

Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors

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McEWAN, R. W. (Department of Biology, The University of Dayton, Dayton, OH 45469), M. K. BIRCHFIELD (School of Biological Sciences, Washington State University–Vancouver, Vancouver, WA 98686), A. SCHOERGENDORFER (Department of Statistics, University of Kentucky, Lexington, KY 40546), AND M. A. ARTHUR (Department of Forestry, University of Kentucky, Lexington, KY 40546). Leaf phenology and freeze tolerance of the invasive shrub Amur honeysuckle and potential native competitors. *J. Torrey Bot. Soc.* 136: 212–220. 2009.—The non-native invasive deciduous shrub *Lonicera maackii* causes a reduction in plant growth and species diversity under its canopy. The mechanisms of these effects are not fully understood, but an apparent difference between *L. maackii* and native shrub species is its extended leaf duration. We tested the hypothesis that *L. maackii* has a longer leaf duration than native shrub species found in the same habitats. Leaf phenology of *L. maackii* and the native deciduous shrubs *Asimina triloba* and *Lindera benzoin* was observed at four sites in central Kentucky (USA) from March until December, 2007. Additionally, a late spring freeze allowed for examination of freeze tolerance among the three test species. *Lonicera maackii* leaf development was two to three weeks earlier than the natives in March and early April. A hard freeze in early April caused significant ($P < 0.05$) leaf mortality to both of the native species (60–100% leaf mortality at 3 of 4 sites) while *L. maackii* showed no observable damage. *L. maackii* had a later transition to fall color and leaf abscission than the native species, which were at a significantly later stage of development (closer to leaf abscission) for a period of four to six weeks. These data suggest two advantages for *L. maackii* over potential native competitors: 1) greater access to carbon via a longer leaf duration, and 2) a greater capacity to withstand freezing temperatures.

Key words: *Asimina triloba*, exotic species, *Lindera benzoin*, *Lonicera maackii*, non-native species.

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Non-native invasive plants cause significant and often deleterious changes to ecosystem structure, function and composition (Pimental et al. 2000, Evans et al. 2001, Ehrenfeld 2003, Lovett et al. 2006). These species move aggressively into natural areas and can reduce the diversity of plant communities and alter ecosystem function (Mack et al. 2000, Ehrenfeld 2003, Miller and Gorchoff 2004, Hartman and McCarthy 2007). The invasion of non-native shrubs into forest understories has been particularly problematic (Luken and Thieret 1996, Webster et al. 2006, Hartman and McCarthy 2004). A number of hypotheses have been proposed to explain how invasive species dominate habitat space (e.g., Mack et al. 2000, Callaway and Ridenour 2004) and there likely are multiple interacting mechanisms.

The deciduous shrub Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder) is a non-

native invasive plant that has proliferated rapidly in eastern North America (Luken and Thieret 1996, Hutchinson and Vankat 1997, Miller and Gorchoy 2004). Intentionally imported to North America from Asia (Luken and Thieret 1996), this species has become a significant problem in natural areas (Hutchinson and Vankat 1998, Collier et al. 2002, Hartman and McCarthy 2004, 2008). Once established, *L. maackii* reduces the growth of native shrubs and trees, can reduce the reproductive success of native herbs, and causes the loss of native species diversity (Gould and Gorchoy 2000, Collier et al. 2002, Miller and Gorchoy 2004, Hartman and McCarthy 2007). Although the negative influence of this species on native plant communities is well established (e.g., Collier et al. 2002, Gorchoy and Trisel 2003), the mechanism(s) of this influence are not fully understood.

Lonicera maackii has the potential to affect the growing environment of forest understories. The dense growth form of *L. maackii* creates heavy shade at the forest floor which may be a limiting factor for native species (Luken et al. 1997). One difference between *Lonicera maackii* and native shrubs is a notably extended leaf duration relative to native woody species (Trisel 1997). Longer leaf duration has been documented in other invasive species (Harrington et al. 1989) and could confer a competitive advantage over native species (Trisel 1997).

We observed *L. maackii* leaf phenology in four central Kentucky forests. In the same sites we also monitored the phenology of *Lindera benzoin* and *Asimina triloba* which are native shrubs with growth forms and habitat requirements that are similar to *L. maackii*. By monitoring these species through a full growing season we tested the Trisel (1997) hypothesis that *L. maackii* has a longer leaf phenology than potential native competitors. Additionally, our design encompassed urban and rural sites to investigate the potential for heat island effects on shrub phenology. A late spring freeze allowed us to also examine differences in freeze tolerance among the test species.

Materials and Methods. **STUDY SITES.** Phenology observations were made in four sites in central Kentucky. Shrubs were observed in two sites located in an urban/suburban matrix of neighborhoods in wooded portions of Lake-

Table 1. Observation categories used for the assessment of invasive and native shrub phenology in central Kentucky forests.

Vegetative Features	
1)	Bud dormant
2)	Bud swollen/elongated
3)	Part of leaf blade visible
4)	Entire leaf blade visible
5)	Leaf entirely expanded
6)	Leaf at summer green color
7)	Leaf different than summer color
8)	Leaf at fall color
9)	Leaf abscised/bud dormant

view Park and the University of Kentucky Arboretum within the city limits of Lexington, in Fayette County, Kentucky. The two other sites, Sally Brown Nature Preserve and Tom Dorman Nature Preserve, were located within a matrix of farmland and forest in rural Garrard County, Kentucky. The four sites are within 30 km of one another. Forests in all four sites were secondary mixed deciduous forest, approximately 60–80 years old, and composed of oaks (e.g., *Quercus muehlenbergii*, *Quercus rubra*), hickories (e.g., *Carya laciniata*, *Carya ovata*), and a mix of other species including *Acer saccharum*, *Celtis occidentalis*, and *Fraxinus americana*. Botanical nomenclature follows Jones (2005).

EXPERIMENTAL DESIGN AND FIELD METHODS. Within each of the four sites, observations were made on five individual shrubs of *Lonicera maackii*, *Lindera benzoin* and *Asimina triloba*, from early March 2007 until December 2007. Within Lakeview Park, *A. triloba* was not present and only two individuals of *L. benzoin* were found. A single branch was selected from the south facing side of each shrub. Leaf observations (Table 1) were made on 10 bud locations from each of these branches (behind the growing tip to avoid confusing meristematic activity and phenology of dormant buds). Observations were made approximately every 3 days beginning in mid-March, and ending once leaves had entirely emerged and arrived at growing season color (Table 1). Over the summer, when the leaves were consistently at summer green color, leaves were observed approximately every 14 days. During the fall, observations of leaf color were made approximately every 7 days until all leaves had fallen (Table 1). Within each site, temperature measurements were recorded by Hobo H8 Pro Series data loggers

(Onset Computer Corp. Pocasset, MA) every hour throughout the study.

ANALYTICAL METHODS. Phenology data were divided into two periods for the purpose of analysis. The first period captured the spring leaf development from March 16 until leaves on all plants were fully elongated; the second period included fall color changes and leaf drop, from September 18 until December 13. Statistical analyses were performed using the MIXED procedure of the SAS software, Version 9.1 (SAS Institute Inc. 2003). All tests were conducted at a significance level of $\alpha = 0.05$. Leaf development of the three species was analyzed for each season separately using a non-parametric repeated measures analysis with dependent replications (Brunner et al. 2001). In these analyses, repeated measures models were fitted to the mean ranks of each sampling date for each shrub, using the observations from the 10 bud location subsamples of each experimental unit, the shrub. Covariance parameters were estimated using minimum variance quadratic unbiased estimation (MIVQUE0) as suggested by Brunner et al. (2001). As there was a significant interaction between time and species, mean ranks of *Lonicera maackii* were compared to those of the two native species using pairwise comparisons for each sampling date. Because the data structure necessitated non-parametric rank-based statistical methods, the median (rather than the mean) was used to construct the phenology figures.

We also observed substantial leaf damage from an early spring freeze. Freeze damage was evaluated from April 6, the last date previous to the freeze, up to May 16, beyond which freeze damage previously present had been replaced by a new flush of leaves. Freeze damage was recorded as the number of (completely) dead leaves out of 10 observations made on a single branch of each shrub. The observations were transformed using a square root arcsine transformation for normalization. Differences in severity of freeze damage between the species were evaluated in a repeated measures analysis using restricted maximum likelihood (REML) estimation of the covariance parameters. Due to a significant interaction between time and species, pairwise comparisons were performed between each of the native species and *Lonicera maackii* for each date. Although the experiment was set up to examine urban/rural

differences, there was no evidence in the data for the hypothesized effect (data not shown). For spring and fall phenology, as well as for freeze damage, there were significant three-factor interactions between site, time and species ($P < 0.05$); consequently, the analysis of differences among species was performed for each site separately.

Results. Spring leaf development of *Lonicera maackii* was earlier than that of the two native shrubs, which were similar to one another (Fig. 1). Pairwise comparisons of native species to *L. maackii* indicated that leaves of both natives at all sites (*Asimina triloba* not present at Lakeview) were significantly less developed than those of *L. maackii* for a minimum period of March 16 through March 27 ($P < 0.05$, Fig. 1). For instance, on day one of observations at the Brown site, median leaf development for *L. maackii*, *A. triloba*, and *Lindera benzoin* were 3, 1, and 1.5, respectively (Fig. 1). Leaves of *L. maackii* had developed to median of category 4 (entire leaf blade visible) at all sites by March 24, while this level of development did not occur until March 30 to April 6 for *L. benzoin*, and on or after April 6 for *A. triloba*. At Lakeview, leaves of *L. benzoin* were significantly less developed than those of *L. maackii* through March 30 ($P < 0.05$, Fig. 1). At Arboretum, leaves of both natives remained significantly less developed than *L. maackii* through April 2 ($P < 0.05$, Fig. 1), whereas leaves of *A. triloba* remained significantly less developed than *L. maackii* through April 6 at both the Dorman and Brown sites ($P < 0.05$; Fig. 1).

An abnormally warm spring followed by five consecutive nights of freezing temperatures (from April 6 through 10) caused substantial damage to native species, but *Lonicera maackii* was ostensibly unaffected (Fig. 2). Overall, high percentages (60–100%) of leaf mortality occurred and persisted through most of April for both of the native species at all sites except Dorman, where only a small percentage of the leaves on the native shrubs were damaged by the freeze (Fig. 2). Least squares means analysis showed no significant leaf mortality (compared to null hypothesis of 0% leaf mortality) for *L. maackii* whereas maximum mean percentage of leaf mortality for *Asimina triloba* was 98.6% (on April 11 at Brown) and that of *Lindera benzoin* was 100.0% (on April 9 at Lakeview). Pairwise

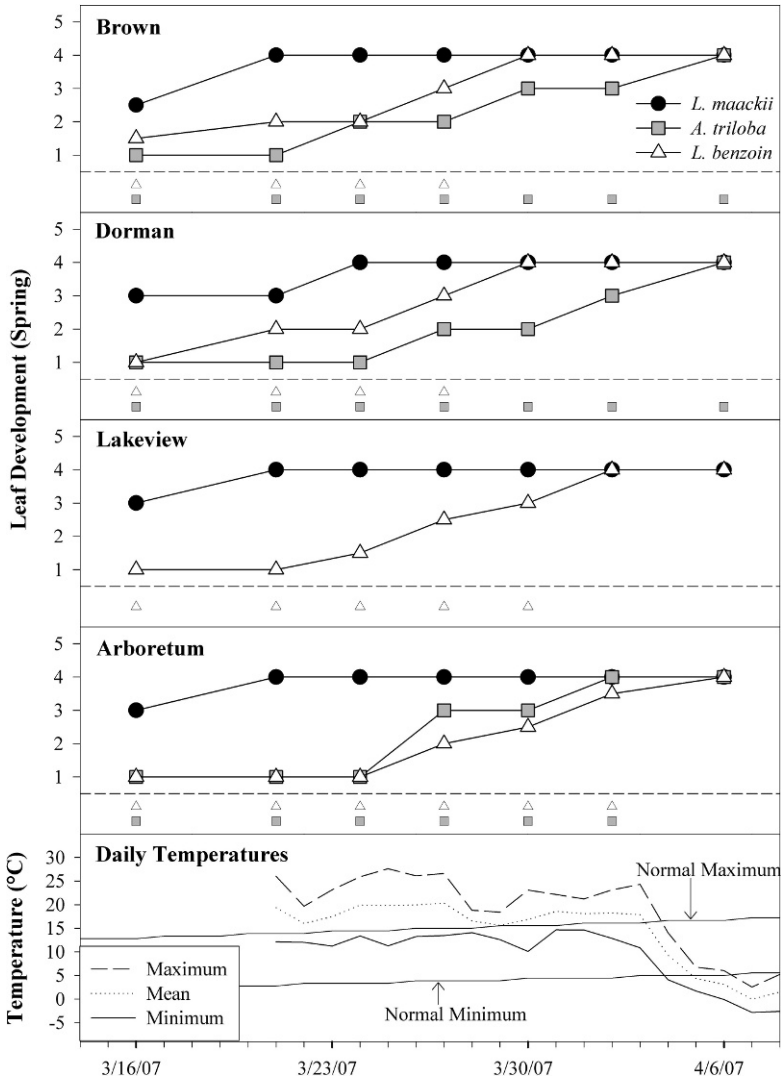


FIG. 1. Top four graphs: Median early spring leaf development from 1 = buds dormant, to 5 = leaf entirely expanded (Table 1) of two native shrubs (*Asimina triloba* and *Lindera benzoin*) and a non-native, invasive shrub (*Lonicera maackii*) at four sites in Central Kentucky, USA (note: the maximum development during this time period was 4). Presence of species symbol below dashed line indicates statistical significance ($\alpha = 0.05$) between corresponding median values for native species and *L. maackii*. Bottom Graph: Mean daily maximum, mean, and minimum temperatures recorded at each site and averaged across all four. Reference lines are normal maximum and minimum temperatures for Lexington, Kentucky, USA (30-year average, 1971–2000; NOAA 2008).

comparisons of *L. maackii* to each of the natives showed mean percentages of leaf mortality were significantly greater than that of *L. maackii* for the natives from April 9 until May 3 at Brown, Arboretum, and Lakeview ($P < 0.05$; Fig. 2). At Dorman, mean percentages of leaf mortality for *A. triloba* were only found to be significantly greater than those of *L. maackii* from April 9 until April 26, while leaf mortality of *L. benzoin* was significantly

greater than *L. maackii* on April 23 solely ($P < 0.05$; Fig. 2).

Lonicera maackii held its leaves for a longer period of time than the native species (Fig. 3). Transition from summer green to leafless conditions occurred for *Lindera benzoin* and *Asimina triloba* from approximately October 15 to November 21. *L. benzoin* had arrived at fully leafless conditions (i.e., reached a median leaf development of 9, leaf abscised) at all sites

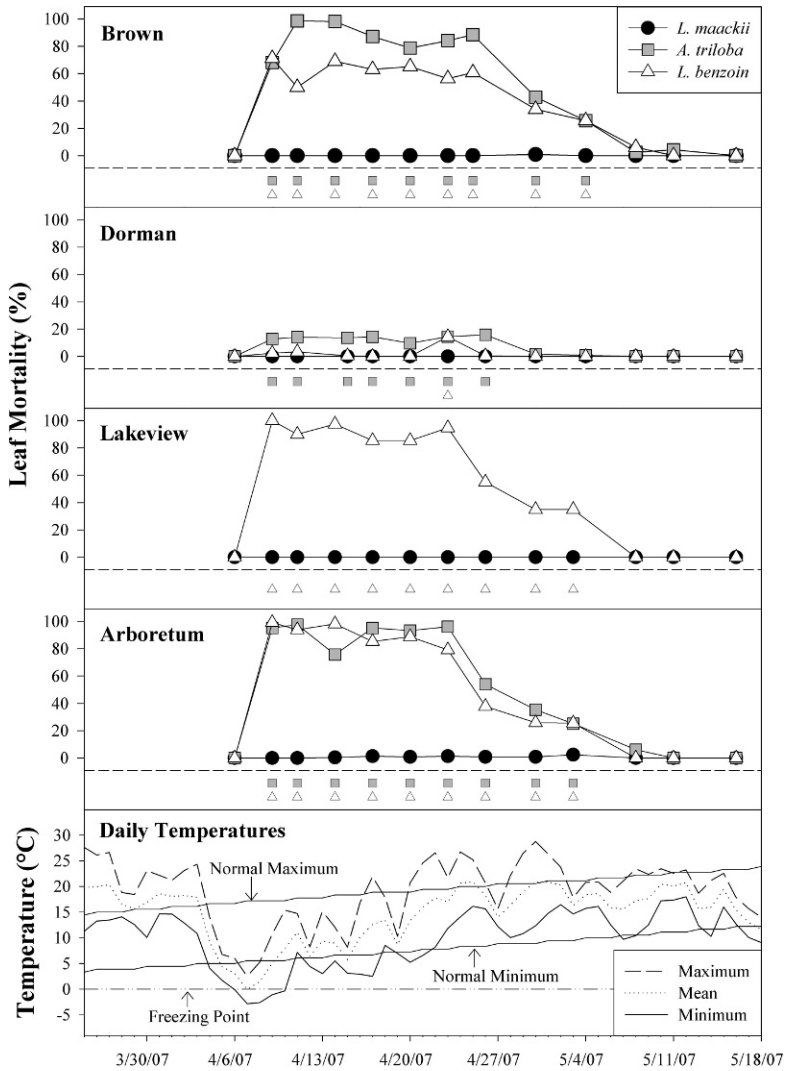


FIG. 2. Top four graphs: Mean percent leaf mortality for two native shrubs (*Asimina triloba* and *Lindera benzoin*) and a non-native, invasive shrub (*Lonicera maackii*) resulting from abnormal late spring freeze (April 6–10, 2007) at four sites in Central Kentucky, USA. Presence of species symbol below dashed line indicates statistical significance ($\alpha = 0.05$) between corresponding native species and *L. maackii*. Bottom Graph: Mean daily maximum, mean, and minimum temperatures recorded at each site and averaged across all four sites. Reference lines are normal maximum and minimum temperatures for Lexington, Kentucky, USA (30-year average, 1971–2000; NOAA 2008) and freezing point (0 °C).

by November 21 (Fig. 3). Leafless condition was recorded for *A. triloba* by November 30 at all sites. In contrast, *L. maackii* did not transition to leaf drop until early-to-mid December (Fig. 3). Pairwise comparisons of *L. benzoin* and *L. maackii* showed that *L. benzoin* was at a significantly later stage of development (closer to leaf abscission) than *L. maackii* for a period starting October 22nd at both Brown and Arboretum, October 29 at

Dorman, and November 6 at Lakeview, and continuing until December 7 at all four sites ($P < 0.05$; Fig. 3), a period of four to six weeks. Similarly, pairwise comparisons between *A. triloba* and *L. maackii* indicated leaf phenology of *A. triloba* was at a significantly later stage than *L. maackii* from November 6 at Brown and Dorman, and November 12 at Arboretum, until December 7 at all three sites ($P < 0.05$; Fig. 3).

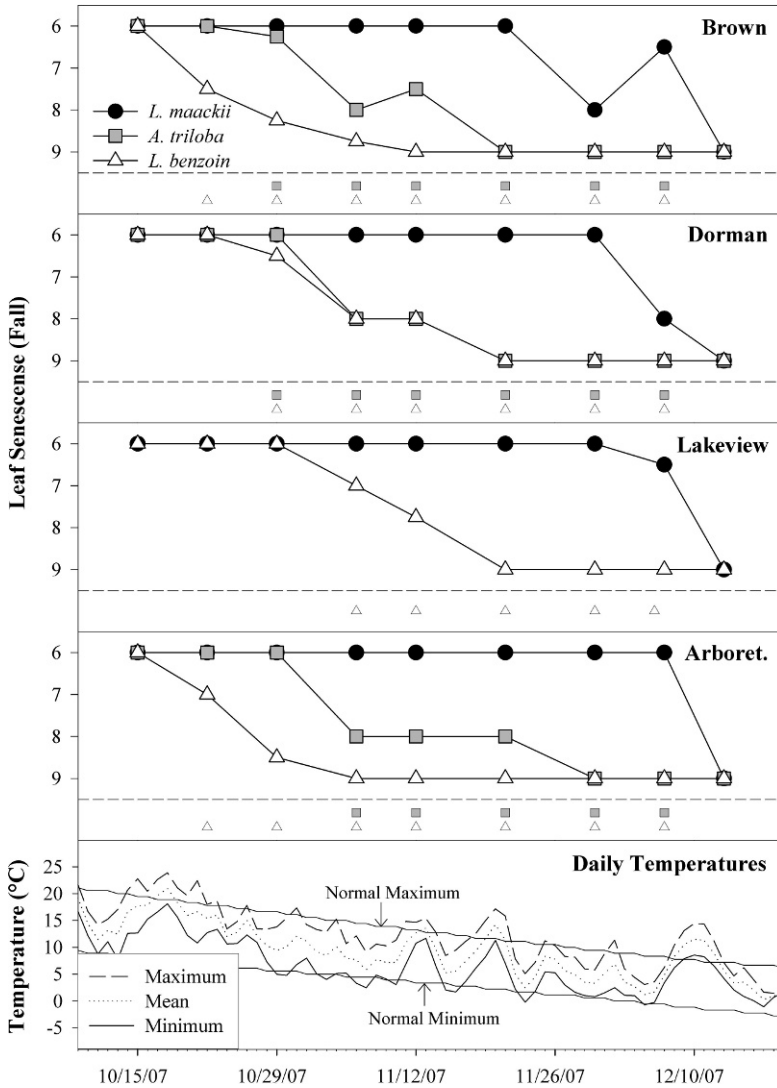


FIG. 3. Top four graphs: Median fall leaf phenological development (from 6 = leaf at summer green, to 9 = leaf abscised/buds dormant; Table 1) of two native shrubs (*Asimina triloba* and *Lindera benzoin*) and one exotic, invasive shrub (*Lonicera maackii*) at four sites in Central Kentucky, USA. Presence of species symbol below dashed line indicates statistical significance ($\alpha = 0.05$) between corresponding median values for native species and *L. maackii*. Bottom Graph: Mean daily maximum, mean, and minimum temperatures recorded at each site and averaged across all four sites. Reference lines are normal maximum and minimum temperatures for Lexington, Kentucky, USA (30-year average, 1971–2000; NOAA 2008).

Discussion. Invasive plants are one of the most important threats to biodiversity and ecosystem function in many forests of eastern North America (e.g., Webster et al. 2006, Kohli et al. 2009). *Lonicera maackii*, in particular, is a significant problem in natural areas (Luken and Thieret 1996) causing deleterious effects for native species (Collier et al. 2002, Hartman and McCarthy 2004) and ecosystem productivity (Hartman and McCarthy 2007). This

already problematic species may be poised to expand its habitat dominance in response to the loss of ash (*Fraxinus* spp.) due to the emerald ash borer (*Agrilus planipennis*; e.g., Poland and McCullough 2006) which will create canopy openings in many forests where *L. maackii* is present. Understanding the mechanism(s) that facilitate the invasion of this species is an important and ongoing challenge (e.g., Luken and Thieret 1996,

Hutchinson and Vankat 1997, Hartman and McCarthy 2008, Cipollini et al. 2008).

Lonicera maackii possesses a diverse profile of traits that enable it to obtain habitat space (Luken and Theiret 1996, Gorchoy and Trisell 2003, Hartman and McCarthy 2004). It grows faster than potential native competitors (Luken and Thieret 1996) and has a more flexible response to changing light environments (Luken et al. 1995, Luken et al. 1997). *Lonicera maackii* responds by increased growth when clipped (Luken and Mattimiro 1991). This species also contains chemicals that confer defense against insect herbivores (McEwan et al. 2009) and suppresses the seed germination of native species via allelopathy (Dorning and Cipollini 2006, Cipollini et al. 2008). Our data support evidence that *L. maackii* has substantially longer leaf duration than potential native competitors (Trisell 1997), and we found that *L. maackii* was considerably more frost resistant than native species.

A longer leaf phenology may provide a substantial competitive advantage for *Lonicera maackii* (Trisell 1997). In a forest understory, light availability is significantly lower during the closed-canopy conditions of summer than when the canopy is leafless in late fall, winter, and early spring. For instance, Gill et al. (1998) found that sunlight at the forest floor was about 55% of full sun in the understory of a temperate deciduous forest prior to overstory leaf-out, and only 1–3% of full sun once the overstory canopy had entirely developed. *Lonicera maackii* leaf development was substantially earlier than native species and it also held leaves longer than native species in the fall, ostensibly taking advantage of high understory irradiance in leafless canopy conditions at both extremes of the growing season. This created an opportunity for greater annual photosynthesis in *L. maackii* relative to native shrubs. An early leaf emergence in spring (prior to overstory leaf expansion) is particularly advantageous. Harrington et al. (1989) found that early spring photosynthesis accounted for 25–35% of annual carbon gain for several understory shrubs including Bell's honeysuckle (*Lonicera ×bella*), and Gill et al. (1998) demonstrated that shrub photosynthesis prior to overstory leaf emergence was higher than any other time of the year. A longer leaf phenology in fall is also advantageous, but some data suggest less so than spring (Harrington et al. 1989) due to

declining leaf area and photosynthetic capacity (Gill et al. 1998) as the understory shrubs transition toward winter dormancy. These factors may not limit photosynthesis for *L. maackii* as our data indicated that it was at summer green color well after the native species had begun fall color change, or had dropped their leaves entirely. Future research that quantifies the carbon gain associated with its extended leaf phenology would enhance understanding of *L. maackii* invasion ecology.

The extended leaf phenology of *Lonicera maackii* also has important consequences for plant biodiversity. Herbaceous species are negatively impacted by *L. maackii* (Gould and Gorchoy 2000, Collier et al. 2002, Miller and Gorchoy 2004), and this negative impact is partially a result of intense shading. The early spring leaf-out may be particularly deleterious for spring ephemeral herbs that complete their lifecycle prior to leaf development of woody vegetation (e.g., *Erythronium americana*; Muller 1978). Miller and Gorchoy (2004) did not detect a stronger negative effect on the spring ephemeral *Allium burdickii* than on herbaceous species that mature in the summer and are adapted to canopy shading. Work with *Trillium erectum*, a spring flowering herb found in the invasion range of *L. maackii*, indicates that the length of early spring canopy-less conditions is important to its growth and reproductive success (Routhier and Lapointe 2002). The spring flora in the invasive range is species rich (Small and McCarthy 2003, McEwan et al. 2005), and further work is needed with other herbaceous species to determine potentially negative effects of *L. maackii* early leaf-out.

Lonicera maackii did not suffer leaf mortality associated with the spring freeze, and was thus provided with (at least) two potential advantages. First, for approximately 20 days, *L. maackii* had green leaves, which had the potential for photosynthesis, while the photosynthetic apparatus of native species was damaged or absent. This period could have provided *L. maackii* with a substantially increased annual carbon gain. Secondly, unlike the native species, *L. maackii* did not have to spend energy rebuilding leaf tissue. The energetic cost to the natives of growing a second “flush” of leaves is unknown, though it can be safely assumed that not having to go through this process was comparatively advantageous for *L. maackii*.

This study adds to a substantial and growing understanding of how *Lonicera maackii* acquires habitat space and impacts native species (e.g., Luken and Theiret 1996, Hutchinson and Vankat 1997, Gorchoy and Trisel 2003, Hartman and McCarthy 2007). Even so, much remains unknown. Our data documented greatly extended leaf duration of *L. maackii* relative to native species, which may interact with its dense growth form to create deep shade. This shade may be partially responsible for the previously documented negative influence on forest floor herbaceous species (Gould and Gorchoy 2000, Miller and Gorchoy 2004) and seedlings (Gorchoy and Trisel 2003). Reinhart et al. (2006) found that the invasion of *Acer platanoides* altered both light quantity and quality in the forest understory, negatively impacting native species. Further work is needed to measure the quantity of light occlusion by *L. maackii* (and other invasive shrubs), and to test potential effects on light quality. Secondly, our data indicated that *L. maackii* was vastly more tolerant of freezing temperatures than native species. We hypothesize that freeze tolerance may have to do with solute concentrations within the leaves, although it was not measured in our study. Since *L. maackii* was at a later stage in leaf development its foliage may have been more freeze tolerant due to a more completely developed leaf cuticle, or more lignified tissues. Further research into the capacity of this species to survive freezing could increase our understanding of this mode of competitive advantage.

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