

Invaders do not require high resource levels to maintain physiological advantages in a temperate deciduous forest

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Abstract. Non-native, invasive plants are commonly typified by trait strategies associated with high resource demands and plant invasions are often thought to be dependent upon site resource availability or disturbance. However, the invasion of shade-tolerant woody species into deciduous forests of the Eastern United States seems to contradict such generalization, as growth in this ecosystem is strongly constrained by light and, secondarily, nutrient stress. In a factorial manipulation of light and soil nitrogen availability, we established an experimental resource gradient in a secondary deciduous forest to test whether three common, woody, invasive species displayed increased metabolic performance and biomass production compared to six co-occurring woody native species, and whether these predicted differences depend upon resource supply. Using hierarchical Bayesian models of photosynthesis that included leaf trait effects, we found that invasive species exhibited functional strategies associated with higher rates of carbon gain. Further, invader metabolic and growth-related attributes were more responsive to increasing light availability than those of natives, but did not fall below average native responses even in low light. Surprisingly, neither group showed direct trait or growth responses to soil N additions. However, invasive species showed increased photosynthetic nitrogen use efficiencies with decreasing N availability, while that of natives remained constant. Although invader advantage over natives was amplified in higher resource conditions in this forest, our results indicate that some invasive species can maintain physiological advantages over co-occurring natives regardless of resource conditions.

Key words: *Bayesian hierarchical models; forest invasion; functional traits; light addition; nitrogen fertilization; photosynthesis; resource limitation; understory shrubs.*

INTRODUCTION

Habitats characterized by high resource availability, frequent disturbance, or low environmental stress are generally considered to be more susceptible to invasion by nonnative plant species (e.g., Elton 1958, Hobbs and Huenneke 1992, Burke and Grime 1996, Alpert et al. 2000), which Davis et al. (2000) formalized as the theory of fluctuating resources. Comparisons with native resident species often indicate invasive species display “early successional” traits associated with high resource acquisition and increased productivity (Daehler 2003, Leishman et al. 2010, van Kleunen et al. 2010). In contrast, environments where light, water, and/or nutrients place significant constraints on plant productivity are generally thought to be invasion resistant (e.g., Alpert et al. 2000, Daehler 2003).

Many plant invaders in the Eastern United States (hereafter, EUS), however, are Eurasian shade-tolerant woody species that are actively spreading into mid- to late-successional deciduous forests (Fridley 2008, Martin et al. 2009), despite the presumably strong light- and nutrient-related constraints on plant growth (Pacala et al. 1994, Reich et al. 1997, Finzi and Canham 2000). Common garden studies have found these species to senesce their leaves later and assimilate proportionally more carbon into the autumn (Fridley 2012), possess both more productive (C gains) and efficient (C gains per unit resource cost) resource-use strategies (Heberling and Fridley 2013), and exhibit root traits associated with more efficient nutrient foraging (Jo et al. 2015) compared to native species. However, it is unclear whether such differences in a common garden are found in limiting resource conditions typical to secondary forests. Field surveys indicate invasive species abundance is generally increased in forests of high soil nitrate and seasonal light availability (Dreiss and Volin 2013), but few experimental field manipulations of resources have been performed in the context of native and invasive

Manuscript received 10 September 2015; revised 28 October 2015; accepted 5 November 2015. Corresponding Editor: D. C. Laughlin.

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TABLE 1. Woody, deciduous species measured in this study, including nativity status in Eastern North America and general growth form.

Code	Species	Common name	Nativity	Growth form
ACSA	<i>Acer saccharum</i> Marsh.	sugar maple	native	tree
CORA	<i>Cornus racemosa</i> Lam.	gray dogwood	native	shrub
FRAM	<i>Fraxinus americana</i> L.	white ash	native	tree
LOBE	<i>Lonicera</i> × <i>bella</i> Zabel [<i>L. morrowii</i> × <i>tatarica</i>]	Bell's honeysuckle	nonnative	shrub
OSVI	<i>Ostrya virginiana</i> (Mill.) K. Koch	hophornbeam	native	shrub, tree
PRSE	<i>Prunus serotina</i> Ehrh.	black cherry	native	tree
PRVI	<i>Prunus virginiana</i> L.	chokecherry	native	shrub, tree
RHCA	<i>Rhamnus cathartica</i> L.	common buckthorn	nonnative	shrub, tree
ROMU	<i>Rosa multiflora</i> Thunb.	multiflora rose	nonnative	subshrub, vine

forest species' ecophysiology and performance (but see Cassidy et al. 2004).

Prevailing forest succession models highlight strong species-specific responses to light, indicating growth rates under high light trade off with low-light survival (Pacala et al. 1994, 1996, Kobe et al. 1995, Walters and Reich 1996). Shade tolerance can define strategy variation in forest species worldwide (Valladares and Niinemets 2008). Secondarily, many mesic temperate ecosystems are considered to be nitrogen limited (Vitousek and Howarth 1991), with experiments showing increased growth with N fertilization (LeBauer and Treseder 2008). Nitrogen addition experiments in temperate forests have reported complex responses to N, with seedling survivorship variously a function of both nitrogen and light availabilities (Catovsky and Bazzaz 2002), no growth or photosynthetic trait differences with increased soil N (Walters and Reich 1996), or species-dependent growth responses (Catovsky et al. 2002, Zaccherio and Finzi 2007). In general, understory growth is correlated more with light than with N availability in EUS trees (Finzi and Canham 2000).

In a two-yr factorial manipulation of light and soil nitrogen in a deciduous forest in central New York, USA, we tested (1) the responsiveness of physiological traits of co-occurring native and invasive woody species to variation in resource supply, (2) how such responses relate to carbon gain across resource supply gradients, and (3) the degree to which invasive species maintain physiological advantages over natives under low light and nutrient availabilities.

We had two hypotheses: (H1) Under low resource conditions, invasive species maintain greater carbon gain and resource-use efficiencies (carbon gains per resource cost) compared to native species. (H2) In contrast, in high resource environments, efficient use of resources might not convey fitness advantages. Therefore, invasive and native species may have similar resource-use efficiencies in high resource conditions, but invaders exhibit faster growth rates as a consequence of greater investment in photosynthetic capacity.

METHODS

Study site

Plots were selected in a closed canopy secondary forest in central New York (42°55' N, 76°02' W; town of Pompey, south of Syracuse, New York, USA). The overstory primarily consisted of *Acer saccharum* (sugar maple) and *Fraxinus americana* (white ash), along with other native deciduous tree species *Prunus serotina* and *Ostrya virginiana*.

Light and soil nitrogen additions

Sixteen, spatially separated, 5 m radius plots were selected in summer 2012, following field surveys of species occurrences and light availabilities. We chose study species based on common occurrence with a subset of three invasive species (minimum of two) and six native woody species (minimum of three) in each plot (Table 1).

Nitrogen was added as granular NH_4NO_3 in five applications from March to August totaling $133 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$. This high fertilization rate was chosen to ensure any potential N growth limitations were relieved, yet consistent with other long and short term understory forest N additions (e.g., Catovsky and Bazzaz 2002, Cassidy et al. 2004, Magill et al. 2004). This rate is roughly double the average N mineralization rates in mesic temperate forests (Reich et al. 1997). Light availability was increased in half of the plots through overstory canopy thinning or tree felling in November 2012 (post leaf fall). Any woody debris was removed from each plot to minimize site disturbances.

Plot- and plant-level light levels were estimated as integrated growing season light availability through hemispherical photographs taken in the center of each plot in pre-treatment year (2012), treatment year one (2013), and year two (2014), as well as directly above each plant canopy in 2014. Images were analyzed with Gap Light Analyzer (GLA) software (Frazer et al. 1999) to calculate the gap light index (GLI; Canham 1988), which estimates combined incident diffuse and

TABLE 2. Model parameters, data, prior distributions, and literature sources used in photosynthesis model.

Symbol	Definition (units)	Attribute	Distribution (mean μ , SD σ)	Literature source
A_{net}	net photosynthetic rate, observed ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	dependent variable	data	–
μA_{net}	net photosynthetic rate, modeled ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	dependent variable	predicted value	–
τ	model precision (variance ⁻¹)	parameter	(model σ^2) ⁻¹ $\sigma \sim \text{dunif}(0, 100)$	non-informative prior
R_d	mitochondrial daytime respiration rate ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	parameter	dnorm ($\mu = 0$, $\sigma^2 = 10^3$)	non-informative prior based on Patrick et al. (2009)
V_{cmax}	maximum carboxylation rate of rubisco ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	parameter	dnorm ($\mu = 25$, $\sigma^2 = 10^3$)	non-informative prior based on Peltier and Ibanez (2015)
C_i	intercellular CO ₂ partial pressure (Pa)	independent variable	data	–
Γ^*	CO ₂ compensation point (Pa)	parameter	dnorm ($\mu = 4.275$, $\sigma^2 = 0.1$)	informative prior based on Patrick et al. (2009), Bernacchi et al. (2001)
O	intercellular O ₂ partial pressure (kPa)	constant	21	Farquhar et al. (1980)
K_c, K_o	Michaelis-Menten constants for CO ₂ (Pa) and O ₂ (kPa), respectively	constant	40.49, 27.84 (adjusted to 25°C)	Bernacchi et al. (2001)
β_N	slope of fixed effect of leaf N on V_{cmax}	parameter	dnorm ($\mu = 0$, $\sigma^2 = 10^4$)	non-informative prior
N	leaf nitrogen concentration (g/m ²)	covariate	data	–
Chl	leaf chlorophyll index (unitless; 0–100)	covariate	data	–
J_{max}	maximum electron transport rate ($\mu\text{mol e}^-\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	parameter	dnorm ($\mu = 55$, $\sigma^2 = 10^3$)	non-informative prior based on Peltier and Ibanez (2015)
$\text{RE}_{p,s}, \text{RE}_{p,i}$	random individual effects for species, s , or individual, i , on parameter, p	parameter	($\text{RE } \sigma^2$) ⁻¹ $\sigma \sim \text{dunif}(0, 100)$	non-informative prior
α	quantum efficiency of electron transport (mol e ⁻ ·mol quanta ⁻¹)	parameter	dnorm ($\mu = 0.24$, $\sigma^2 = 0.01$)	informative prior Feng and Dietze (2013)
β_{chl}	slope of fixed effect of leaf chl on α	parameter	dnorm ($\mu = 0$, $\sigma^2 = 10^4$)	non-informative prior
q	photosynthetic photon flux density ($\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	independent variable	–	–
SLA	specific leaf area (m ² /g)	covariate	data	–
β_{SLA}	slope of fixed effect of Chl on α	parameter	dnorm ($\mu = 0$, $\sigma^2 = 10^4$)	non-informative prior

direct beam radiation over a growing season (percentage of full sun). Plant-available nutrients were quantified using plant root simulator (PRS) ion exchange probes (Western Ag Innovations, Saskatoon, Saskatchewan, Canada) deployed for 4 weeks on separate occasions in May and July 2013. For each deployment, four cation and four anion probes were inserted into the soil of each plot and were pooled by plot for analysis. See Appendix S2 for final light and soil N levels.

Leaf gas exchange

Gas exchange measurements were performed on cut branches, following the protocol of Niinemets et al.

(2005), widely used for temperate woody species. Gas-exchange measurements were made using a LI-6400 portable photosynthesis system equipped with CO₂ and temperature control modules (Li-Cor, Lincoln, Nebraska, USA). Leaves were photoinduced at a moderate irradiance level (300 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) prior to measuring CO₂ response curves (A/C_i) and light response curves (A/q). See Appendix S1 for further details.

Leaf structural and biochemical traits

Leaves were scanned for leaf area and oven dried at 60°C for 48 h. Specific leaf area (cm²/g) was

calculated as the surface area per dry mass. Leaf construction costs (CC) were calculated as described in Heberling and Fridley (2013). Mass-based leaf nitrogen (N_{mass}) and carbon (C_{mass}) concentrations were determined using an elemental analyzer (CE Elantech, Lakewood, New Jersey, USA). Area-based concentrations (N_{area} , C_{area}) were determined by multiplying mass-based units by SLA. Due to similarity between years, we pooled leaf chemical data from two collection years.

To measure leaf N resorption, recently senesced leaves were collected in autumn (October–November 2013) on tagged individuals by gently shaking the plant and collecting fallen leaves, aiming to collect leaves from the same cohort as the mature leaf collection. Mass loss during senescence was corrected following Vergutz et al. (2012). Senesced leaf N concentration (senesced N_{mass}) was calculated by multiplying N_{mass} by the MLCF (mass loss correction factor [dry mass of senesced leaves]/[dry mass of mature leaves]).

Leaf chlorophyll concentrations (chl) were measured with a chlorophyll meter (atLEAF+; FT GREEN LLC, Wilmington, Delaware, USA), using the mean of six readings per leaf (avoiding midrib; 5–10 leaves/plant). The atLEAF+ measures leaf absorbance difference between 660 and 940 nm and has been shown perform similarly to other readers and correlated to total chl content (Zhu et al. 2012). Species-specific leaf out and senescence dates for each plot were recorded in 2013, as well as biweekly chl measurements from September 2014 through senescence.

Leaf and branch production (ANPP)

Aboveground growth was tracked on at least one individual per species per plot by tagging growing point terminuses on every branch in early spring 2013 and 2014 (pre-leaf out) using colored tape and remarked throughout the year. In a few cases where plants were too large to feasibly monitor, a subset of branches were tagged. Leaf counts were done annually to quantify leaf mass production. Aboveground net primary productivity (ANPP; excluding radial growth, flower production) was estimated as stem and leaf dry mass produced over the 2-yr study. We assumed radial woody growth and other production was negligible compared to stem elongation and foliage production during our study, and therefore refer to stem and leaf dry mass production rate as ANPP.

Data analysis

We implemented a version of the Farquhar-von Caemmerer-Berry (FvCB) photosynthesis model (Farquhar et al. 1980) using a hierarchical Bayesian (HB) framework (Patrick et al. 2009). We chose the HB framework for several reasons, based on its ability to (1) efficiently fit a complex model with multiple parameters relating to biochemical limitations of

photosynthesis (Patrick et al. 2009, see Table 2), many of which are treated as constants or assigned subjectively in conventional maximum likelihood-based model fitting approaches (Dubois et al. 2007); (2) use data from multiple sources (A/q , A/C_i) simultaneously to inform species and individual-level parameters, rather than fitting data individually curve-by-curve; (3) explicitly incorporate the influence of plant traits on photosynthetic processes to improve model fits and make direct inferences on biologically relevant, mechanistic hypotheses (Feng and Dietze 2013); (4) estimate posterior probability distributions, as opposed to single point estimates, to account for uncertainty in subsequent models; and (5) incorporate prior information (Table 2) to improve model performance for biochemical parameters that are well studied but might be poorly informed by our data alone, while still accounting for this uncertainty based on recognized interspecific variation in these parameters (Patrick et al. 2009).

We included fixed effects for the influence of functional traits on photosynthetic processes following Feng and Dietze (2013) and included species- and individual-level random effects into the process model. Trait effects in the full model included effects of leaf N on maximum carboxylation rate (β_N), SLA (β_{SLA}), and Chl (β_{chl}) on quantum efficiency. Prior distributions were derived at a broad taxonomic level, centered on literature values (Peltier and Ibanez 2015) or uninformative. Abbreviations, units, definitions, and distributions are listed in Table 2. See Appendix S1 for further description of the modeling methods.

Statistical inference

The photosynthetic model was implemented for native and invasive species separately and the 95% Bayesian credible intervals were used to compare parameters across native and invasive species. Due to constraints in our model structure, we also ran models separately by species (removing species random effects) to obtain species-level estimates in order to visualize species variation (Fig. 1), but group-level inferences are made using the full model with random effects. To test for differences between native and invasive species by resource availability, posterior means for each parameter were compared with HB models with non-informative priors (with species and plot random effects) and incorporating parameter uncertainty into the data models. GLI and soil N values were standardized by their mean and standard deviation to facilitate comparisons across data sets. Potential photosynthetic nitrogen-use efficiency (PNUE) was calculated as $A_{\text{max}}/N_{\text{area}}$ (Funk and Vitousek 2007).

Similarly, we modeled ANPP as a function of (1) light, soil N, and their interaction; and (2) photosynthetic capacity (A_{max}) using posterior estimates of model parameters under ambient CO_2 and saturating light, and leaf duration (90% senesced minus leaf expansion

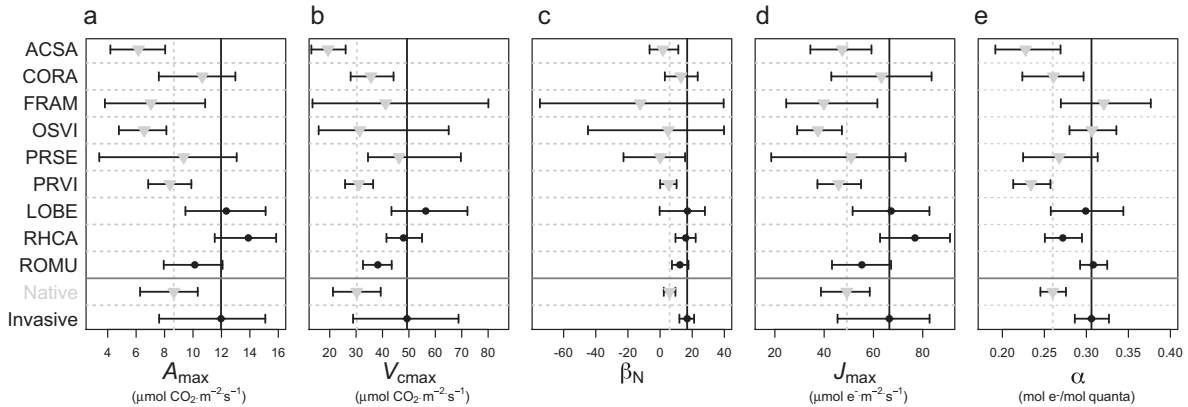


FIG. 1. Means and 95% credible intervals across all plots according to species and nativity group for (a) maximum photosynthetic rate (A_{\max}), (b) maximum carboxylation rate ($V_{c\max}$), (c) slope of fixed effect of leaf N on $V_{c\max}$ (β_N), (d) maximum electron transport rate (J_{\max}), and (e) quantum utilization efficiency (α). Native, gray triangles; invasive, black circles. Vertical lines denote group-level means. See Table 1 for species codes. Species-level estimates were calculated from separate models.

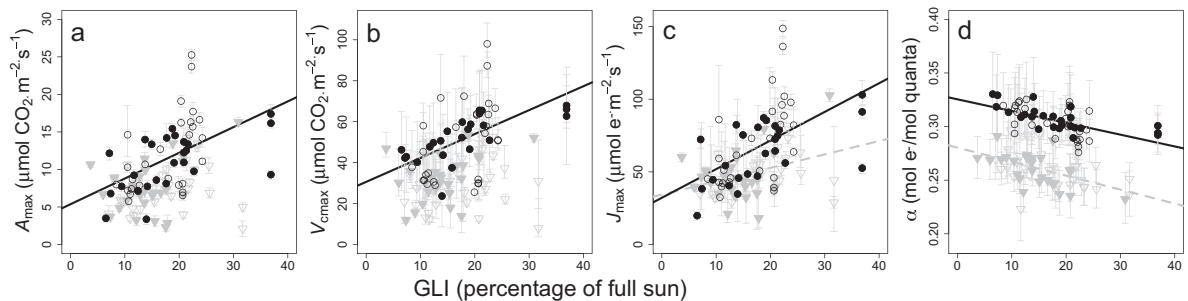


FIG. 2. Photosynthetic model parameters as a function of light availability (gap light index, GLI) for (a) maximum photosynthetic rate (A_{\max} ; 95% slope CIs $\times 10$, native $[-5.7, 0.2]$, invasive $[14.5, 22.9]$), (b) maximum carboxylation rate ($V_{c\max}$; 95% slope CIs $\times 10$, native $[-10.0, 12.0]$, invasive $[24.0, 49.3]$), (c) maximum electron transport rate (J_{\max} ; 95% slope CIs $\times 10$, native $[-27.2, -3.7]$, invasive $[89.9, 125]$), (d) quantum utilization efficiency (α ; 95% slope CIs $\times 10$, native $[-0.15, -0.15]$, invasive $[-0.14, 0.00]$). Light gray error bars denote 95% credible intervals on posterior means. Solid points show individuals in N-addition plots for invasive (black circles) and native (gray triangles) species. Regression lines with slope 95% CIs outside zero are drawn (native, dashed; invasive, solid).

dates). Because differences in ANPP might be confounded by initial plant biomass, we included starting wood biomass as a covariate in all ANPP models.

Analyses were performed in JAGS (Plummer 2003) using R2jags (Su and Yajima 2015) in R (R Core Team 2014; see Supplement 1 for code). Final models were run with three parallel Markov chain Monte Carlo (MCMC) chains for 100 000 iterations, discarding the initial 50 000 for burn-in. Trace plots and \hat{R} (Gelman-Rubin diagnostic; Gelman and Rubin 1992) were used to confirm convergence.

RESULTS

Experimental resource gradients

Tree removal significantly increased plot-level light availability (change in GLI = $14.0\% \pm 1.5\%$ full sun [mean \pm SE]; Appendix S2: Table S1, Fig. S1). Compared to unfertilized plots, fertilized plots showed increased

N availability by roughly five-fold (Fig. B1). N addition had the biggest influence on nitrate availabilities. Spring and summer soil N were similar (data not shown), so total soil inorganic N (ammonium + nitrate) means were used in analyses.

Photosynthetic trait responses

Photosynthetic model parameters showed significant variation across species (Fig. 1; Appendix S3) and treatments (Fig. 2). Final models for both native and invasive groups excluded the fixed effect of chlorophyll (Chl) on α (β_{chl}), but included all other fixed and random effects. When included with SLA, β_{chl} 95% CIs included zero (native $[-0.010, 0.017]$; invasive $[-0.031, 0.040]$) and removal of this term facilitated convergence and substantially improved model fit for both native (DIC = 1667 vs. 1609) and invasive (DIC = 2841 vs. 2830) species, likely due to collinearity between SLA and Chl. Predicted photosynthetic

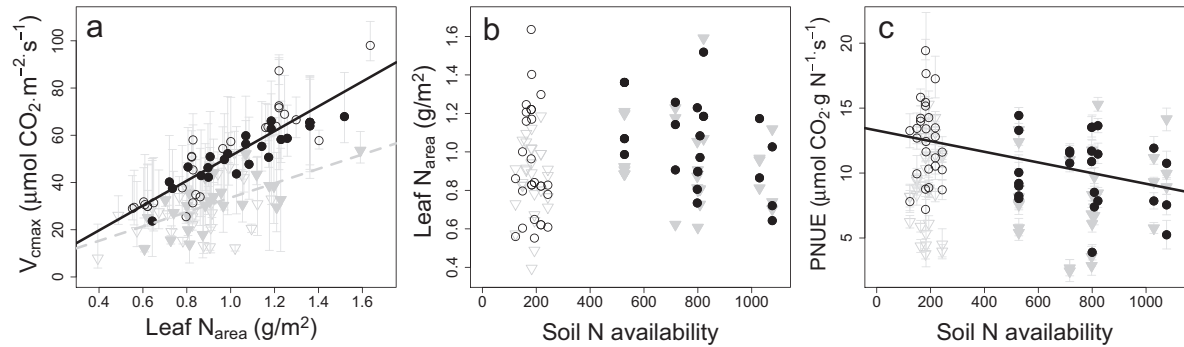


Fig. 3. Functional relationships between leaf nitrogen, photosynthesis, and available soil N. (a) Carboxylation capacity leaf N; 95% slope CIs (β_{N_c}), native (2.3, 9.6), invasive (12.0, 21.2). (b) Leaf nitrogen-available soil N; 95% slope CIs, native ($-0.008, 0.099$), invasive ($-0.045, 0.080$). (c) PNUE (photosynthetic nitrogen use efficiency)-available soil N; 95% slope CIs, native ($-11.54, 8.92$), invasive ($-21.9, -4.51$). Light gray error bars denote 95% credible intervals on posterior means. Closed points show individuals in N addition plots for invasive (black circles) and native (gray triangles) species. Only significant regression lines are drawn (native, dashed; invasive, solid).

rates (μA_{net}) in final models for both native and invasive species were closely correlated to observed A_{net} ($R^2 > 0.97$).

Leaf nitrogen significantly influenced carboxylation capacity (V_{cmax}) in both native and invasive species, but the effect size (β_{N_c}) was significantly greater in invaders (Fig. 1; Appendix S3). Invasive species had higher mean V_{cmax} and J_{max} (maximum electron transport rates), but their corresponding 95% CIs overlapped (Fig. 1b,d). Native and invasive species groups had significant but similar SLA influences on α (β_{SLA} ; Appendix S3).

All species displayed significant photosynthetic differences across the light gradient. In general, invasive species were more responsive to light availability, with greater coordinated variation in photosynthetic parameters (V_{cmax} , J_{max}) and parameter-derived traits (A_{max} , PNUE; Fig. 2; Appendix S3). Invasive species displayed a greater range of A_{max} and significant responses to increases in light availability (Figs. 1 and 2a; β_{GLI} coefficients in Appendix S3: Table S1). Invasive species also had greater V_{cmax} , J_{max} , and α at a given light level (Fig. 2b,c).

Soil N had no direct influences on any parameter ($\beta_{soil N}$ in Appendix S3; Fig. 2) and leaf N showed minimal responses to fertilization (Fig. 3b). However, the interaction between light and soil $\beta_{soil N \times GLI}$ was significant for several parameters (V_{cmax} , J_{max} , A_{max} ; Table B2), with contrasting responses between native and invasive species. Soil N \times light effects were significant for invasive species for both parameters (95% CI V_{cmax} $\beta_{soil N \times GLI}$ [$-3.9, -1.5$]; 95% CI J_{max} $\beta_{soil N \times GLI}$ [$-9.7, -6.3$]). Only the J_{max} effect was significant for natives, but the estimated coefficient was positive (95% CI $\beta_{soil N \times GLI}$ [$2.2, 4.6$]). As a result, there was a significant negative response of nitrogen availability on PNUE, but no response for natives (Table C2; Fig. 3c; $R^2 < 0.01$, invasive: $R^2 = 0.32$). Including only a soil N fixed effect ($\beta_{soil N}$) confirmed this

difference, with 95% CIs for natives essentially centered at zero ($-0.003, 0.002$) but negative for invasive species ($-0.007, -0.001$).

Phenological trait responses

Invasive species tended to lose their leaves later into the autumn than native species, in terms of 50% and 90% leaf loss (Fig. 4e,f). Later senescence subsequently permitted invaders to retain significant Chl later into autumn (Fig. 4a–d). Compared to control plots, light and light + N addition plots showed slight increases in mid-season Chl for invaders, but no response in natives. Leaves in native species showed rapid declines in Chl beginning in September. Invasive species maintained mid-season Chl levels into mid-October and showed slower declines and higher Chl at senescence. In addition to Chl, invasive species invested more total nitrogen in their leaves. Similar to Chl at senescence, senesced leaf N was greater in invasive species, indicating significantly lower nitrogen resorption proficiencies than natives (Fig. 5).

Structural leaf trait responses

Leaf structural adjustments were consistent across species in response to light. SLA declined with increasing light availabilities (invasive, $R^2 = 0.50$, $P < 0.001$; native, $R^2 = 0.27$, $P < 0.001$), while LDMC and leaf thickness increased (Appendix S4). Leaf trait responses to the soil N gradient were minimal and inconsistent across species (Figs. 2 and 3b). At a given light level, invasive species showed greater SLA and lower LDMC than natives (Appendix S4).

Growth responses

Sapling growth responses in all species were difficult to estimate in the field and were highly variable. Despite

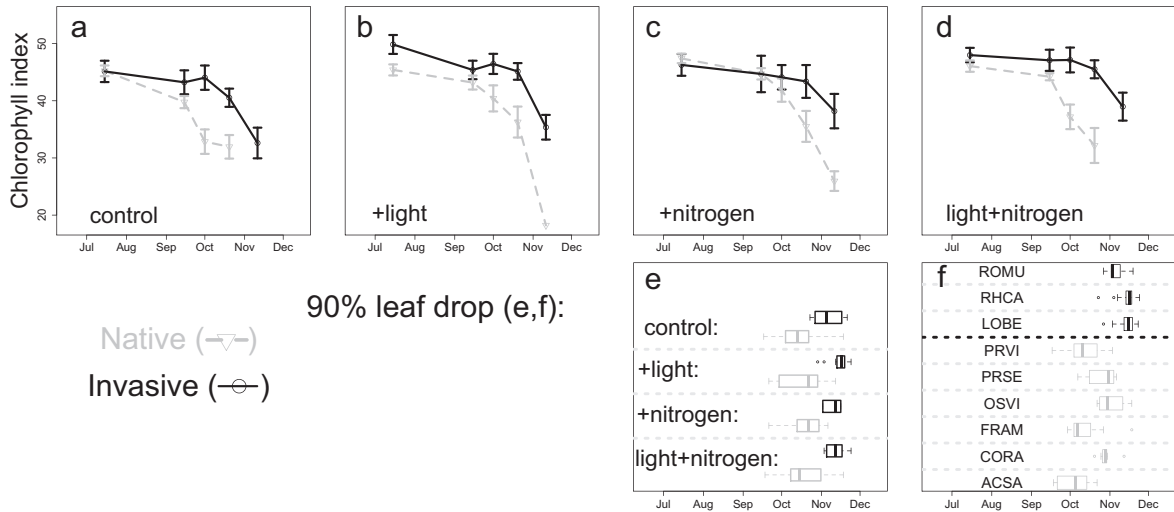


FIG. 4. Seasonal trajectory of relative leaf chlorophyll concentration (chlorophyll index) across (a) control, (b) light, (c) nitrogen, and (d) light + nitrogen treatments for native (gray, dashed line) and invasive (black, solid line) species. (e and f) Boxplots of date of 90% leaf drop by treatment and species, respectively. Points represent mean (\pm SE) by group. Boxplots denote dates of approximate 90% leaf loss as determined through weekly censuses. Boxes show first and third quartiles with median as heavy line, whiskers extend to 1.5 times the interquartile range, and points are outliers outside that range.

this variation, invasive species had the higher maximum rates of stem and leaf production (ANPP) regardless of treatment, but these differences were particularly pronounced at higher light levels (Fig. 6a). Neither invasive nor native species showed ANPP responses to increasing soil N (Fig. 6b; Table 3a). As with leaf trait–environment responses, invasive species were more responsive to the light availability gradient, with light-mediated ANPP increases in invasive species only (Table 3a). Native and invasive species were influenced by initial plant size similarly ($\beta_{\text{initial biomass}} \approx 0.2$; Table 3) and native and invasive species did not differ by group in pre-treatment biomass.

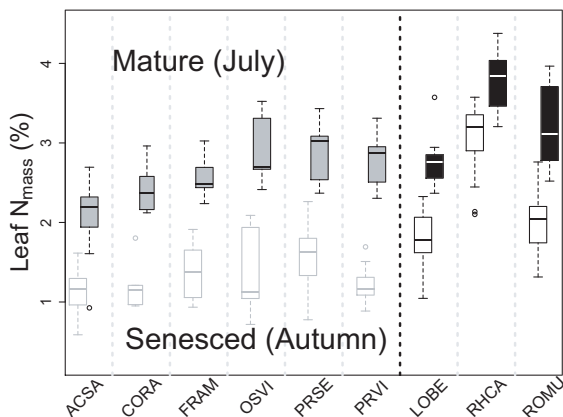


FIG. 5. Leaf nitrogen concentrations across treatments for mature (solid boxplots) and senesced (open boxplots) for native (left, gray) and invasive (right, black) species. Senesced leaf N was corrected to account for leaf mass loss at senescence. See Table 1 for species codes.

Maximum photosynthetic rate (A_{max}) significantly influenced ANPP for invasive species but not native species (Table 3b). ANPP models that also included growing season (leaf duration) showed no response to growing season length in native or invasive species length ($\beta_{\text{leaf duration}}$ was near zero in both groups), so the term was removed in the final models. However, leaf display duration and A_{max} were positively related across all individuals ($R^2 = 0.53$, $P < 0.001$).

DISCUSSION

To date, mechanistic understanding of plant invasions is derived to a large degree from foundational perspectives based in resource-rich ecosystems of anthropogenic disturbance (Elton 1958). However, habitats that constrain productivity through resource limitations, including water, nutrients, or light, are frequently invaded by species with unique adaptations for these environments (Funk 2013). In the EUS, many natural area invaders of management concern are found in forest understories (Fridley 2008), an environment where light and, occasionally, nitrogen have been shown to limit native woody growth and constrain community dynamics (e.g., Bazzaz 1979, Pacala et al. 1994, Finzi and Canham 2000). With an experimental resource gradient in an EUS deciduous forest, we tested two hypotheses: first, invader trait advantages over natives are maintained at low resource levels; and second, natives and invaders may not differ in resource-use efficiency in high resources, but invaders are capable of investing more resources toward C gain. Unlike previous research that emphasized the importance of disturbance and resource availability in plant invasions

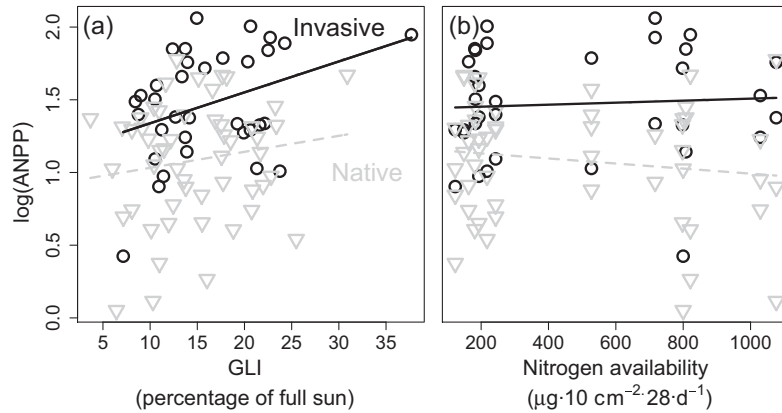


FIG. 6. Growth responses (ANPP, g/2 yr) measured after 2 yr of treatment across (a) light levels (invasive, $R^2 = 0.13$, $P < 0.05$; native, $R^2 = 0.02$, $P > 0.1$) and (b) soil nitrogen (invasive, $R^2 < 0.01$, $P > 0.7$; native, $R^2 = 0.02$, $P > 0.3$). Native, gray triangles, dashed line; invasive, black circles, solid line.

(e.g., Burke and Grime 1996, Davis et al. 2000, Leishman et al. 2010), we found invasive species in this ecosystem maintain physiological advantages compared to resident natives, even under low light conditions, and invader trait advantages are magnified at higher light levels. Unexpectedly, direct responses to nitrogen availability were negligible in both native and invasive species.

As predicted in our first hypothesis, invasive species displayed greater photosynthetic rates overall (Fig. 1), regardless of environment. Supporting our second hypothesis, these differences were magnified at increasing understory light levels (Fig. 2). Quantum efficiency (α) differences between groups were particularly evident. In addition, invaders displayed greater carboxylation efficiency in response to leaf N (β_N). Trait shifts along the light gradient were frequently in the same direction for both native and invasive species, but these shifts were stronger for invasive species. Invasive species exhibited higher A_{max} at higher light levels and this

difference led to greater rates of biomass production.

It was surprising that ANPP in native species did not respond to increased light levels in this experiment, given that previous studies on similar species found light responses in radial stem growth (e.g., Pacala et al. 1994, Finzi and Canham 2000). Relative to these studies, our range of light levels was not as dramatic and may not have captured variation in native ANPP responses. Pacala et al. (1994) reported growth rate saturation at extremely low light levels for late successional shade tolerant species (e.g., 1% full sun to achieve half its maximum growth rate for *Acer saccharum*). The range of light levels in the current study was broad (around 5% to >30% full sun) and representative of many deciduous forest conditions in the region, supporting the conclusion that invasive species appear more responsive to a wider gradient of understory light levels in these forests.

Table 3. Effects of (a) light (GLI) and nitrogen (N) availability and (b) photosynthesis on branch and leaf production (ANPP; g new biomass over 2 yr treatment period) as assessed through Bayesian linear mixed effects models with random effects for species.

ANPP as function of	Native			Invasive		
	Mean	95% CI		Mean	95% CI	
a) Resource availability						
β_{GLI}	0.48	-0.40	1.38	1.61	0.43	2.76
$\beta_{\text{soil N}}$	-0.83	-1.74	0.08	0.21	-0.93	1.25
$\beta_{\text{soil N} \times \text{GLI}}$	-0.3	-1.27	0.67	-0.41	-1.47	0.62
$\beta_{\text{initial biomass}}$	2.73	1.87	3.62	1.65	0.42	2.92
b) Photosynthesis						
$\beta_{A_{\text{max}}}$	0.22	-0.62	1.07	1.19	0.24	2.15
$\beta_{\text{initial biomass}}$	2.03	1.22	2.83	2.30	1.39	3.20

Notes: Pre-treatment biomass was included as a covariate ($\beta_{\text{initial biomass}}$). Significant fixed effects (credible intervals not overlapping zero) are shown in boldface type. Slope coefficients are $\times 10$ and ANPP was log-transformed.

Unexpectedly, plant responses to soil nitrogen were much less striking, even though N availabilities varied by a factor of five. A lack of ANPP responses to soil N implies that growth in this forest was not nitrogen-limited. Responses may have become significant if we had reduced N availability below ambient levels (Cassidy et al. 2004). Although leaf N significantly influenced V_{cmax} in both groups, invasive species displayed greater photosynthetic adjustments to leaf N. While leaf N was significantly higher in invasive species, neither group showed obvious increases in leaf N with increasing soil N availability. This result is in contrast with previous long-term N addition studies including similar native species that reported increases in leaf N following fertilization (e.g., Magill et al., 2004; Bauer et al. 2004). Leaf N differences might become significant with time. However, even in a 14-yr N addition experiment in Michigan, Bethers et al. (2009) found no differences in A_{max} for *A. saccharum*. In a related study, this species showed increased growth from fertilization, but not photosynthetic rates, suggesting soil N might affect C allocation, rather than C assimilation (Talhelm et al. 2011). Despite lack of treatment effects on leaf N, we found significant light \times soil N effects for photosynthetic parameters, indicating N toxicity at high light. A previous study found N additions to alter leaf N allocation in native *Pinus resinosa* and result in a 50% decrease in photosynthetic capacity in fertilized trees (Bauer et al. 2004). It is unclear whether N additions caused similar shifts in allocation in invasive species in the current study.

In addition to differences in biomass and carbon gains, invasive species showed significantly greater PNUE than native species, but only in unfertilized plots (Fig. 3c). The PNUE–light availability relationship was positive, but interestingly, the relationship between PNUE and soil N was negative, due to similar leaf N across treatments combined with lower A_{max} at higher soil N availabilities. Decreases in PNUE with increasing soil N might suggest that resource use efficiencies are meaningful only at lower nutrient conditions. An intuitive explanation for our result is that invasive species are better able to adjust their strategies along nitrogen gradients, whereas natives' strategies appear to be insensitive. Supporting this hypothesis, common garden comparisons revealed these forest invaders are less conservative with nitrogen (low resorption rates), but have root traits (increased specific root length and fine root production) that enable higher uptake rates and rapid N cycling (Jo et al. 2015).

Does resource availability determine understory invasion success?

Current invasion theory emphasizes the mediating roles of disturbance and resource conditions (Burke and Grime 1996, Davis et al. 2000; but see Ordóñez

and Olf 2013) and propagule pressure (von Holle and Simberloff, 2005) in driving invader success. Yet, shade-tolerant woody species actively colonize relatively undisturbed, low-light forest understories in EUS and other temperate regions, including Europe. The context of these invasions suggests forest invaders might substantially differ from those of other studies where invasive trait strategies depend upon physiological advantages at high resources (Leishman et al. 2010). To complicate the search for general mechanisms, species-specific case studies suggest that invasion mechanisms for EUS forests invaders may even differ between species and forests. *Ailanthus altissima*, an invasive tree in EUS, is a “gap-obligate” species that can invade late-successional forests, but only in high light (Knapp and Canham 2000, Martin et al. 2010). It is likely that many forest invaders, particularly those confined to gaps or forest edges, follow similar mechanisms reported for invasions into other ecosystems. However, many invaders are well adapted to low resource conditions. Our conclusions might be generalizable to other groups invasive in deciduous forests. Wilson et al. (2015) found the success of the invasive grass, *Microstegium vimineum*, was similarly unconstrained by resource availability.

Our results are supported by previous studies that implicate functional differences between native and invasive species, where invasive advantages seem to be independent of resource or disturbance conditions. Demographic comparisons with native EUS tree species indicate that invasive *Acer platanoides* follows a different life history trade-off between low-light survivorship and growth in high light (Martin et al. 2010). Along with common garden results (Fridley 2012, Heberling and Fridley 2013, Jo et al. 2015), our results confirm in the field that resource availability does not in itself determine understory invasion success. We found invasive species to follow different responses to light than natives, particularly in α and β_N .

CONCLUSION

Contrary to the widespread expectation that native species show trait and growth advantages under certain environmental conditions, we found no evidence that woody invasive species performed more poorly than natives under the decreased light or nitrogen conditions common in EUS forest understories, although rates of invasion are likely to be higher as light levels increase. It is possible an unmeasured axis of differentiation exists (e.g., toward defense) that can account for the apparent functional superiority of invaders in this forest. Future work should focus on the lack of apparent physiological tradeoffs in many invaders, and whether there exist any common forest conditions that preclude invader establishment.

ACKNOWLEDGMENTS

We are grateful to Tom and Randi Starmer for support, assistance and property access, and to Allison Heberling, Mara McPartland, and Elise Hinman for invaluable field and laboratory assistance. This work was supported by a U.S. NSF Graduate Research Fellowship to J. M. Heberling.

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