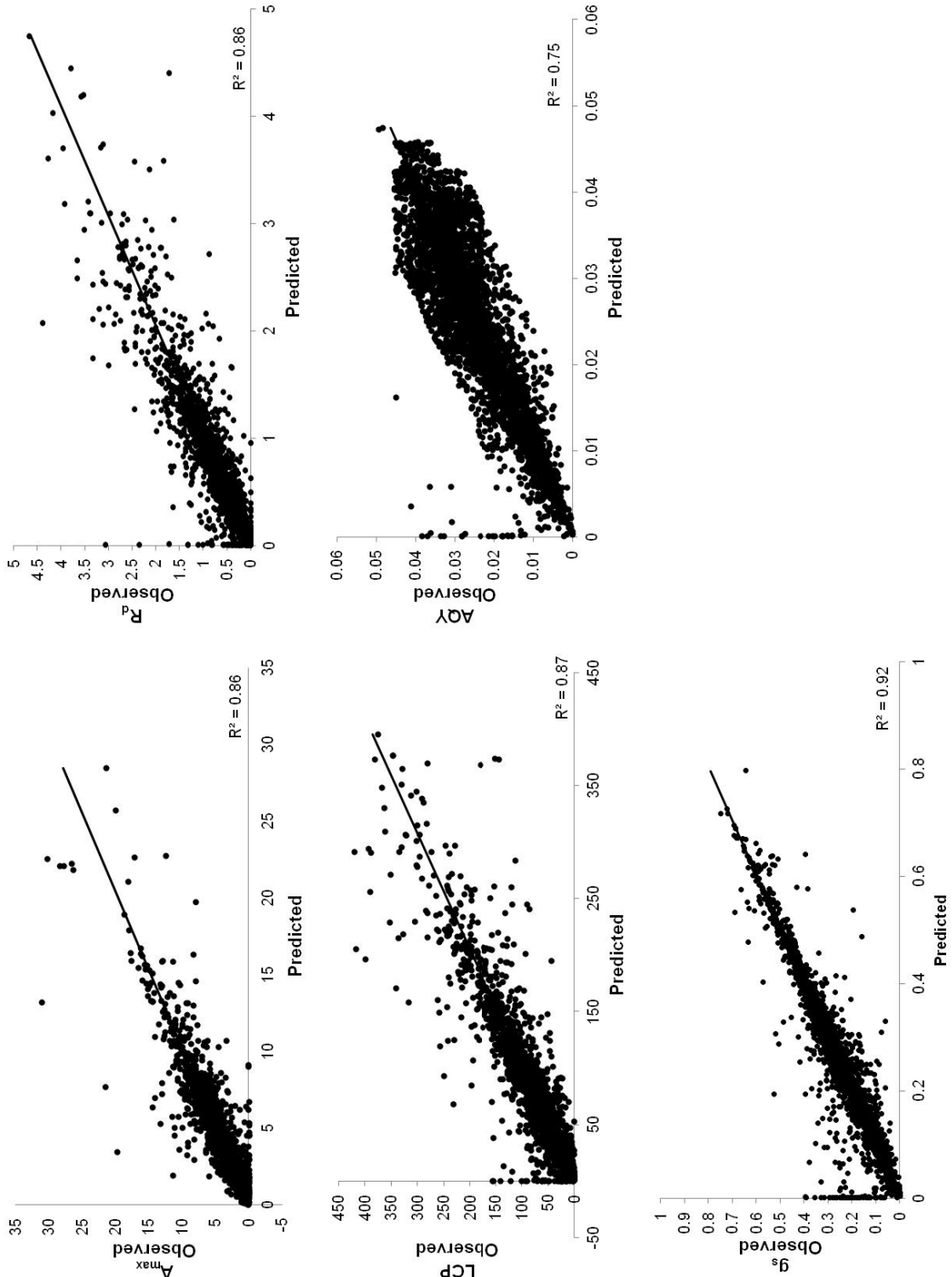


Figure 2

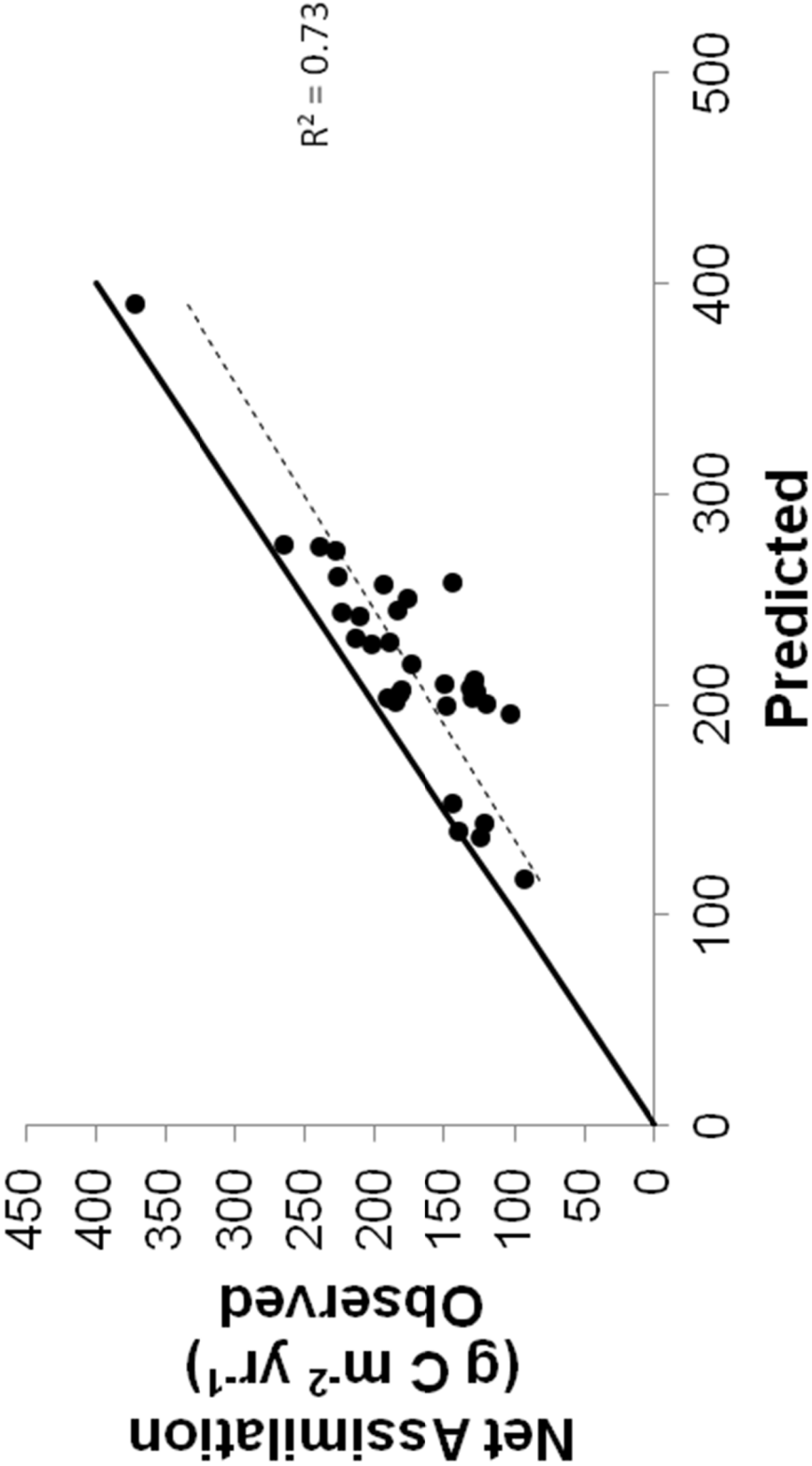
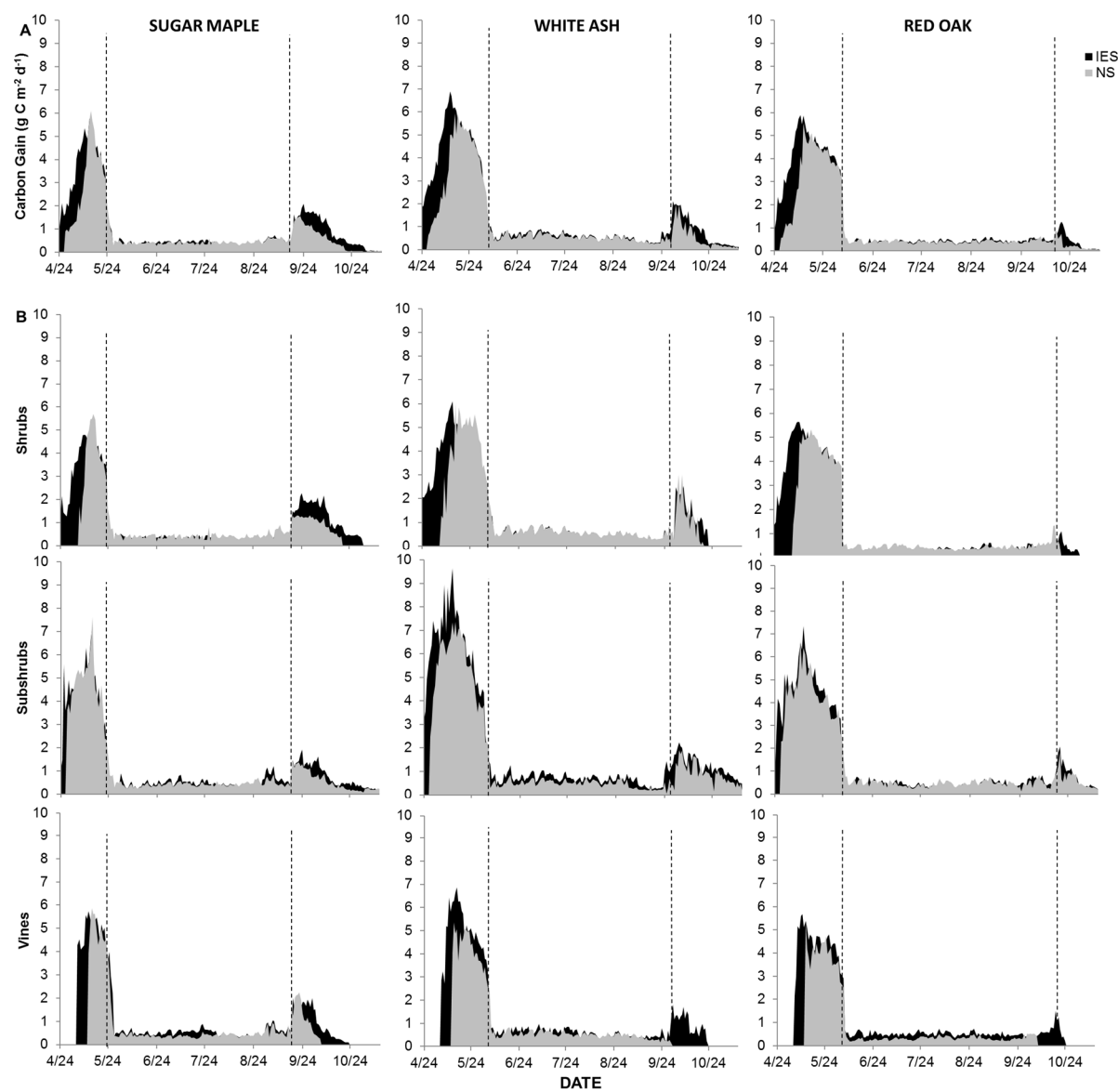


Figure 3



SUPPORTING INFORMATION

Table S1. Average (\pm SE) activation energies and temperature normalized values for model input parameters representing eight understory species per canopy type and growing season month. Numbers below the month name refer to the temperature ($^{\circ}\text{C}$) to which parameters for that month were normalized. Due to a lower sample size, July measurements were grouped with August values for model parameterization. Months followed by the same lowercase letter within a variable are not significantly different at $P < 0.05$. Abbreviations and units: A_{max} = area-based maximum photosynthetic rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$); R_d = dark respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$); LCP = light compensation point ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

Parameter/Species	Activation Energy (KJ mol^{-1})					Temperature-Normalized				
	May	June	August	September	October	May	June	August	September	October
						(20)	(23)	(25)	(25)	(20)
<i>A_{max}</i>										
White Ash										
BETH	7.75 \pm 2.1a	6.81 \pm 1.8a	7.54 \pm 1.3a	7.15 \pm 2.3a	6.45 \pm 2.7a	5.27 \pm 0.5ab	7.53 \pm 0.9a	3.16 \pm 0.7b	2.97 \pm 0.5b	2.76 \pm 0.8b
EUAL	8.3 \pm 1.1a	4.9 \pm 1.5a	7.2 \pm 1.4a	7.7 \pm 1.3a	7.3 \pm 1.6a	4.4 \pm 0.3a	5.56 \pm 0.5a	5.65 \pm 0.6a	3.88 \pm 0.4a	3.87 \pm 0.5a
CEOR	6.3 \pm 1.4a	6.4 \pm 1.7a	6.81 \pm 1.5a	5.2 \pm 1.6a	4.1 \pm 1.1a	6.2 \pm 0.5a	4.77 \pm 0.4b	4.46 \pm 0.3b	4.21 \pm 0.3b	3.95 \pm 0.2b
ROMU	5.2 \pm 1.7a	5.4 \pm 1.3a	5.8 \pm 1.2a	5.9 \pm 1.1a	4.9 \pm 1.5a	5.74 \pm 0.4a	5.82 \pm 0.4a	6.76 \pm 0.5a	5.23 \pm 0.3a	2.09 \pm 0.6b
LIBE	10.9 \pm 2.3a	10.0 \pm 2.1a	5.1 \pm 1.9a	6.2 \pm 1.7a	6.6 \pm 1.4a	4.13 \pm 0.4a	4.02 \pm 0.3a	4.62 \pm 0.4a	2.63 \pm 0.2bc	2.28 \pm 0.4c
KALA	5.8 \pm 1.5a	7.1 \pm 1.4a	8.6 \pm 2.3a	9.2 \pm 2.5a	7.3 \pm 2.1a	5.77 \pm 0.3a	5.23 \pm 0.4a	5.7 \pm 0.5a	4.39 \pm 0.3a	4.47 \pm 0.3a
PAQU	18.5 \pm 1.2a	7.4 \pm 1.8b	5.0 \pm 1.1b	6.6 \pm 2.2b		5.84 \pm 0.6a	3.59 \pm 0.3b	4.53 \pm 0.3ab	2.45 \pm 0.3b	
RUID	12.4 \pm 1.3a	6.5 \pm 1.2b	5.6 \pm 1.4b	5.3 \pm 1.6b	4.8 \pm 1.3b	6.13 \pm 0.3a	5.25 \pm 0.3ab	4.57 \pm 0.5ab	3.52 \pm 0.4b	4.25 \pm 0.5b
Sugar Maple										
BETH	5.03 \pm 1.7a	6.12 \pm 1.4a	6.98 \pm 1.5a	6.54 \pm 1.9a	5.99 \pm 1.7a	5.04 \pm 0.3ab	5.99 \pm 0.7a	3.29 \pm 0.8bc	2.81 \pm 0.2c	1.98 \pm 0.4c
EUAL	9.3 \pm 2.3a	8.3 \pm 1.7a	8.6 \pm 1.7a	6.2 \pm 1.4a	5.6 \pm 2.3a	4.6 \pm 0.2b	9.54 \pm 0.6a	5.04 \pm 0.3b	4.48 \pm 0.3b	3.04 \pm 0.5b
CEOR	9.7 \pm 2.6a	7.2 \pm 1.8a	6.7 \pm 1.3a	6.9 \pm 1.6a	4.7 \pm 1.2a	4.7 \pm 0.4a	3.08 \pm 0.2b	3.82 \pm 0.3ab	4.1 \pm 0.2ab	3.08 \pm 0.4b
ROMU	6.5 \pm 1.5a	7.3 \pm 1.3a	7.6 \pm 1.4 a	6.3 \pm 2.1a	5.6 \pm 1.5a	7.08 \pm 0.5a	9.07 \pm 0.6a	7.28 \pm 0.4a	3.99 \pm 0.5b	4.71 \pm 0.6b

133	LIBE	8.2 ± 2.1a	6.1 ± 1.1a	5.4 ± 1.1a	6.5 ± 1.4a	4.9 ± 1.3a	3.09 ± 0.3ab	3.8 ± 0.2ab	3.98 ± 0.3a	4.08 ± 0.3a	2.74 ± 0.3b
	KALA	8.6 ± 1.9a	7.5 ± 1.6a	6.8 ± 2.3a	5.6 ± 1.2a	6.5 ± 1.9a	6.27 ± 0.4a	6.01 ± 0.5a	5.94 ± 0.2a	3.80 ± 0.2b	3.55 ± 0.3b
	PAQU	5.6 ± 1.7a	7.6 ± 1.8a	4.6 ± 1.0a	6.4 ± 1.6a		4.71 ± 0.3a	4.65 ± 0.3a	5.58 ± 0.3a	3.81 ± 0.3a	
	RUID	8.5 ± 1.5a	9.8 ± 2.2a	7.3 ± 1.5a	6.8 ± 1.3a	5.6 ± 1.3a	4.56 ± 0.3ab	4.04 ± 0.2b	5.68 ± 0.4a	5.45 ± 0.3a	4.5 ± 0.2b
	Red Oak										
	BETH	8.60 ± 2.0a	7.45 ± 1.5a	7.22 ± 1.5a	7.04 ± 2.1a	6.52 ± 2.1a	5.83 ± 0.5a	6.22 ± 0.6a	3.04 ± 0.3b	2.84 ± 0.3b	2.25 ± 0.4b
	EUAL	5.2 ± 1.6a	6.4 ± 1.7a	7.4 ± 1.1a	6.3 ± 1.4a	5.6 ± 1.4a	4.14 ± 0.3bc	8.51 ± 0.5a	4.92 ± 0.4b	3.03 ± 0.2c	2.93 ± 0.4c
	CEOR	7.9 ± 1.2a	8.5 ± 1.4a	6.4 ± 1.2a	4.8 ± 1.1a	4.2 ± 1.1a	4.61 ± 0.2ab	4.62 ± 0.4ab	4.95 ± 0.3a	3.49 ± 0.2bc	3.29 ± 0.3c
	ROMU	6.7 ± 1.8a	8.0 ± 1.2a	7.8 ± 1.6a	6.2 ± 1.2a	6.6 ± 1.7a	6.27 ± 0.4ab	5.39 ± 0.5b	7.85 ± 0.5a	7.14 ± 0.4a	5.01 ± 0.5b
	LIBE	6.2 ± 1.3a	6.8 ± 1.3a	5.7 ± 1.4a	6.2 ± 1.6a	5.3 ± 1.4a	3.09 ± 0.2ab	3.94 ± 0.3a	3.86 ± 0.4ab	2.84 ± 0.2b	3.1 ± 0.2ab
	KALA	8.6 ± 2.2a	8.1 ± 2.1a	7.1 ± 1.9a	5.7 ± 1.1a	5.4 ± 1.3a	5.14 ± 0.3b	6.61 ± 0.4a	4.95 ± 0.3b	2.91 ± 0.3c	3.38 ± 0.2c
	PAQU	6.9 ± 1.7a	8.0 ± 1.6a	5.7 ± 1.1a	6.2 ± 1.3a		5.23 ± 0.3a	3.98 ± 0.2b	5.49 ± 0.3a	2.83 ± 0.2c	
	RUID	5.4 ± 1.4a	8.6 ± 1.3a	7.5 ± 2.0a	7.1 ± 1.4a	7.5 ± 1.5a	6.4 ± 0.3a	4.48 ± 0.4b	4.52 ± 0.2b	4.84 ± 0.3b	4.73 ± 0.2b
	Rd										
	White Ash										
	BETH	89.7 ± 3.2a	97.4 ± 3.5a	84.7 ± 5.3a	79.4 ± 6.6ab	62.1 ± 7.2b	1.12 ± 0.18a	0.49 ± 0.17ab	0.55 ± 0.14ab	0.72 ± 0.18ab	0.46 ± 0.18b
	EUAL	69.6 ± 5.4a	80.3 ± 4.1a	85.8 ± 2.6a	40.1 ± 2.7b	83.1 ± 3.6a	0.48 ± 0.11a	0.63 ± 0.14a	0.46 ± 0.09a	0.78 ± 0.16a	0.45 ± 0.09a
	CEOR	95.6 ± 6.1a	81.5 ± 2.7a	81.2 ± 3.1a	31.1 ± 4.2b	40.1 ± 2.5b	1.27 ± 0.09a	0.82 ± 0.12ab	0.48 ± 0.13b	0.89 ± 0.14ab	0.93 ± 0.11ab
	ROMU	84.3 ± 4.8a	86.7 ± 3.2a	87.5 ± 4.7a	79.7 ± 3.8a	78.2 ± 4.1a	0.79 ± 0.12a	0.82 ± 0.16a	0.92 ± 0.11a	0.68 ± 0.11a	0.41 ± 0.15a
	LIBE	77.6 ± 4.7a	61.4 ± 3.5b	63.5 ± 2.9ab	20.9 ± 3.3d	44.4 ± 3.4c	1.35 ± 0.20a	0.86 ± 0.13ab	0.69 ± 0.12b	0.72 ± 0.12b	0.53 ± 0.11b
	KALA	89.2 ± 5.3ab	96.8 ± 4.1a	65.4 ± 3.6c	81.3 ± 2.5b	24.5 ± 2.9d	1.05 ± 0.17a	0.99 ± 0.12a	0.59 ± 0.12ab	0.44 ± 0.09b	0.69 ± 0.16ab
	PAQU	83.6 ± 7.1a	77.7 ± 2.8a	61.2 ± 3.3b	77.4 ± 2.1a		1.17 ± 0.13a	1.09 ± 0.11a	0.77 ± 0.17ab	0.34 ± 0.14b	
	RUID	70.4 ± 4.4a	79.3 ± 3.6a	83.7 ± 4.1a	36.1 ± 5.3b	92.6 ± 6.7a	1.19 ± 0.15a	0.94 ± 0.11ab	1.03 ± 0.14ab	0.62 ± 0.11b	0.57 ± 0.10b
	Sugar Maple										
	BETH	81.8 ± 7.5a	89.7 ± 4.6a	75.5 ± 5.6ab	70.4 ± 5.9ab	56.8 ± 6.4b	0.51 ± 0.14a	0.73 ± 0.25a	0.58 ± 0.11a	0.65 ± 0.20a	0.53 ± 0.16a

134	EUAL	72.8 ± 5.3ab	90.6 ± 3.4a	70.0 ± 6.2b	83.7 ± 4.6ab	77.9 ± 4.8ab	0.52 ± 0.09ab	0.85 ± 0.13a	0.9 ± 0.05a	0.57 ± 0.10ab	0.38 ± 0.15b
	CEOR	96.5 ± 5.5a	77.6 ± 4.4ab	51.6 ± 3.1b	61.6 ± 3.3b	55.4 ± 5.1b	1.43 ± 0.18a	1.27 ± 0.12a	0.96 ± 0.09ab	0.62 ± 0.13b	0.72 ± 0.11b
	ROMU	81.0 ± 3.7ab	89.9 ± 5.2a	85.1 ± 4.3	73.1 ± 5.1ab	66.9 ± 3.9b	0.63 ± 0.11a	0.78 ± 0.11a	0.86 ± 0.10a	0.64 ± 0.14a	0.46 ± 0.14a
	LIBE	68.9 ± 3.1a	54.6 ± 3.1bc	53.4 ± 3.5bc	62.9 ± 3.8ab	48.3 ± 3.3c	1.01 ± 0.13a	0.97 ± 0.09ab	0.84 ± 0.06ab	0.87 ± 0.11ab	0.53 ± 0.17b
	KALA	75.1 ± 4.1a	81.2 ± 4.6a	67.1 ± 3.2a	66.1 ± 4.2a	42.9 ± 4.3b	0.93 ± 0.15ab	1.12 ± 0.14a	0.83 ± 0.10ab	0.62 ± 0.13ab	0.58 ± 0.12b
	PAQU	73.0 ± 3.3a	61.6 ± 3.3a	70.7 ± 3.8a	67.3 ± 3.7a		1.15 ± 0.17a	1.19 ± 0.12a	1.19 ± 0.05a	0.59 ± 0.18b	
	RUID	74.2 ± 2.9ab	71.7 ± 3.7ab	80.3 ± 4.1a	76.6 ± 2.5ab	64.7 ± 2.6b	0.95 ± 0.14a	0.73 ± 0.11a	1.06 ± 0.10a	0.73 ± 0.16a	0.81 ± 0.11a
	Red Oak										
	BETH	82.9 ± 6.2ab	96.3 ± 4.1a	85.4 ± 4.8ab	71.3 ± 5.4b	64.6 ± 6.3b	0.92 ± 0.12a	0.53 ± 0.14a	0.60 ± 0.09a	0.50 ± 0.15a	0.49 ± 0.12a
	EUAL	62.7 ± 3.4b	71.5 ± 3.3ab	88.4 ± 5.1a	82.1 ± 4.2a	69.5 ± 5.7b	1.04 ± 0.16a	0.76 ± 0.12ab	0.79 ± 0.13ab	0.82 ± 0.11ab	0.32 ± 0.22b
	CEOR	99.6 ± 5.6a	73.3 ± 2.4ab	82.9 ± 3.7a	61.8 ± 7.1b	51.6 ± 4.3b	0.84 ± 0.13a	0.99 ± 0.16a	1.04 ± 0.11a	0.62 ± 0.09a	0.93 ± 0.21a
	ROMU	89.5 ± 4.1a	89.0 ± 4.1a	85.7 ± 4.2a	74.8 ± 3.8ab	69.5 ± 5.1b	0.91 ± 0.10a	0.69 ± 0.13a	0.95 ± 0.09a	0.61 ± 0.14a	0.49 ± 0.16a
	LIBE	72.4 ± 3.2a	68.8 ± 3.3ab	54.1 ± 3.2b	58.9 ± 2.9b	31.7 ± 2.7c	1.15 ± 0.11a	0.90 ± 0.12a	0.92 ± 0.14a	0.93 ± 0.13a	0.69 ± 0.18a
	KALA	70.6 ± 3.8a	72.2 ± 4.7a	54.9 ± 3.3b	52.5 ± 3.1b	34.7 ± 3.5c	0.81 ± 0.07ab	1.04 ± 0.14a	0.62 ± 0.18ab	0.52 ± 0.11b	0.64 ± 0.13ab
	PAQU	91.9 ± 5.3a	64.3 ± 3.2b	76.5 ± 3.6b	74.3 ± 3.3b		1.12 ± 0.14a	0.98 ± 0.11ab	0.92 ± 0.12ab	0.58 ± 0.14b	
	RUID	84.5 ± 4.7a	87.2 ± 4.5a	86.4 ± 5.1a	60.0 ± 4.0b	57.3 ± 3.6b	1.06 ± 0.10ab	0.73 ± 0.15b	1.38 ± 0.21a	1.03 ± 0.12ab	0.72 ± 0.18b
	LCP										
	White Ash										
	BETH	123.8 ± 11.2a	110.3 ± 9.1a	97.8 ± 7.1a	41.4 ± 14.5b	21.4 ± 11.5b	37.2 ± 5.4b	58.9 ± 6.2a	61.4 ± 4.0ab	42.1 ± 3.1b	24.2 ± 5.2c
	EUAL	70.2 ± 6.7b	96.9 ± 5.2a	92.2 ± 4.6a	67.5 ± 3.7b	23.8 ± 3.2c	52.6 ± 6.5ab	71.5 ± 5.9a	56.2 ± 3.6	70.5 ± 4.3a	33.2 ± 3.7b
	CEOR	98.5 ± 7.1a	86.6 ± 4.8a	99.1 ± 3.5a	64.1 ± 4.6b	57.1 ± 5.1b	91.9 ± 7.1a	56.8 ± 4.7b	78.2 ± 4.4a	30.7 ± 3.4c	52.1 ± 5.4b
	ROMU	94.1 ± 5.9ab	99.1 ± 3.5a	98.4 ± 4.1a	80.9 ± 3.3b	48.5 ± 4.5c	76.5 ± 5.4a	69.4 ± 5.2a	74.8 ± 3.8a	67.4 ± 2.6a	23.7 ± 6.1b
	LIBE	88.1 ± 4.3a	79.3 ± 3.2ab	76.9 ± 3.3abc	67.6 ± 4.1b	62.9 ± 5.2c	36.2 ± 3.8c	85.8 ± 6.1a	64.3 ± 2.6b	54.9 ± 3.3b	32.4 ± 4.6c
	KALA	74.6 ± 5.4a	82.1 ± 4.4a	78.1 ± 5.1a	33.1 ± 4.5b	37.6 ± 4.3b	61.6 ± 4.2b	82.3 ± 4.3a	91.4 ± 3.4a	75.5 ± 4.8b	21.9 ± 5.2c
	PAQU	59.6 ± 5.1b	91.8 ± 7.1a	86.9 ± 6.5a	51.5 ± 5.2b		65.6 ± 4.4a	56.0 ± 3.4ab	48.7 ± 2.8b	68.4 ± 3.6a	

RUID	60.3 ± 6.3a	71.8 ± 3.5a	65.5 ± 4.4a	66.8 ± 3.6a	31.1 ± 4.4b	92.1 ± 6.1ab	103.6 ± 5.1a	74.4 ± 4.2b	53.3 ± 4.4c	45.5 ± 3.6c
Sugar Maple										
BETH	103.8 ± 12.7a	96.9 ± 11.3a	94.2 ± 10.4a	31.2 ± 13.2b	45.7 ± 10.8b	41.4 ± 4.5b	59.0 ± 5.3ab	77.5 ± 5.1a	52.5 ± 4.3b	33.8 ± 4.8c
EUAL	68.1 ± 7.8b	101.6 ± 5.4a	91.4 ± 6.3a	75.4 ± 5.5ab	36.4 ± 6.1c	34.9 ± 3.2b	55.5 ± 4.1a	49.4 ± 2.9a	52.9 ± 3.1a	55.5 ± 3.3a
CEOR	81.4 ± 6.2a	93.3 ± 4.3a	87.1 ± 5.1a	54.5 ± 3.7b	38.3 ± 4.8b	67.2 ± 5.1a	66.6 ± 2.4a	63.2 ± 3.3a	37.4 ± 2.5b	26.7 ± 2.1b
ROMU	72.3 ± 5.8a	71.0 ± 2.5ab	88.4 ± 6.5a	71.1 ± 4.4ab	51.8 ± 5.5b	91.4 ± 6.5a	67.3 ± 3.7b	59.9 ± 3.2b	64.5 ± 2.8b	41.9 ± 3.6c
LIBE	74.7 ± 6.6a	62.1 ± 5.7a	57.5 ± 4.2ab	54.1 ± 3.1b	54.5 ± 4.2b	47.1 ± 4.3b	75.1 ± 5.1b	72.5 ± 2.7b	80.6 ± 3.5b	24.4 ± 5.1c
KALA	81.7 ± 5.3a	76.3 ± 6.1a	80.1 ± 4.6a	62.8 ± 4.7a	75.2 ± 4.9a	76.3 ± 3.8a	91.2 ± 5.4a	63.9 ± 4.2b	58.4 ± 2.6b	32.4 ± 3.2c
PAQU	58.6 ± 7.1b	87.2 ± 4.4a	85.8 ± 6.1a	72.6 ± 5.3ab		64.0 ± 4.4a	61.8 ± 3.2ab	49.9 ± 3.6b	56.2 ± 3.2ab	
RUID	63.6 ± 6.8a	71.8 ± 5.1a	65.6 ± 4.5a	77.2 ± 5.6a	53.1 ± 6.3a	78.1 ± 3.1a	76.1 ± 2.4a	65.4 ± 3.1b	57.4 ± 2.4bc	44.8 ± 3.1c
Red Oak										
BETH	134.4 ± 15.6a	106.6 ± 13.2ab	101.3 ± 8.7ab	77.8 ± 11.6b	64.5 ± 12.1b	44.6 ± 7.6b	56.2 ± 4.7ab	64.4 ± 3.6a	50.8 ± 3.8ab	26.9 ± 3.3c
EUAL	81.8 ± 5.3ab	95.7 ± 4.3a	89.9 ± 4.5a	75.2 ± 3.3b	64.0 ± 7.3b	35.7 ± 6.8b	70.4 ± 5.6a	53.4 ± 4.5ab	48.9 ± 3.5b	29.9 ± 4.4c
CEOR	84.8 ± 6.1a	87.7 ± 3.1a	84.8 ± 3.8a	89.1 ± 4.1a	40.6 ± 5.6b	77.0 ± 5.4a	52.3 ± 4.8bc	55.4 ± 3.2b	60.7 ± 4.1b	39.1 ± 3.2c
ROMU	83.1 ± 4.6ab	85.7 ± 5.2ab	93.0 ± 3.1a	81.5 ± 4.7ab	74.1 ± 4.2b	52.2 ± 4.3b	51.1 ± 2.5b	44.2 ± 4.4bc	71.5 ± 5.4a	35.6 ± 4.1c
LIBE	85.2 ± 4.4a	86.7 ± 3.6a	74.6 ± 2.7ab	58.1 ± 3.2c	60.3 ± 6.3bc	36.6 ± 4.6b	69.9 ± 5.1a	78.3 ± 3.8a	49.5 ± 4.7b	46.2 ± 3.6b
KALA	94.1 ± 6.5a	67.3 ± 3.2b	89.4 ± 4.1ab	79.3 ± 5.2ab	72.1 ± 5.3b	73.3 ± 5.5b	94.5 ± 6.2a	66.4 ± 4.1b	60.4 ± 3.3b	26.5 ± 6.1c
PAQU	99.9 ± 5.5a	79.4 ± 4.6b	83.4 ± 3.6b	86.3 ± 4.4ab		59.5 ± 3.8a	65.7 ± 4.1a	53.2 ± 4.5a	61.9 ± 2.6a	
RUID	78.8 ± 4.9a	76.1 ± 3.1a	75.5 ± 5.5a	72.1 ± 3.6a	51.7 ± 5.2b	61.4 ± 4.4a	42.9 ± 3.9b	56.4 ± 3.3b	48.4 ± 3.2b	19.4 ± 6.8c

Table S2. Average (\pm SE) percent annual carbon gained for each day of growth during pre-, during-, and post-canopy periods for four invasive species (IES) (*Berberis thunbergii*, *Euonymus alatus*, *Celastrus orbiculatus*, and *Rosa multiflora*) and four native species (NS) (*Lindera benzoin*, *Kalmia latifolia*, *Parthenocissus quinquefolia*, and *Rubus allegheniensis*) grown under three different overstory canopy types. Canopy species included sugar maple (*Acer saccharum*), white ash (*Fraxinus americana*), and red oak (*Quercus rubra*). Values are also pooled by invasive (IES) and native groups (NS) as well as functional groups. Invasive exotic species are highlighted in gray cells and NS in white. Two-way ANOVAs compare variables across species (n = 3), IES and NS groups (n = 6) and interactions, where site was a random effect and month was a fixed effect. Variables followed by the same lowercase letter within a canopy type are not significantly different at $P < 0.05$. P values are reported, with significant effects denoted with an asterisk: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Additionally, bolded values indicate significant differences ($p < 0.05$) between IES and NS within a column.

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	<i>Acer saccharum</i>			<i>Fraxinus americana</i>			<i>Quercus rubra</i>			All		
	%Pre	%During	%Post	%Pre	%During	%Post	%Pre	%During	%Post	%Pre	%During	%Post
<i>B. thunbergii</i>	1.35 \pm 0.5a	0.40 \pm 0.1b	0.91 \pm 0.4b	1.61 \pm 0.2a	0.41 \pm 0.1b	0.42 \pm 0.3b	1.79 \pm 0.2a	0.48 \pm 0.1b	0.22 \pm 0.1b	1.67 \pm 0.2	0.41 \pm 0.01	0.47 \pm 0.1
<i>L. benzoin</i>	0.95 \pm 0.1a	0.57 \pm 0.2b	0.58 \pm 0.2b	1.37 \pm 0.2a	0.54 \pm 0.1b	0.50 \pm 0.2b	1.04 \pm 0.2a	0.51 \pm 0.2b	0.50 \pm 0.1b	0.89 \pm 0.1	0.52 \pm 0.03	0.46 \pm 0.2
<i>E. alatus</i>	1.75 \pm 0.3b	0.38 \pm 0.1a	0.75 \pm 0.3b	1.67 \pm 0.3a	0.38 \pm 0.1b	0.62 \pm 0.4b	1.85 \pm 0.2a	0.35 \pm 0.1b	0.29 \pm 0.1b	1.77 \pm 0.1	0.35 \pm 0.03	0.36 \pm 0.1
<i>K. latifolia</i>	1.07 \pm 0.2a	0.47 \pm 0.1b	0.70 \pm 0.3b	1.56 \pm 0.4a	0.48 \pm 0.1b	0.70 \pm 0.5b	1.81 \pm 0.3a	0.47 \pm 0.1b	0.30 \pm 0.1b	1.14 \pm 0.4	0.47 \pm 0.03	0.53 \pm 0.1
<i>C. orbiculatus</i>	1.72 \pm 0.5a	0.47 \pm 0.1b	0.40 \pm 0.2b	2.22 \pm 0.3a	0.43 \pm 0.1b	0.37 \pm 0.3b	2.16 \pm 0.4a	0.43 \pm 0.1b	0.35 \pm 0.2b	2.28 \pm 0.2	0.43 \pm 0.02	0.31 \pm 0.1
<i>P. quinquefolia</i>	1.51 \pm 0.3a	0.57 \pm 0.1b	0.61 \pm 0.3b	1.00 \pm 0.5a	0.58 \pm 0.2b	0.12 \pm 0.1b	1.71 \pm 0.3a	0.51 \pm 0.2b	0.0 \pm 0.0b	0.93 \pm 0.4	0.55 \pm 0.01	0.23 \pm 0.2
<i>R. multiflora</i>	1.92 \pm 0.3a	0.46 \pm 0.1b	0.41 \pm 0.4b	1.89 \pm 0.2a	0.39 \pm 0.1b	0.36 \pm 0.1b	2.01 \pm 0.4a	0.40 \pm 0.1b	0.29 \pm 0.1b	1.97 \pm 0.1	0.37 \pm 0.01	0.32 \pm 0.1
<i>R. allegheniensis</i>	1.71 \pm 0.3a	0.41 \pm 0.1b	0.34 \pm 0.2b	1.66 \pm 0.7a	0.41 \pm 0.1b	0.35 \pm 0.1b	1.94 \pm 0.5a	0.40 \pm 0.2b	0.23 \pm 0.1b	1.72 \pm 0.2	0.38 \pm 0.03	0.31 \pm 0.1
IES	1.78 \pm 0.1a	0.43 \pm 0.1b	0.62 \pm 0.2b	1.85 \pm 0.1a	0.41 \pm 0.1b	0.45 \pm 0.1b	1.98 \pm 0.1a	0.42 \pm 0.1b	0.29 \pm 0.1b	1.92 \pm 0.1	0.41 \pm 0.02	0.37 \pm 0.03
NS	1.32 \pm 0.2a	0.50 \pm 0.1b	0.54 \pm 0.1b	1.40 \pm 0.1a	0.48 \pm 0.1b	0.42 \pm 0.1b	1.62 \pm 0.2a	0.47 \pm 0.1b	0.26 \pm 0.1b	1.47 \pm 0.1	0.48 \pm 0.04	0.38 \pm 0.07
Summary of ANOVA												
Canopy												
Group	(0.05)*	(0.08)	(0.55)	(0.01)*	(0.17)	(0.83)	(0.02)*	(0.43)	(0.75)	(0.05)*	(0.81)	(<0.01)**
Canopy*Group										(0.001)**	(0.07)	(0.72)
Direction	IES>NS			IES>NS			IES>NS			(0.88)	(0.88)	(0.64)
Shrub	1.30 \pm 0.2a	0.45 \pm 0.1b	0.74 \pm 0.1b	1.52 \pm 0.1a	0.45 \pm 0.1b	0.57 \pm 0.1b	1.65 \pm 0.2a	0.45 \pm 0.1b	0.33 \pm 0.1b	1.36 \pm 0.2	0.44 \pm 0.1	0.46 \pm 0.1
Vine	1.69 \pm 0.4a	0.52 \pm 0.1b	0.50 \pm 0.1b	1.62 \pm 0.6a	0.51 \pm 0.1b	0.23 \pm 0.1b	1.83 \pm 0.2a	0.47 \pm 0.1b	0.18 \pm 0.2b	1.60 \pm 0.7	0.49 \pm 0.1	0.27 \pm 0.2
Subshrub	1.81 \pm 0.1a	0.43 \pm 0.1b	0.38 \pm 0.1b	1.77 \pm 0.1a	0.39 \pm 0.1b	0.35 \pm 0.1b	1.97 \pm 0.1a	0.40 \pm 0.1b	0.26 \pm 0.1b	1.84 \pm 0.1	0.36 \pm 0.1	0.32 \pm 0.1

SYNTHESIS

Community-level phenology influences IES understory success in temperate deciduous forests

Phenological observations have provided information regarding the natural calendar and plant communities since ancient agricultural times, but with strong evidence of warming shifts in climate, the study of phenology has gained renewed interest with questions emerging regarding species, community, and ecosystem performance under changing conditions. Most studies of invasive exotic species (IES) suggest that phenology may be one such mechanism supporting their success in introduced environments. Phenology may be used to exploit ecosystem resources through several means including extended temporal niche breadth in which IES benefit by assimilating more energy (Richards *et al.* 2006; Wolkovich & Cleland 2011) and occupying a vacant niche to utilize resources not being used by resident species (Elton 1958; Mack *et al.* 2000). These hypotheses present the potential for individual plant photosynthetic activity and carbon gain based on community-level processes, which may be more appropriate for investigating communities with complex compositions and high seasonal variability such as temperate deciduous forests. The deciduous nature of vegetation along with phenological asynchrony across strata results in seasonal variability of understory resource availability. Windows of opportunity for resources also vary spatially across the forest landscape, as species-specific traits lead to differential phenology and light availability across forest stands. Given this complexity, few studies have taken a community-level, mechanistic approach to understanding the role of phenology in IES success. Due to the apparent influence of overstory phenology on understory growth success and the incomplete knowledge regarding IES and NS growth sensitivities to seasonal light availability, the objectives of my dissertation were to evaluate the role of community-level phenology in IES success and the underlying mechanistic basis for IES and NS growth differences in temperate deciduous forest understories.

To address this issue, I conducted a replicated common garden experiment with four IES and four NS grown under three canopy types differing in phenology and light transmittance. Understory species

were chosen because they commonly co-occur in local forests and they allow testing of the following hypotheses within and across multiple functional groups: 1) annual growth of IES exceeds that of NS, 2) IES growth advantage is most pronounced under canopies that allow greater understory light availability (*i.e.*, later spring phenophases, higher transmittance, and shorter leaf lifespans), 3) growth variation among IES and NS is related to differences in several intrinsic growth determinants, and 4) IES advantage is more greatly influenced by spring than autumn phenological variation. Critical phenophases in overstory and understory vegetation were monitored in all gardens as were understory PAR and temperature. Diagnostic gas exchange was measured *in situ* using photosynthetic light responses assessed across a range of leaf temperatures throughout the growing season. Comparisons of seasonal growth rates among IES and NS grown under the various canopy types were based on a combination of destructive measures and nondestructive, allometric estimates of plant biomass.

As hypothesized, annual growth was greater for IES than NS under all canopy types and was highly and positively related to total seasonal light accessible to understory seedlings. As IES were more likely to exhibit longer leaf lifespans, they also achieved greater seasonal growth. This trend was supported within and across all functional groups except subshrubs for which IES and NS did not differ in either leaf lifespan or growth. However, because growth was related to seasonal light availability, it was also explained by dates of canopy flush and abscission and differed with canopy type. In support of my second hypothesis, greater growth was achieved in white ash understories which received the greatest amount of light, due to both higher light transmission when canopy leaves were present and relatively shorter leaf lifespans (*i.e.*, later spring and earlier fall phenophases). IES growth advantage was evident under all canopy types, but significantly greater under canopies with greater seasonal light availability. Although IES exhibited greater seasonal growth rates, which is often characteristic of fast-growing, resource-demanding species, they also exhibited longer leaf lifespans, suggesting that IES may benefit from traits attributed to successful competitors in both high- and low-resource environments

Beyond extended leaf lifespans, growth in temperate deciduous forest understories was also explained by a number of intrinsic growth determinants. Overall, growth was explained by the daily

integral of photosynthesis expressed per unit leaf area (A_{area}), leaf mass (A_{mass}), and plant mass (A_{plant}), with whole-plant photosynthesis explaining the greatest amount of variation as it represents physiological (A_{area}), morphological (specific leaf area, SLA), and allocational (leaf mass ratio, LMR) determinants of growth. In general, leaf area ratio (LAR) and, in particular, SLA had the highest relative influence on growth under all canopy types which is often the case for growth in low-light environments. In a comparison of IES and NS species groups, SLA, mass-based, and whole-plant photosynthesis were significantly greater in IES. However, steeper relationships between relative growth rates (RGR) and assimilation rates (A_{area} and A_{plant}) suggested more efficient resource use and carbon capture in IES compared to NS. My findings indicate that growth variation cannot generally be ascribed to a sole determinant (Kruger & Volin 2006) as slightly larger SLA, greater assimilation efficiency, greater phenological extension were all factors in IES growth advantage. However, greater assimilation efficiency together with greater leaf lifespans could amplify IES success in deciduous forest understories.

Field measurements of diagnostic gas exchange and environmental conditions were used to build a stochastic model of photosynthesis and further emphasized the significance of phenology and seasonal variability in IES success. Model predictions supported empirical observations that IES achieve greater carbon gain and growth than NS, especially under canopies that provided slightly greater seasonal understory light conditions, albeit low light, such as the white ash canopies used in my study. While IES advantages were in part due to longer leaf lifespans, they were also due to a faster and more plastic response to seasonal changes in temperature in spring and summer months. Photosynthetic capacities also significantly declined in autumn, resulting in greater contributions of pre-canopy physiological activity to annual carbon gain in all species under all canopy types. The carbon gain in spring before canopy closure was more important to acquiring an annual carbon subsidy, suggesting earlier leaf flush is an important mechanism of IES establishment and growth. This was consistent with higher photosynthetic capacity and temperature light responses in spring and early summer, supporting the hypothesis that IES have an advantage during these periods, especially under canopies with late spring phenophases. Given the apparent influence of phenology and seasonal temperature sensitivities of growth, climate warming and

associated phenological shifts will likely have important implications for the susceptibility of temperate forest understories to IES.

Overall, this dissertation elucidates the role of community-level predictors such as canopy species composition, plant phenology, and environmental site characteristics in understory growth and IES success. This dissertation is the first to incorporate 1) community-level phenological interactions, 2) direct measures of carbon gain (*i.e.*, destructive harvests), 3) extensively sampled gas exchange measurements, and 4) temperature-dependence modeled from photosynthetic temperature light response curves to investigate extended leaf lifespan as a mechanism for IES advantage over NS. Furthermore, by focusing on community-level phenology and associated seasonal variations in environmental conditions, this dissertation addressed prominent questions in invasive plant ecology regarding niche partitioning, traits conferring invasive success, and growth responses to resource availability and temperature variation. Answers to these questions advance our understanding of the ecological and physiological basis for IES success. For IES in temperate deciduous forest understories, occupying a greater temporal niche breadth and a vacant niche for light integration significantly contributed to their seasonal growth advantage over NS. More efficient light integration, along with greater SLA, also provided a plausible mechanism for IES growth advantage in these low-light environments. Finally, seasonal physiological responses to temperature contributed to support of a critical period for carbon acquisition in the spring and suggest that such information will be essential in building a greater understanding of plant communities and invasions given future climate warming projections and associated climate-driven shifts in phenology.

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