



**The influence of light habitat on the physiology, biomass allocation, and fecundity of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae) 1**

Author: Lieurance, Deah

Source: The Journal of the Torrey Botanical Society, 143(4) : 415-426

Published By: Torrey Botanical Society

URL: <https://doi.org/10.3159/TORREY-D-15-00056.1>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

# The influence of light habitat on the physiology, biomass allocation, and fecundity of the invasive shrub Amur honeysuckle (*Lonicera maackii*, Caprifoliaceae)<sup>1</sup>

Deah Lieurance<sup>2</sup>

Center for Aquatic and Invasive Plants, Institute of Food and Agricultural Sciences  
University of Florida, P.O. Box 110500, Gainesville, FL 32611

Kim Landsbergen

Science Division, Antioch College  
One Morgan Place, Yellow Springs, OH 45387

**Abstract.** Many exotic invasive plants exhibit plasticity in form and function across a range of environmental conditions, optimizing available resources in a manner that frequently outcompetes native organisms. The invasive shrub *Lonicera maackii* is one of the most prominent invasive plant species in the Midwestern United States. The objectives of this research were to investigate the morphological and physiological plasticity of this invasive shrub across light environments, and to study allometric parameters that will help estimate the aboveground biomass of *L. maackii* of all size classes. Shrubs were selected from open, forest edge, and understory habitats. Photosynthetic responses to light and leaf nitrogen content were measured throughout the growing season in 2003 and shrubs were harvested in October 2003. The maximum photosynthetic assimilation rates for open grown shrubs were more than double the values measured in the edge and understory. Maximum photosynthesis rates were strongly correlated with leaf nitrogen content, yet the photosynthetic nitrogen use efficiency was uniform across habitats. Open-grown shrubs had the highest values of total and partitioned biomass, although shrubs from all locations showed a proportional distribution to leaf, branch, trunk, and fruit. Although reproductive shrubs can produce copious amounts of fruits and seed in high light environments, fruit production still occurred in forest interior environments and is a direct source of seeds in the understory. Results suggest that because *L. maackii* exhibits physiological and morphological plasticity coupled with prolific fecundity (even in the understory), this species can persist in all habitats.

Keywords: allometry, Amur honeysuckle, fecundity, photosynthesis, Photosynthetic nitrogen use efficiency (PNUE)

As the ecological and economic costs of biological invasion increase, we must refine our understanding of many of the attributes that make invaders successful in their new habitats. Invasive plant species have many common life history traits, such as high leaf longevity, superior physiological performance, increased growth rates, high phenotypic plasticity, and abundant seed production and dispersal (Bazzaz 1986, Reichard and Hamilton 1997, Davidson, Jennions, and

Nicotra 2011, Jelbert *et al.* 2015). An important component of an invasive plant's ability to compete with and persist among native plants is the efficiency of the plant in utilizing available resources such as light and nutrients (Bazzaz 1986, Heberling and Fridley 2013). Subsequently, by understanding the characteristics influencing photosynthetic performance, light availability, and nitrogen use, one can gain useful information regarding the competitive success of an invasive plant.

Although attempts have been made to evaluate which plant physiological and morphological features are correlated with invasiveness (*e.g.*, Reichard and Hamilton 1997, Smith and Knapp 2001, Richards *et al.* 2006, Van Kleunen, Weber, and Fischer 2010), a single “smoking gun” trait that effectively predicts plant invasive potential has yet to be identified. Phenotypic plasticity in the form of growth, morphology, physiology, and fitness traits has often been identified as an important mechanism of invasion for plants (Davidson *et al.* 2011). Additionally, plant morphological and physiological features, such as

---

<sup>1</sup> Funding for this research was provided by Ohio University's Department of Environmental and Plant Biology, the Masters in Environmental Studies program, and Ohio University's John Houk Memorial Research Grant. We would also like to thank Chris Dauner and the staff of East Fork State Park for access to field sites. D. Black, J. Bascom, J. Chiang, K. Hartman, and R. McEwen assisted throughout this research.

<sup>2</sup> Author for correspondence: [dmlieurance@ufl.edu](mailto:dmlieurance@ufl.edu)  
doi: 10.3159/TORREY-D-15-00056.1

©Copyright 2016 by The Torrey Botanical Society

Received for publication September 8, 2015, and in revised form July 14, 2016; first published September 8, 2016.

reduced construction cost and dark respiration, increased leaf density, nitrogen use efficiency, and maximum photosynthesis, correlate with competitive success of invasive plants (Nagel and Griffin 2004, Osunkoya *et al.* 2010). Furthermore, others have found leaf mass per unit area (LMA,  $\text{g/m}^2$ ) and its inverse specific leaf area (SLA) to be a robust correlate of physiological capacity as well as a trait measured to evaluate phenotypic plasticity (Reich *et al.* 1999, Poorter *et al.* 2009). Deconstructing the aspects of invasive plant success could lead to improved management, and the presence of certain traits could help identify potentially invasive plants before they reach a novel ecosystem.

First introduced in the late 1800s, *Lonicera maackii* (Rupr.) Maxim (Caprifoliaceae) has become one of the most prominent invasive plant species in the midwestern and northeastern parts of the United States (Luken and Thieret 1996). *Lonicera maackii*, a deciduous woody shrub native to China, Japan, Korea, and southeastern Russia, was introduced for horticultural purposes, and is still commercially available today (Luken and Thieret 1996). Even now, *L. maackii* plants and seeds can still be found online for purchase in the United States, although increasing numbers of states are banning its sale and import.

*Lonicera maackii* demonstrates many traits attributed to successful invasive species, such as extended leaf phenology, high fecundity, allelopathic suppression of other plants, tolerance to a variety of habitats, and high photosynthetic rates that facilitate the establishment and spread of this species (Luken *et al.* 1995a, Luken *et al.* 1997, Dorning and Cipollini 2006, McEwan *et al.* 2009, McEwan *et al.* 2010, Cipollini, Titus, and Wagner 2012, Lieurance and Cipollini 2013, Ali, Lieurance, and Cipollini 2015). Due to its moderately high light requirements, it is particularly successful in fragmented habitats, and this is a trait that *L. maackii* shares with many other prominent invasive plants (Luken and Goessling 1995, With 2002, Fan *et al.* 2013). Fragmentation of forests in rural areas and suburban woodlots has provided adequate habitat for *L. maackii* establishment. High tolerance to a variety of habitats has allowed this species to persist across the landscape, with *L. maackii* bushes comprising up to 50% of the species composition in the understory of small woodlots in southwest Ohio (Medley 1997; Gorcho, Henry, and Frank 2014).

Much is known about the population structure, dispersal, and ecosystem effects of *L. maackii* as well as the morphological and physiological plasticity of seedling and juvenile plants (*e.g.*, Luken *et al.* 1997, Gorcho and Trisel 2003, Bartuszevige and Gorcho 2006, Poulette and Arthur 2012, Castellano and Gorcho 2013). Luken *et al.* (1995a) examined the branch architecture plasticity of *L. maackii* in open- and closed-canopy light environments, finding the open-grown shrubs able to reach larger heights and diameters due to changing ratios of long to short shoots and continuous growth habit. Harrington, Brown, and Reich (1989a) and Harrington *et al.* (1989b) investigated physiological traits and biomass allocation of exotic shrubs including the hybrid honeysuckle, *Lonicera ×bella* and found differences in SLA, photosynthesis, leaf nitrogen content, and other measures of leaf morphology and biomass allocation/carbon gain based on available light resources in the field. To our knowledge, however, no physiological research has been conducted on mature plants growing in the field, specifically in edge habitats, such as roadsides and forest-meadow interfaces, where *L. maackii* is exceedingly successful. It is reasonable to presume the amount of edge habitat will only increase over time due to anthropogenic disturbance and increased fragmentation. Therefore, the study of *L. maackii* in edge habitat is integral to our understanding of the successful colonization and persistence of this invasive woody shrub.

Allometric equations in the form of regression models are often employed to estimate above-ground biomass and primary productivity of woody species without the need of a destructive harvest (*e.g.*, Niklas 1994, Clark *et al.* 2001, Chave *et al.* 2005, Basuki *et al.* 2009). Allometry can also provide an efficient method for determining plant management strategies such as the dosage of herbicide required for treatment or the duration of grazing to reduce aboveground biomass (Grace and Fownes 1998, Itou *et al.* 2015). Additionally, allometric equations are used routinely in the estimation of carbon storage in terrestrial systems (*e.g.*, Litton and Kauffman 2008, Singh *et al.* 2011, Corona *et al.* 2012). In the case of *L. maackii*, accurate equations estimating aboveground biomass, leaf area, and fecundity of a population in an invaded habitat can assist in our understanding of carbon acquisition, the proportion of aboveground carbon sequestered

by *L. maackii* in the ecosystem, propagule pressure, and potential dispersal across the landscape and can help simplify management planning in the natural areas of the Midwest.

Our objectives were to assess the physiological and morphological plasticity of mature *L. maackii* shrubs growing in three habitat types of open field, forest edge, and forest interior, and to examine the allometric relationships between plant diameter and aboveground biomass. We predicted that: (a) net photosynthesis (and other measures of physiology), leaf nitrogen content, and leaf density (leaf mass per unit area) will increase with proportional increases in light availability; (b) leaf nitrogen and nitrogen use efficiency will increase under increasing light conditions with the operational assumption that *L. maackii* is a shade intolerant shrub (Luken *et al.* 1995a, b); and (c) biomass and fecundity will increase with increasing light availability.

**Materials and Methods.** **SITE DESCRIPTION.** We evaluated *L. maackii* shrubs located within the East Fork State Park in Clermont County, Ohio, USA (39°1'31.4"N, 84°5'32.1"W) beginning March 2003. The park is a mosaic of successional phases, consisting of reclaimed agricultural land, remnant prairie habitat, and red maple (*Acer rubrum*) dominated forest fragments. The 30-year mean annual precipitation was 107.95 cm and the mean annual temperature was 12.6 °C (maximum 18.2 °C and minimum 6.9 °C). In addition to *L. maackii*, the site contains several other invasive plant species including Japanese honeysuckle (*Lonicera japonica*), kudzu (*Pueraria montana*), Russian olive (*Elaeagnus angustifolia*), and garlic mustard (*Alliaria petiolata*). *Lonicera maackii* bud break was observed the third week of March 2003.

Shrubs were randomly selected in three light environments: open meadow, forest edge, and forest interior. Plant canopy openness was measured with hemispherical photography at each shrub and mean openness was  $62.86 \pm 4.7\%$ ,  $13.85 \pm 0.3\%$ , and  $12.17 \pm 0.4\%$ , respectively (Lieurance 2004). Within each location, a range of size classes were selected and all were reproductively mature (between 7 and 10 years). Open-grown shrubs ( $N = 5$ ) were located in open fields (no overstory), edge-grown shrubs ( $N = 23$ ) were located on the periphery of forest patches within 10 m from the forest meadow interface, and interior-grown shrubs ( $N = 23$ ) were selected in the

center of the forest past the 10-m edge-defining parameter. The imbalance in sample size was due to the management practices of this state park (mowing open areas), resulting in a scarcity of open-grown *L. maackii* shrubs in meadows.

**GAS EXCHANGE AND LEAF STRUCTURE MEASUREMENTS.** Leaf gas exchange measurements were performed on 4 open, 6 edge, and 12 interior shrubs using a LI-6400 infra-red gas exchange analyzer (Li-Cor Inc., Lincoln, NE) in May, July, and September 2003, on one to three fully developed leaves per shrub. Responses were recorded at 10 PPFD levels: 0, 75, 100, 200, 400, 600, 800, 1000, 1200, and 1600  $\mu\text{mol m}^{-2}\text{s}^{-1}$ . Transitions between PAR were made once photosynthesis was stable (minimum 5 min). Measurements were made between 8:00 am and 3:00 pm, the relative humidity (RH) and temperature within the leaf chamber were set at 70% and 20 °C, respectively, and CO<sub>2</sub> reference partial pressure was set to match ambient values (350  $\mu\text{mol mol}^{-1}$ ). Leaf CO<sub>2</sub> assimilation ( $A$ ) as a function of photosynthetic photon flux density ( $Q$ ) curves were generated for each leaf sampled (SigmaPlot; Systat Software, Inc., Chicago, IL). Maximum photosynthesis ( $A_{\text{max}}$ ), respiration ( $R_d$ ), quantum yield (QE), light compensation point (LCP), and light saturation point (LSP) were estimated from A/Q curves using the Photosyn Assistant software (Dundee Scientific, Dundee, Scotland, UK). Leaves used for gas exchange were immediately removed, bagged, and placed on ice until returned to the lab for further analysis.

Leaf nitrogen is often positively correlated with  $A_{\text{max}}$  and other measures of physiology (*e.g.*, Evans 1989). To determine leaf nitrogen content and leaf mass per area (LMA), leaf area was measured for all leaves sampled for gas exchange using a LI-3100 leaf area meter (Li-Cor Inc., Lincoln, NE). Leaves were dried to a constant weight at 70 °C. Total leaf nitrogen was measured using the MicroDumas combustion method of elemental analysis (Carlo Erba NA 1500 CHN analyzer; Carlo Erba Co., Milan, Italy) at the University of Georgia Stable Isotope/Soil Biology Laboratory. Photosynthetic nitrogen use efficiency (PNUE;  $\mu\text{mol CO}_2 \text{ mg}^{-1} \text{ N s}^{-1}$ ) was calculated by dividing  $A_{\text{max}}$  by mass of N per unit area ( $N_a$ ).

**STATISTICAL ANALYSES OF PHYSIOLOGICAL PARAMETERS.** Our hypotheses concerning open, edge, and interior environments address questions at the

individual shrub level; as a result, shrub means were used for a repeated measures ANOVA to test for seasonal differences and interactions between locations for LMA,  $N_a$ , PNUE, and the parameters derived from leaf level physiological measurements ( $R_d$ ,  $A_{max}$ , QE, and LCP; Version 9.2, SAS Institute, Cary, NC). We determined there was no effect of time in our repeated measures model ( $P < 0.05$ ). Therefore, we present physiological data from the midseason (July) measurements of shrub means. Because leaf level physiological differences can be partially explained by LMA, an analysis of covariance (ANCOVA) was used with the dependent variables  $R_d$ ,  $A_{max}$ , QE, LCP,  $N_a$ , and PNUE with LMA as the covariate and location as the class variable (Version 9.2; SAS Institute). Least squares means were calculated *post hoc* to determine significant differences between locations. For all analyses, differences were considered significant at  $P \leq 0.05$ .

**HARVEST AND ALLOMETRIC SAMPLING.** An end-of-season harvest was conducted October, 2003. All shrubs were cut within 5 cm of the soil surface and the fresh mass of all the aboveground biomass for each shrub was measured in the field with a spring instrument scale. Due to the volume of biomass, approximately 10% of the total biomass of large shrubs was randomly subsampled using a two person "blind" sampling technique (Lieurance, 2004). In brief, all stems larger than 1 cm in diameter were cut from the shrub and placed in a pile. One researcher with a random numbers table stood with their back to another researcher who counted stems. The stems that corresponded to a random number from 1–10 from the table were identified by the "blind" person. Hence, the person choosing the branch from the pile selected a truly unbiased subsample of approximately 10% of the shrub. Also, 10% of the total wood for large shrubs was selected in a similar manner. All biomass was collected for the small and medium size classes. Samples brought back to the lab were separated into leaf, stem, and fruit, then dried to a constant weight at 70 °C and weighed. The dry weight of the subsample was used to estimate the total dry weight of subsampled large shrubs.

Total leaf area for each shrub was calculated using a type II reduced major axis regression model with leaf area as dependent variable and leaf mass as independent variable (RMA 1.17; Bohonak and van der Linde, 2004). We chose this model because RMA minimizes the error associ-

ated with variation in both the dependent and independent variables (Sokal and Rohlf 1995). Because there was no statistical difference between edge and interior data for leaf weight and leaf area, values were pooled to develop the estimation equation ( $R^2 = 0.920$ , coefficient = 0.011,  $N = 784$ ) and open-grown leaf data were analyzed separately ( $R^2 = 0.953$ , coefficient = 0.026,  $N = 141$ ). The coefficient for each regression was multiplied by the total dry leaf weight for each shrub to estimate whole-shrub leaf area. Leaf area ratio (LAR) was calculated by dividing total leaf area by total shrub mass. Leaf weight ratio (LWR) was calculated by dividing total dry leaf weight by total dry biomass per shrub. Fruit weight per leaf area (FRUIT/LA) was also calculated in our biomass analysis. Fruit enumerations were estimated for whole shrubs by counting out multiple samples of fruits from open, edge, and interior ( $N = 100$  per location). Fruits were then dried at 70 °C and weighed. The resulting number and biomass data were used with the fruit biomass data to estimate total number of fruit per shrub at the time of harvest. Results of mean number of seeds per fruit (4–6 seeds per fruit) from a related 2003 study using plant material collected from the same site (Bascom, unpublished data) were used to estimate total fecundity of each shrub.

**STATISTICAL ANALYSIS OF ALLOMETRIC DATA.** A one-way analysis of variance (ANOVA) was performed to test for differences in biomass allocation, allocation analysis parameters, basal area, and measurements of fecundity in differing light environments (Version 9.2; SAS Institute, Cary, NC). Percent of total biomass allocated to wood, leaf, and fruit were arcsine transformed to meet the assumptions of normality before ANOVA procedure was performed. Mean differences were considered significant at  $P \leq 0.05$ . Comparisons of means between locations were tested using Bonferroni *post hoc* tests.

To determine allometric equations for biomass parameters, harvest data from all shrubs were pooled across locations to give a complete range of shrub sizes and to account for the small sample size for open grown shrubs ( $n = 5$  open vs.  $N = 48$  total). Dry weights for partitioned components of each shrub (total aboveground plant biomass, wood biomass, leaf biomass, fruit biomass, and estimated total leaf area) as well as the diameter at base (DAB; explanatory variable) were log transformed (double-sided natural logarithm) for

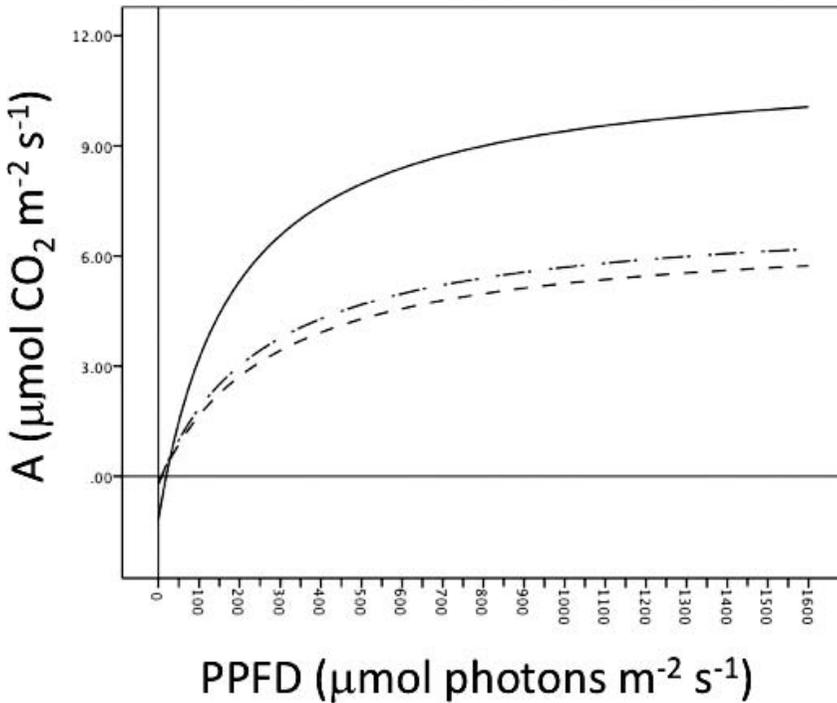


FIG. 1. Photosynthesis light curves based on mean midseason (July) data. All measurements were made July 22–27, 2003 on two fully expanded leaves per shrub. Shrub replication and legend are as follows: Solid line = open ( $N = 5$ ), dotted line = edge ( $N = 6$ ), dashed line = interior ( $N = 12$ ). Light curve model fitting was performed on treatment means using the method of Lobo *et al.* (2013).

regression analysis. Linear regression analysis and coefficients of determination ( $R^2$ ) were used to compare the predictability DAB for biomass estimation (Version 9.2; SAS Institute, Cary, NC). Other research has indicated that an inherent bias occurs when ln-transformed data analyzed with linear regression models is used to predict arithmetic units (Sprugel 1983; Clough, Dixon, and Dalhaus 1997, Rayachhetry *et al.* 2001). Sprugel (1983) suggested the correction factor anti-ln (standard error)<sup>2</sup>/2 to be multiplied with back-transformed estimations (anti-ln( $y$ )) to remove the bias introduced in transformation.

**Results.** Initial analyses indicated there were no significant effects of time on all measurements of gas exchange or leaf structure, subsequent analyses are presented for midseason data (July; Lieurance 2004, Appendix). Open-grown shrubs out-performed the edge and interior shrubs in their photosynthetic response to increasing light, with observed mean maximum photosynthesis rates ( $A_{\max}$ ) of approximately  $14.77 \mu\text{mol m}^{-2} \text{s}^{-1}$  (open) versus  $7.48 \mu\text{mol m}^{-2} \text{s}^{-1}$  (edge and interior; Fig.

1). Plants from these edge and interior habitats displayed similar physiological capacities for all measured parameters. Open-grown *L. maackii* shrubs had values of  $R_d$ ,  $A_{\max}$ , LCP, LMA, QE, and  $N_a$  that were approximately twice that of edge and interior shrubs (Fig. 1; Table 1). Open-grown shrubs had a lower PNUE (Table 1) and all physiological variables were positively correlated with LMA. Edge and interior shrubs also displayed a similar leaf-level physiology and structure. Notably, open-grown shrubs exhibited more physiological variance with increasing LMA for all parameters. For each location, foliar N per unit area ( $N_a$ ) was correlated with  $A_{\max}$  with an  $R^2$  value of 0.622 (data not shown).

Results of the ANCOVA using LMA as the covariate indicate that, after adjusting for LMA, there were significant differences among locations for  $R_d$  ( $F_{2,18} = 8.15$ ,  $P = 0.003$ ),  $A_{\max}$  ( $F_{2,18} = 23.64$ ,  $P < 0.0001$ ), QE ( $F_{2,18} = 5.45$ ,  $P = 0.01$ ),  $N_a$  ( $F_{2,18} = 62.31$ ,  $P < 0.0001$ ), and PNUE ( $F_{2,18} = 47.15$ ,  $P = 0.0001$ ). *Post hoc* tests revealed differences in location where  $R_d$ ,  $A_{\max}$ , QE,  $N_a$ , and PNUE for open-grown *L. maackii* shrubs were

Table 1. Mean values ( $\pm$  SE) for midseason (July) leaf physiological, morphological, and nutrient profiles from shrubs located in open ( $N = 4$ ), edge ( $N = 6$ ), and forest interior ( $N = 12$ ) habitats. Superscript letters indicate differences in mean values for locations ( $P < 0.05$ ).

	Open	Edge	Interior
$R_d$ ( $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$ )	-1.17 (0.38) <sup>a</sup>	-0.27 (0.09) <sup>b</sup>	-0.33 (0.06) <sup>b</sup>
$A_{\text{max}}$ ( $\mu\text{mol CO}_2/\text{m}^2/\text{sec}$ )	14.77 (1.79) <sup>a</sup>	8.31 (0.93) <sup>b</sup>	6.65 (0.42) <sup>b</sup>
QE	0.13 (0.06) <sup>a</sup>	0.03 (0.01) <sup>b</sup>	0.03 (0.01) <sup>b</sup>
LCP ( $\mu\text{mol photon}/\text{sec}/\text{m}^2$ )	17.02 (3.16) <sup>a</sup>	12.91 (5.21) <sup>a</sup>	11.95 (2.02) <sup>a</sup>
LSP ( $\mu\text{mol photon}/\text{sec}/\text{m}^2$ )	329.88 (103.53) <sup>a</sup>	300.17 (27.54) <sup>a</sup>	391.05 (73.71) <sup>a</sup>
LMA ( $\text{g}/\text{m}^2$ )	74.69 (1.82) <sup>a</sup>	41.76 (6.09) <sup>b</sup>	37.46 (1.77) <sup>b</sup>
$N_a$ ( $\text{g}/\text{m}^2$ )	1.50 (0.08) <sup>a</sup>	0.69 (0.04) <sup>b</sup>	0.67 (0.03) <sup>b</sup>
PNUe ( $\mu\text{mol}/\text{gN}/\text{sec}$ )	9.86 (1.04) <sup>a</sup>	10.70 (0.54) <sup>b</sup>	9.96 (0.43) <sup>b</sup>

significantly different than edge/interior shrubs. In contrast, there were no significant differences for LCP or LSP ( $F_{2,18} = 1.26$ ,  $P = 0.31$ ;  $F_{2,18} = 0.04$ ,  $P = 0.96$ , respectively).

Whole plant, component biomass (leaf, wood, and fruit), and basal area ( $\text{cm}^2$ ) were significantly greater in open habitat ( $P < 0.0001$ ) than in edge and interior, which were not different (Table 2). Per shrub total leaf area was roughly 15.5 times greater for open-grown than edge- or interior-grown shrubs. There were differences among all locations for FRUIT/LA ( $\text{g}/\text{m}^2$ ) ratios, the number of fruits per shrub and seeds per shrub were highest in open habitats, and did not differ significantly between edge and interior habitats (Table 2).

There were no differences in allocation to wood or leaf biomass, but there was a significant

difference in percent of total biomass allocated to fruit between interior and open/edge-grown shrubs ( $P < 0.05$ ; Fig. 2). The linear relationship between DAB and the total and partitioned biomass components of *L. maackii* is:

$$\ln(y) = y_0 + a \ln(\text{DAB}),$$

where  $y$  is the dry weight of either a plant component, total biomass, or estimated total leaf area, the intercept is  $y_0$ ,  $a$  is the slope, and DAB is diameter at the base of the shrub. Regression coefficients for predicting partitioned biomass are presented in Table 3. Total aboveground biomass, wood, and leaf weights were positively and significantly correlated with basal area ( $R^2$  values ranging from 0.66 to 0.74). In contrast, there were low correlations between basal area and total leaf

Table 2. Mean values ( $\pm$  SE) for end-of-season biomass, basal area values, allocation proportions, and fecundity of *Lonicera maackii* shrubs grown in open ( $N = 5$ ), edge ( $N = 23$ ), and interior ( $N = 23$ ) habitats. Superscript letters indicate differences in mean values for locations ( $P < 0.05$ ). Leaf area ratio (LAR) is the total leaf area/total aboveground biomass and leaf mass ratio (LMR) is the total leaf mass/total aboveground biomass.

	Open	Edge	Interior
A. Biomass			
Total (g)	23,200.68 (11,015.92) <sup>a</sup>	1,165.47 (370.71) <sup>b</sup>	1,094.88 (261.69) <sup>b</sup>
Wood (g)	18,640.06 (8,811.43) <sup>a</sup>	985.88 (321.84) <sup>b</sup>	954.03 (240.98) <sup>b</sup>
Leaf (g)	4,034.53 (1,950.85) <sup>a</sup>	139.68 (44.83) <sup>b</sup>	130.11 (22.14) <sup>b</sup>
Fruit (g)	526.08 (314.76) <sup>a</sup>	15.71 (5.38) <sup>b</sup>	11.26 (4.17) <sup>b</sup>
B. Basal area ( $\text{m}^2/\text{ha}$ )			
Leaf area ( $\text{m}^2$ )	44.380 (21.459) <sup>a</sup>	3.632 (1.218) <sup>b</sup>	3.383 (0.576) <sup>b</sup>
C. Allocation analysis			
LAR ( $\text{m}^2/\text{g}$ ) <sup>*</sup>	0.0019 (0.00037) <sup>a</sup>	0.0034 (0.00035) <sup>a</sup>	0.0040 (0.011) <sup>a</sup>
LMR ( $\text{g}/\text{g}$ )	0.174 (0.0336) <sup>a</sup>	0.130 (0.0134) <sup>a</sup>	0.154 (0.0108) <sup>a</sup>
FRUIT/LA ( $\text{g}/\text{m}^2$ )	10.27 (2.36) <sup>a</sup>	5.05 (1.12) <sup>b</sup>	2.32 (0.62) <sup>c</sup>
D. Fecundity			
Fruits/shrub	7,294.69 (4,364.46) <sup>a</sup>	286.15 (97.95) <sup>b</sup>	260.76 (96.52) <sup>b</sup>
Seeds/shrub	31,586.00 (18,898.10) <sup>a</sup>	1,181.78 (404.56) <sup>b</sup>	764.04 (282.82) <sup>b</sup>

\* General ANOVA yielded significant results ( $P = 0.046$ ), but the conservative Bonferroni *post hoc* test did not reveal significant differences among means.

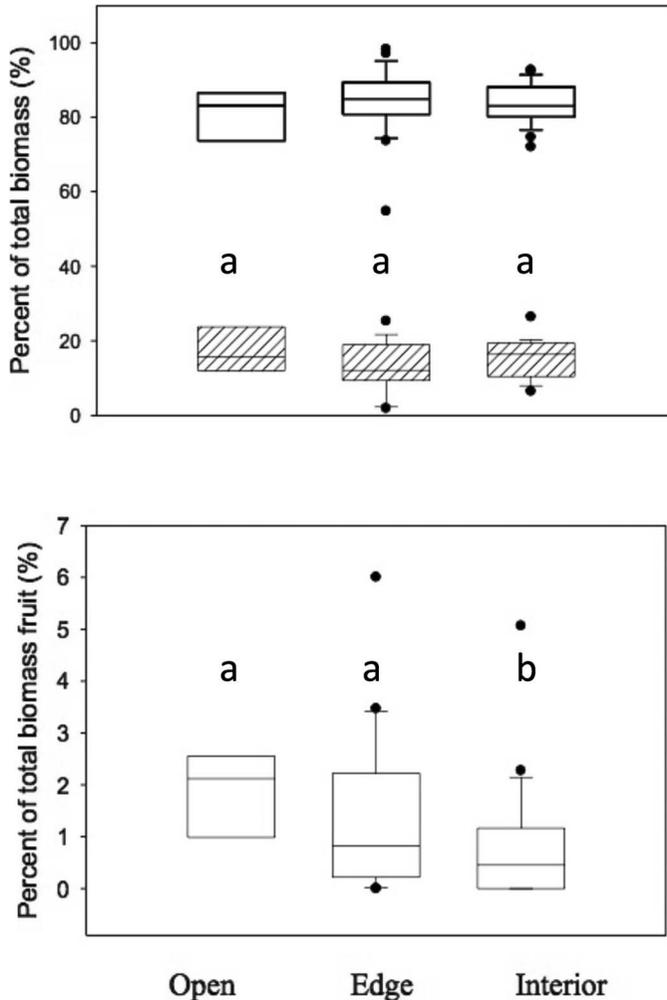


FIG. 2. Percent of total biomass of *Lonicera maackii* shrubs located in open, edge, and interior habitats allocated to wood (A-top, bold), leaf (A-bottom, hatched), and fruit (B). Small letters indicate differences in means for fruit allocations at  $P < 0.05$ . There was no significant difference in means for wood or leaf allocation.

area and fruit weight ( $R^2 = 0.30$  and  $0.13$ , respectively).

**Discussion.** Overall, results of our study supported our prediction that net photosynthesis, leaf N content, and LMA would increase with light availability but, contrary to our predictions, edge and interior shrubs performed the same. Furthermore, high photosynthetic potential in conjunction with low  $R_d$  and LCP rates suggest that *L. maackii* can operate in a positive carbon balance in a wide range of light conditions. This, in combination with other traits measured in this and other studies, indicates *L. maackii* employs many traits associ-

ated with shade tolerance as well as traits associated with phenotypic plasticity (Luken 1988; Luken *et al.* 1995a, b; Luken *et al.* 1997; Valladares and Niinemets 2008). This is contrary to observations of the co-occurring invasive shrub *Rosa multiflora* that exhibits many of the traits associated with shade-avoidance (Dlugos *et al.* 2015). In general, shade-tolerant plants are often thought to exhibit reduced plasticity, but this often dependent on the traits that are measured (Valladares and Niinemets 2008).

Our findings also suggest that, physiologically, the leaves of shrubs growing in edge habitats respond like those growing in the interior. One

Table 3. Parameters for estimating total aboveground biomass and the component biomass for *Lonicera maackii* shrubs growing in open, edge, and interior habitats in Ohio based on the following equation:  $\ln(y) = y_0 + a \ln(\text{DAB})$ , where  $y$  is the dry weight of either a plant component, total biomass, or estimated total leaf area; the intercept is  $y_0$ ;  $a$  is the slope; and DAB is diameter at the base of the shrub. Values represent least square means (standard errors) from two-sided ln-transformed regression.

Dependent variable	DAB <sup>1</sup>		R <sup>2</sup>
	Intercept (± SE)	Slope (± SE)	
Total leaf area (cm <sup>2</sup> )	9.05 (0.23)	0.63 (0.10)	0.48
Total biomass (g)	5.39 (0.19)	0.74 (0.08)	0.65
Wood (g)	5.21 (0.19)	0.74 (0.08)	0.65
Leaf (g)	3.41 (0.23)	0.70 (0.10)	0.52
Fruit (g)	0.10 (0.36)	0.88 (0.15)	0.42

might anticipate clearer distinctions between locations because edge habitats, although shaded, are warmer and generally have more light than interior locales (Matlack 1993). However, our hemispherical photography results indicated that percent canopy openness was roughly four times as great in the open habitat (~ 64%) compared to the edge and interior locations, which were similar in their mean canopy openness values (~ 13%). *Lonicera maackii* had considerable responses to increasing PPFD, and  $A/Q$  light-response curves suggest plasticity of leaf level physiology (high  $A_{\text{max}}$ , low  $R_d$ , and low LCP) might give *L. maackii* a competitive advantage in shadier environments where low light compensation points are a benefit. It should be noted, however, that our estimates of LCP might have been more precise with more observations at lower PPFD. Additionally, our study observed morphological plasticity where lower LMA in low light environments results in increased foliar area to maximize light capture (Niinemets, Kull, and Tenhunen 1998). The leaf traits observed here, with the plastic branching traits observed by Luken *et al.* (1995a), in turn, could ensure the persistence of this shrub in the fragmented forests and woodlots of the Midwest and furthermore, *L. maackii* shrubs could rapidly capitalize on increased light availability if a disturbance were to occur that presented a canopy gap.

The results for leaf N content supported our prediction that foliar  $N_a$  content would increase with increasing light availability.  $N_a$  and LMA were strongly correlated with  $A_{\text{max}}$ . The positive

correlation between LMA,  $N_a$ , and photosynthetic performance parameters is a broadly observed phenomenon in woody species (Niinemets 1999). Additionally, there was no seasonal variation in  $N_a$  content observed from May to late September and shrubs were observed producing new shoots, leaves, flowers and fruit through the growing season until the harvest date in early October. Perhaps the continuous flushing of leaves, flowering, and fruiting requires a constant demand for nitrogen throughout the entire growing season.

Consistent with previous research, increased resource availability, specifically light, resulted in higher productivity and reproductive output of *L. maackii*, (Luken 1988; Luken and Goessling 1995; Luken *et al.* 1995a, b; Luken *et al.* 1997). Open-grown shrubs had more than three times greater photosynthetically active radiation than edge and interior-grown shrubs and approximately 20 times the total biomass and 25 times the number of fruits per shrub. Although open-grown shrubs produced more biomass and seeds, this site was dominated by edge- and interior-grown shrubs providing a significant seed source in shaded habitats. The amount of fruit in the forest interior was surprising, based on the assumption that the interior would be too shady for successful reproduction in an invasive shrub known to thrive in high light environments. Current *L. maackii* pollination research in Ohio fragmented forests has demonstrated ample pollinator availability for fertilization and seed set in forest interior habitats (Goodell, McKinney, and Chia-Hua 2010).

Analysis revealed no significant differences in LAR or LWR with habitat, indicating similar allocation patterns of carbon to leaf area and mass across differing amounts of available light. This differed from previous studies showing changes in LAR and LWR of *L. maackii* seedlings in a shadehouse to be dependent upon light availability (Luken *et al.* 1997). The discrepancy between these studies could be due differences in the length of experiments (11 wk and 6 mo), or due to ontogeny (0–1 yr-old seedlings versus 7–20 yr-old shrubs). Even though the architectural appearance of the shrubs looked very different, the percentage of partitioned biomass to total biomass did not differ by light environment for leaf or wood and was marginally significant for fruit. Therefore, the plasticity to light demonstrated in other studies applies to architecture, not allocation patterns (Luken *et al.* 1995b).

There was a strong correlation between stem basal diameter and aboveground biomass (and the component parts) and our results were consistent with those calculated by Hartman and McCarthy (2008). The resulting allometric equations provide an easy to measure estimation of aboveground biomass of *L. maackii* in similar habitats and will prove useful in management planning (Grace and Fownes 1998; Itou *et al.* 2015). Our study investigated shrub-level responses to light habitat, but more research is needed to integrate the physiological function to estimate the impact of *L. maackii* at the ecosystem level. Recent studies have shown understory *L. maackii* to contribute 1% to 6% of stand transpiration in a northern Kentucky forest (Boyce, Durtsche, and Fugal 2012). Future ecosystem studies may find the allometric data provided here useful for scaling up estimates of aboveground carbon content and shifts in shrub biomass communities with invasion.

The results presented here support previous observations of high productivity and plasticity in high- and low-light shadehouse conditions (Luken *et al.* 1995a; Luken *et al.* 1997), yet this field-based approach is more extendable to the urban/suburban interface where this woody invasive shrub is such a persistent problem. Clearly, *L. maackii* shrubs growing in very high light environments must be targeted as a priority for removal, but no habitat is resistant to invasion. The physiological plasticity and shade tolerance exhibited by *L. maackii* enables this woody invasive to grow, reproduce, and persist in closed canopy environments. Because light availability determines growth rates, canopy fragmentation is all that is needed for shaded, slow-growing shrubs to accelerate productivity. Shrubs growing in edge and forest interior habitats frequently lie undetected with the potential for fast growth through high productivity and reproductive input when opportunity arises with new canopy openings. This is particularly relevant in Midwestern forests with the advance of the invasive insect Emerald Ash Borer (*Agilus planipennis* Fairmaire, 1888) and the resulting canopy gaps resulting from *Fraxinus* decline.

Additionally, previous studies have provided only crude estimates of seed production for this well studied species. The results of this study provide new estimates of per-shrub fecundity that are an improvement on the nonrandom sampling techniques from previous research (Ingold and

Craycraft 1983). Overall, the ecophysiology, phenotypic plasticity, shade tolerance, and reproduction capacity of *L. maackii* as documented here and elsewhere are reasons that describe the spread and persistence of this formidable woody invasive. Once established in the landscape, *L. maackii* becomes a transformative agent in forest communities and further questions exist about food web, biodiversity, and biogeochemical impacts of this species in Eastern deciduous forests.

### Literature Cited

- ALI, J., D. LIEURANCE, AND D. CIPOLLINI. 2015. Soil biota affect mycorrhizal infection and growth of *Impatiens capensis* and alter the effects of *Lonicera maackii* rhizosphere extracts. *J. Torrey Bot. Soc.* 142: 1–11.
- BARTUSZEVIĆ, A. M. AND D. L. GORCHOV. 2006. Avian seed dispersal of an invasive shrub. *Biol. Invasions* 8: 1013–1022.
- BASUKI, T. M., P. E. VAN LAAKE, A. K. SKIDMORE, AND Y. A. HUSSIN. 2009. Allometric equations for estimating the above-ground biomass in tropical lowland Dipterocarp forests. *Forest Ecol. Manag.* 257: 1684–1694.
- BAZZAZ, F. A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features, pp. 96–110. *In* H. Mooney and J. Drake [eds.], *Ecology of Biological Invasions of North America and Hawaii*. Springer-Verlag, New York, NY.
- BOHONAK, A. J. AND K. VAN DER LINDE. 2004. RMA software for Reduced Major Axis regression, Java version. Retrieved August 10, 2016 from San Diego State University, San Diego, CA.
- BOYCE R. L., R. D. DURTSCHKE, AND S. L. FUGAL. 2012. Impact of the invasive shrub *Lonicera maackii* on stand transpiration and ecosystem hydrology in a wetland forest. *Biol. Invasions* 14: 671–680.
- CASTELLANO, S. M. AND D. L. GORCHOV. 2013. White-tailed deer (*Odocoileus virginianus*) disperse seeds of the invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Nat. Areas J.* 3: 78–80.
- CHAVE, J., C. ANDALO, S. BROWN, M. A. CAIRNS, J. Q. CHAMBERS, D. EAMUS, H. FÖLSTER, F. FROMARD, N. HIGUCHI, T. KIRA, AND J. P. LESQUIRE. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145: 87–99.
- CIPOLLINI, K., K. TITUS, AND C. WAGNER. 2012. Allelopathic effects of invasive species (*Alliaria petiolata*, *Lonicera maackii*, *Ranunculus ficaria*) in the Midwestern United States. *Allelopath. J.* 29: 63–75.
- CLARK, D. A., S. BROWN, D. W. KICKLIGHTER, J. Q. CHAMBERS, J. R. THOMLINSON, AND J. NI. 2001. Measuring net primary production in forests: concepts and field methods. *Ecol. Appl.* 11: 356–370.
- CLOUGH, B. F., P. DIXON, AND O. DALHAUS. 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. *Aust. J. Bot.* 45: 1023–1031.
- CORONA, P., S. PASTA, G. GIARDINA, AND T. LA MANTIA. 2012. Assessing the biomass of shrubs typical of Mediterranean pre-forest communities. *Plant Biosyst.* 146: 252–257.

- DAVIDSON, A. M., M. JENNIONS, AND A. B. NICOTRA. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecol. Lett.* 14: 419–431.
- DLUGOS, D. M., H. COLLINS, E. M. BARTEME, AND R. E. DRENOVSKY. 2015. The non-native plant *Rosa multiflora* expresses shade avoidance traits under low light availability. *Am. J. Bot.* 102: 1323–1331.
- DORNING, M. AND D. CIPOLLINI. 2006. Leaf and root extracts of the invasive shrub, *Lonicera maackii*, inhibit seed germination of three herbs with no autotoxic effects. *Plant Ecol.* 184: 287–296.
- EVANS, J. R. 1989. Photosynthesis and nitrogen relationships in leaves of C<sub>3</sub> plants. *Oecologia* 78: 9–19.
- FAN, Z., W. K. MOSER, M. H. HANSEN, AND M. D. NELSON. 2013. Regional patterns of major nonnative invasive plants and associated factors in Upper Midwest forests. *For. Sci.* 59: 38–49.
- GOODSELL, K., A. M. MCKINNEY, AND L. CHIA-HUA. 2010. Pollen limitation and local habitat-dependent interactions in the invasive shrub *Lonicera maackii*. *Int. J. Plant Sci.* 171: 63–72.
- GORCHOV, D. L. AND D. E. TRISEL. 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecol.* 166:13–24.
- GORCHOV, D. L., M. C. HENRY, AND P. A. FRANK. 2014. Invasion of an exotic shrub into forested stands in an agricultural matrix. *Invasive Plant Sci. Manag.* 7: 336–344.
- GRACE, K. T. AND J. H. FOWNES. 1998. Leaf area allometry and evaluation of non-destructive estimates of total leaf area and loss by browsing in a silvopastoral system. *Agrofor. Syst.* 40: 139–147.
- HARRINGTON, R. A., B. J. BROWN, AND P. B. REICH. 1989. Ecophysiology of exotic and native shrubs in Southern Wisconsin: I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. *Oecologia* 80: 356–367.
- HARRINGTON, R. A., B. J. BROWN, P. B. REICH, AND J. H. FOWNES. 1989b. Ecophysiology of exotic and native shrubs in Southern Wisconsin: II. Annual growth and carbon gain. *Oecologia* 80: 368–373.
- HARTMAN, K. M. AND B. C. MCCARTHY. 2008. Restoration of a forest understory after the removal of an invasive shrub, Amur honeysuckle (*Lonicera maackii*). *Restoration Ecol.* 12: 154–165.
- HEBERLING, J. M. AND J. D. FRIDLEY. 2013. Resource-use strategies of native and invasive plants in Eastern North American forests. *New Phytol.* 200: 523–533.
- INGOLD, J. L. AND M. J. CRAYCRAFT. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. *Ohio J. Sci.* 83: 256–258.
- ITOU, T., K. HAYAMA, A. SAKAI, H. TANOUCI, S. OKUDA, H. KUSHIMA, AND T. KAJIMOTO. 2015. Developing an effective glyphosate application technique to control *Bischofia javanica* Blume, an invasive alien tree species in the Ogasawara Islands. *J. For. Res.* 20: 248–253.
- JELBERT, K., I. STOTT, R. A. McDONALD, AND D. HODGSON. 2015. Invasiveness of plants is predicted by size and fecundity in the native range. *Ecol. Evol.* 5: 1933–1943.
- LIEURANCE, D. M. 2004. Leaf phenology, fecundity, and biomass allocation of the invasive shrub *Lonicera maackii* (Rupr.) max. M.S. thesis. Ohio University, Athens, OH.
- LIEURANCE, D. AND D. CIPOLLINI. 2013. Environmental influences on growth and defence responses of the invasive shrub, *Lonicera maackii*, to simulated and real herbivory in the juvenile stage. *Ann. Bot.* 112: 741–749.
- LITTON, C. M. AND J. B. KAUFFMAN. 2008. Allometric models for predicting biomass in two widespread woody plants in Hawaii. *Biotropica* 40: 313–320.
- LOBO, F. DE A., M. P. DE BARROS, H. J. DALMAGRO, Á. C. DALMOLIN, W. E. PEREIRA, É. C. DE SOUZA, G. L. VOURLITIS, AND C. E. RODRÍGUEZ ORTÍZ. 2013. Fitting net photosynthetic light-response curves with Microsoft Excel—a critical look at the models. *Photosynthetica* (Prague) 51: 445–456.
- LUKEN, J. O. 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) Maxim. in forest and open habitats. *Am. Midl. Nat.* 119: 258–267.
- LUKEN, J. O. AND N. GOESSLING. 1995. Seedling distribution and potential persistence of the exotic shrub *Lonicera maackii* in fragmented forests. *Am. Midl. Nat.* 133: 124–130.
- LUKEN, J. O. AND J. W. THIERET. 1996. Amur honeysuckle: its fall from grace. *BioScience* 46: 18–24.
- LUKEN, J. O., K. M. KUDES, T. C. THOLEMEIER, AND D. M. HALLER. 1997. Comparative responses of *Lonicera maackii* (Amur honeysuckle) and *Lindera benzoin* (spicebush) to increased light. *Am. Midl. Nat.* 138: 331–343.
- LUKEN, J. O., T. C. THOLEMEIER, L. M. KUDES, AND B. A. KUNKEL. 1995a. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting environments. *Can. J. Bot.* 73: 1953–1961.
- LUKEN, J. O., T. C. THOLEMEIER, B. A. KUNKEL, AND L. M. KUDES. 1995b. Branch architecture plasticity of Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder): initial response in extreme light environments. *J. Torrey Bot. Soc.* 122: 190–195.
- MATLACK, G. R. 1993. Microenvironment variation within and among forest edge sites in the eastern United States. *Biol. Cons.* 66: 185–194.
- MC EWAN, R. W., L. G. ARTHUR-PARATLEY, L. K. RIESKE, AND M. A. ARTHUR. 2010. A multi-assay comparison of seed germination inhibition by *Lonicera maackii* and co-occurring native shrubs. *Flora* 205: 475–483.
- MC EWAN, R. W., M. K. BIRCHFIELD, A. SCHOERGENDORFER, AND M. A. ARTHUR. 2009. Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. *J. Torrey Bot. Soc.* 136: 212–220.
- MEDLEY, K. E. 1997. Distribution of the non-native shrub *Lonicera maackii* in Kramer Woods, Ohio. *Phys. Geogr.* 18: 18–36.
- NAGEL, J. M. AND K. L. GRIFFIN. 2004. Can gas-exchange characteristics help explain the invasive success of *Lythrum salicaria*? *Biol. Invasions* 6: 101–111.
- NIINEMETS, Ü. 1999. Research review. Components of leaf dry mass per area—thickness and density—alter leaf

- hotosynthetic capacity in reverse directions in woody plants. *New Phytol.* 144: 35–47.
- NIINEMETS, Ü., O. KULL, AND J. D. TENHUNEN. 1998. An analysis of light effects on foliar morphology, physiology, and light interceptions in temperate deciduous woody species of contrasting shade tolerance. *Tree Physiol.* 18: 681–696.
- NIKLAS, K. J. 1994. *Plant Allometry: The Scaling of Form and Process.* University of Chicago Press, Chicago, IL. 395 p.
- OSUNKOYA, O. O., D. BAYLISS, F. D. PANETTA, AND G. VIVIAN-SMITH. 2010. Leaf trait co-ordination in relation to construction cost, carbon gain and resource-use efficiency in exotic invasive and native woody vine species. *Ann. Bot.* 106: 371–380.
- POORTER, H., Ü. NIINEMETS, I. J. WRIGHT, AND R. VILLAR. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol.* 182: 565–588.
- POULETTE, M. M. AND M. A. ARTHUR. 2012. The impact of the invasive shrub *Lonicera maackii* on the decomposition dynamics of a native plant community. *Ecol. Appl.* 22: 412–424.
- RAYACHHETRY, M. B., T. K. VAN, T. D. CENTER, AND F. LAROCHE. 2001. Dry weight estimation of the above-ground components of *Melaleuca quinquenervia* trees in southern Florida. *Forest Ecol. Manag.* 142: 281–290.
- REICH P. A., D. S. ELLSWORTH, M. B. WALTERS, J. M. VOSE, C. GRESHAM, J. C. VOLIN, AND W. D. BOWMAN. 1999. Generality of leaf trait relationships: a test across six biomes. *Ecology* 80: 1955–1969.
- REICHARD, S. H. AND C. W. HAMILTON. 1997. Predicting invasions of woody plants introduced into North America. *Conserv. Biol.* 11: 193–203.
- RICHARDS, C. L., O. BOSSDORF, N. Z. MUTH, J. GUREVITCH, AND M. PIGLIUCCI. 2006. Jack of all trades, master of some? On the role of phenotypic plasticity in plant invasions. *Ecol. Lett.* 9: 981–993.
- SINGH, V., A. TEWARI, S. P. S. KUSHWAHA, AND V. K. DADHWAL. 2011. Formulating allometric equations for estimating biomass and carbon stock in small diameter trees. *Forest Ecol. Manag.* 261: 1945–1949.
- SMITH, M. D. AND A. K. KNAPP. 2001. Physiological and morphological traits of exotic, invasive exotic, and native plant species in tallgrass prairie. *Int. J. Plant Sci.* 162: 785–792.
- SOKAL, R. R. AND F. J. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*, 3rd ed. Freeman, NY. 887 p.
- SPRUGEL, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* 64: 209–210.
- VALLADARES, F., AND Ü. NIINEMETS. 2008. Shade tolerance, a key plant feature of complex nature and consequences. *Annu. Rev. Ecol. Evol. Syst.* 39: 237–257.
- VAN KLEUNEN, M., E. WEBER, AND M. FISCHER. 2009. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13: 235–245.
- WITH, K. A. 2002. The landscape ecology of invasive spread. *Conserv. Biol.* 16: 1192–1203.

### Appendix

Repeated measures ANOVA for response variables derived from *L. maackii* light response curves and foliar N content taken during the 2003 growing season. Differences were considered significant at  $P \leq 0.05$ .

Source	df	Means square	<i>P</i>
A) $R_d$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )			
Location	2	2.672	0.002
Season	2	0.041	n.s.
Loc*Season	3	0.071	n.s.
B) $A_{\text{max}}$ ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ )			
Location	2	125.269	<0.001
Season	2	6.860	n.s.
Loc*Season	3	4.574	n.s.
C) QE			
Location	2	0.022	n.s.
Season	2	0.001	n.s.
Loc*Season	3	0.004	n.s.
D) LCP ( $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ )			
Location	2	332.340	0.014
Season	2	8.448	n.s.
Loc*Season	3	39.814	n.s.
E) LMA ( $\text{g m}^{-2}$ )			
Location	2	4,195.067	<0.001
Season	2	263.371	n.s.
Loc*Season	3	40.773	n.s.
F) $N_a$ ( $\text{g m}^{-2}$ )			
Location	2	2.259	<0.001
Season	2	0.095	n.s.
Loc*Season	3	0.026	n.s.
G) PNUE			
Location	2	1.750	n.s.
Season	2	15.044	n.s.
Loc*Season	3	4.983	n.s.