

Competitive Effects of Native and Exotic Shrubs on *Quercus alba* Seedlings

Lars A. Brudvig^{1,*} and Christopher W. Evans^{1,2}

Abstract - The exotic shrub *Lonicera tatarica* (Tartarian honeysuckle) has aggressively invaded woodlands and forests in central and eastern North America; however, its impacts on native plant species are not well understood. We used a greenhouse seedling experiment to examine the effects of *L. tatarica* on *Quercus alba* (white oak), the presettlement dominant tree of many of these forests. Growth-related parameters of *Q. alba* seedlings (height and basal diameter increases, biomass) did not differ between treatments when grown in monoculture or with *L. tatarica* competitors. In addition, when paired with native *Cornus* (dogwood) species, *Q. alba* displayed similar growth as when paired with *L. tatarica*. *Quercus alba* also did not respond differently to native and *L. tatarica* competitors across a range of densities, although greater competitor diversity resulted in somewhat lower height growth than other treatments. Due to the similarity in *Q. alba* growth across native and exotic shrub combinations, we argue that seedling-to-seedling competition with *Q. alba* is not a significant impact of *L. tatarica* invasion.

Introduction

Biological invasions represent one of the greatest agents of global environmental change and have affected virtually every ecosystem on earth (Vitousek et al. 1996). The deleterious impacts of invasive species range from disease vectoring (Vitousek et al. 1996) to economic loss (Pimental et al. 2000) to reductions of biological diversity (Wilcove et al. 1998). Our abilities to predict and control invasive species have been modest at best, although attempts have been made (Hulme 2003). Much of the scientific literature regarding invasive species is based on correlative studies and experiments are needed to better understand the mechanisms of invasion and its consequences (Kareiva 1996).

Comparative studies, including competition experiments, can help elucidate invasive species' pathways and impacts (Daehler 2003). This approach most commonly involves pairing native with exotic plant species and measuring performance-related traits, such as growth rates, leaf area, or fecundity. If specific life stages are examined, comparative studies can help target invader impacts (Grotkopp et al. 2002). For example, direct seedling-to-seedling competition may result in competitive exclusion of a native species by an exotic species, despite minimal adult interactions.

We used a comparative greenhouse experiment to test the hypothesis that *Lonicera tatarica* L. (Tartarian honeysuckle), an exotic understory shrub,

¹Department of Natural Resource Ecology and Management, Iowa State University, 339 Science II Hall, Ames, IA 50011. ²Current address - University of Georgia, PO Box 748, Tifton, GA 31793. *Corresponding author - brudvigl@iastate.edu.

suppresses *Quercus alba* L. (white oak) seedlings by competitive interactions at the seedling stage and, thus, impedes *Q. alba* regeneration. Although greenhouse experiments have been criticized for failing to replicate field conditions (e.g., Diamond 1983), they do provide a controlled and manipulable environment, not available in the field (Gibson et al. 1999).

Quercus alba was the pre-settlement dominant tree of North American central hardwoods and eastern deciduous forests and is arguably the most economically valuable saw timber species of these regions (Abrams 2003). Unfortunately, ecological impacts associated with European settlement have resulted in *Q. alba* now representing a minor and/or declining component of many forests (Abrams 2003). Throughout its range, little *Q. alba* recruitment has occurred since the turn of the 20th century (Cho and Boerner 1991), most likely because of seedling suppression by competing understory vegetation (Lorimer et al. 1994), including exotic understory species (Gorchov and Trisel 2003).

One such understory species is *L. tatarica*, which was introduced from Eurasia sometime before 1800 (Rehder 1927). Although *L. tatarica* has formed nearly impenetrable thickets in some forest understories (Woods 1993), little is known about the consequences of this invasion. Its congener, *Lonicera maackii* Rupr. (Amur honeysuckle), has been shown to reduce growth and survival of native tree seedlings in Ohio forests (Gorchov and Trisel 2003). Past work (Collier et al. 2002, Gorchov and Trisel 2003, Gould and Gorchov 2000, Hutchinson and Vankat 1997) investigated the effects of mature *L. maackii* shrubs on forest understory species, but to date there have been no studies of *Lonicera* seedlings.

To help understand what effects *L. tatarica* might have on *Q. alba* seedling growth, we asked the following questions: (1) Do competitive interactions between *L. tatarica* seedlings and *Q. alba* seedlings result in reduced *Q. alba* growth-related performance? To answer this, we examined *Q. alba* seedlings' growth and post-experiment biomass when in monoculture and when potted with *L. tatarica* at varying densities. (2) Do the competitive effects of *L. tatarica* on *Q. alba* seedlings differ from those of two native *Cornus* species on *Q. alba*? To address this question, we examined *Q. alba* seedlings' growth and post-experiment biomass when paired with *Cornus* seedlings, *L. tatarica*, and in multi-species mixtures involving *Cornus* and *L. tatarica*. Interactions between co-occurring native (i.e., *Cornus*), exotic (i.e., *L. tatarica*), and focal native species (i.e., *Q. alba*) have been rarely attempted, but may provide insight into why some exotic species become invasive pests (Vilà and Weiner 2004).

Materials and Methods

To test whether *L. tatarica* seedlings competitively suppress *Q. alba* seedlings, we used a greenhouse experiment in Iowa. We planted four seedlings in each of one hundred sixty 21.5-cm diameter by 21.5-cm height

circular plastic pots, in a potting soil mixture of 3 parts peat to 1 part vermiculite. *Quercus alba* and *Cornus* seedlings were 1-year-old bare root stock of central Iowa genotype, obtained from the Department of Natural Resources (DNR) state forest nursery, while *L. tatarica* seedlings were obtained from Lawyer Nursery, WA. Seedlings of all species ranged in above-ground height from 15 to 40 cm. To avoid asymmetric competition resulting from initial size differences (Gibson et al. 1999), all attempts were made to match seedlings for size, within each pot. Seedlings were planted on 25 April 2003, and pots were thoroughly watered each day until 20 May 2003, by which time seedling growth had commenced in all pots. From 20 May 2003 through the conclusion of the study, all pots were watered 3 times per week, until water dripped from the bottom of each pot.

In order to compare growth rates and competitive interactions between *Q. alba* and *L. tatarica*, we used a replacement series design (de Wit 1960, Jolliffe 2000). We planted 20 replicate greenhouse pots with each of the following combinations of seedlings: 4 *Q. alba* (4Qa/0Lt), 3 *Q. alba* and 1 *L. tatarica* (3Qa/1Lt), 2 *Q. alba* and 2 *L. tatarica* (2Qa/2Lt), 1 *Q. alba* and 3 *L. tatarica* (1Qa/3Lt), and 4 *L. tatarica* (0Qa/4Lt). This allowed for the assessment of *Q. alba* growth rates in monoculture and in three different density combinations. *L. tatarica* growth is provided for comparison.

In order to compare these results to *Q. alba* seedling performance when growing with native shrubs, we included 20 replicates of each of the following seedling combinations: 2 *Q. alba* and 2 *Cornus foemina* Lam. (gray dogwood) (2Qa/2Cf), 2 *Q. alba* and 2 *Cornus sericea* L. (red osier dogwood) (2Qa/2Cs), and 1 *Q. alba* and 1 *L. tatarica* and 1 *C. foemina* and 1 *C. sericea* (All).

All pots were arranged in a completely randomized design. The initial basal diameters and heights (perpendicular distance from the soil surface to the highest living point) of each seedling were measured between 2 and 4 May 2003, prior to the initiation of seedling growth, and once per week thereafter. On 15 June 2003, the approximate mid-point of this experiment, all pots received 800 ml of 252-26-165 ppm N-P-K fertilizer solution. Upon the completion of the experiment, on 1 August 2003, final height and basal diameter measurements were made. *Q. alba* seedlings were harvested, cut at the root collar, divided into above ground and below ground parts, cleaned, and dried at 105 °C for 48 hours. Dry biomass was determined using a laboratory scale.

Statistical analyses were performed using one-way ANOVAs, with treatment (seedling combination) as the independent variable. We used mean species-level values per pot of the following dependent variables: relative height change, relative basal diameter change, total plant biomass, and ratio of above- to below-ground biomass. Relative height and basal diameter changes were determined by: (final measurement - initial measurement) / (initial measurement). Weekly relative height change was determined by: (present week's height - previous week's height) / (previous week's height).

Ratios of above to below ground biomass were determined by: (biomass of oven dried leaves and stem) / (biomass of washed, oven dried roots). Independent linear contrasts were used to identify differences between *Q. alba* in monocultures and interspecific combinations.

All statistical analyses were performed using the SAS System for Windows, Version 9.00.

Results

After the pots with dead individuals were discarded, this greenhouse experiment resulted in 138 of the original 160 pots: 17 4Qa/0Lt, 17 3Qa/1Lt, 17 2Qa/2Lt, 19 1Qa/3Lt, 20 0Qa/4Lt, 16 Qa/Cf, 16 Qa/Cs, and 16 All. 19 of the 22 discarded pots were a result of a *Q. alba* seedling death, 2 from *C. foemina*, 1 from *C. sericea*, and 0 from *L. tatarica*.

In the replacement series experiment, *Q. alba* seedlings displayed greater relative height increases than *L. tatarica* seedlings ($F = 9.71$, d.f. = 1, $p = 0.0021$; Fig. 1a), while *L. tatarica* seedlings had greater relative basal diameter increases across treatments ($F = 49.08$, d.f. = 1, $p < 0.0001$; Fig. 1b). Visual observation of the replacement series diagrams (Jolliffe 2000) shows the species-level differences to be consistent across all density combinations (Fig. 1). Although *Q. alba* seedlings in monoculture did not differ in basal diameter from seedlings potted with *L. tatarica* (Fig. 1b), *Q. alba* seedlings in the 1Qa/3Lt treatment had greater relative increases in basal diameter than seedlings in the 2Qa/2Lt treatment ($F = 6.21$, d.f. = 1/225, $p = 0.0134$). *Quercus alba* seedlings in monoculture had greater relative height increases than those in the 2Qa/2Lt treatment ($F = 4.11$, d.f. = 1/89.2, $p = 0.0457$). In addition, *Q. alba* seedlings in the 1Qa/3Lt treatment had greater relative increases in height than seedlings in the 2Qa/2Lt treatment ($F = 5.50$, d.f. = 1/204, $p = 0.0200$).

All *Q. alba* seedlings (in monoculture and with *L. tatarica*) displayed high initial relative height increases, followed by minimal growth after the first three weeks of the experiment (Fig. 2). Throughout the experiment, including during this initial period, seedlings in monoculture and with *L. tatarica* did not differ in incremental relative height increases (minimum $p = 0.1212$; week 10).

For treatments where *Cornus* seedlings were included (Fig. 3), *Quercus alba* seedlings in the All treatment had lower relative increases in height than seedlings in the 4Qa ($F = 12.03$, d.f. = 1/179, $p = 0.0007$), 2Qa/2Cf ($F = 4.51$, d.f. = 1/207, $p = 0.0348$), and 2Qa/2Cs ($F = 9.92$, d.f. = 1/207, $p = 0.0019$) treatments (Fig. 3a). *Quercus alba* seedlings in the 2Qa/2Cf treatment had greater relative increases in basal diameter than seedlings in the 4Qa ($F = 4.77$, d.f. = 1/102, $p = 0.0313$), 2Qa/2Lt ($F = 8.03$, d.f. = 1/156, $p = 0.0052$), and 2Qa/2Cs ($F = 6.68$, d.f. = 1/156, $p = 0.0106$) treatments (Fig. 3b).

Mean *Quercus alba* biomass ranged from 19.30 g (4Qa) to 23.69 g (2Qa/2Lt) and did not differ over treatments ($F = 0.46$, d.f. = 6, $p = 0.8357$). The mean

ratio of above to below ground biomass ranged from 0.58 (2Qa/2Cf) to 0.62(1Qa/3Lt) and did not differ over treatments ($F=0.18$, d.f. = 6, $p=0.9819$).

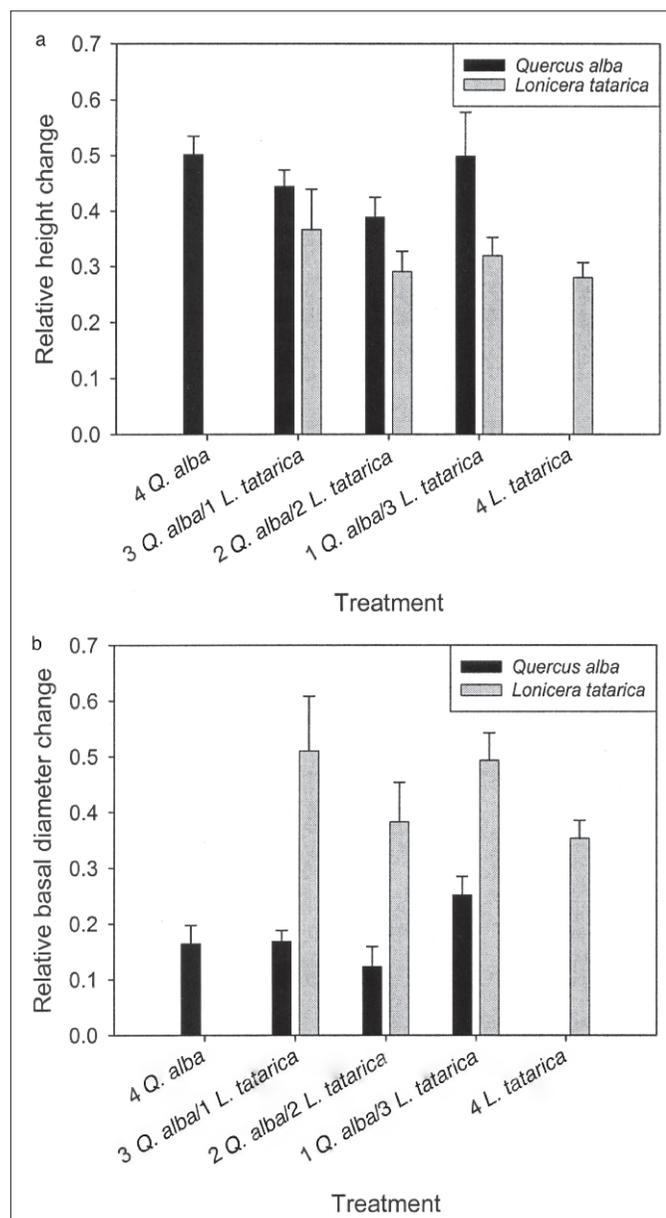


Figure 1. (a) Replacement series diagram comparing relative height changes + 1 standard error for *Quercus alba* and *Lonicera tatarica* seedlings in monocultures and at three different density combinations. *Quercus alba* seedlings displayed greater increases than *L. tatarica* seedlings, a-cross treatments ($p = 0.0021$). *Quercus alba* seedlings in monoculture displayed greater increases than those in the 2Qa/2Lt treatment ($p = 0.0457$).

(b) Replacement series diagram comparing relative basal diameter changes + 1 standard error for *Quercus alba* and *Lonicera tatarica*

seedlings in monocultures and at three different density combinations. *Lonicera tatarica* seedlings displayed greater increases than *Q. alba* seedlings, across treatments ($p < 0.0001$). *Quercus alba* seedlings in monoculture did not differ from those potted with *L. tatarica*.

Discussion

The primary goal of this study was to determine seedling-to-seedling competitive effects of the exotic shrub *L. tatarica* on *Q. alba*. With *Q. alba* displaying similar height, basal diameter, growth rates and biomass when potted in monoculture or with *L. tatarica*, we suggest that these effects were minimal. Furthermore, *Q. alba* growth was similar when potted with native shrubs as with *L. tatarica*. By comparing exotic and native shrubs' effects on *Q. alba*, we are able to ask whether differences in *Q. alba* growth are the result of the exotic shrub, or simply the result of a shrub being present in the pot. At the seedling stage, impacts on *Q. alba* seedlings appear similar for *L. tatarica*, native shrubs, and *Q. alba* itself. Our findings support the idea that invasive species may not always have inherent performance advantages over native species (see Daehler [2003] for review).

Past work has shown that *L. tatarica* and its congener *L. maackii* invade North American forests with deleterious effects on native tree seedlings (Collier et al. 2002, Gorchov and Trisel 2003, Hutchinson and Vankat 1997, Woods 1993). These studies investigated mature *Lonicera* shrubs ($\approx 2\text{--}3$ m height) competing with shorter tree seedlings, which resulted in strong asymmetric competition for light and *Lonicera* dominance. Our

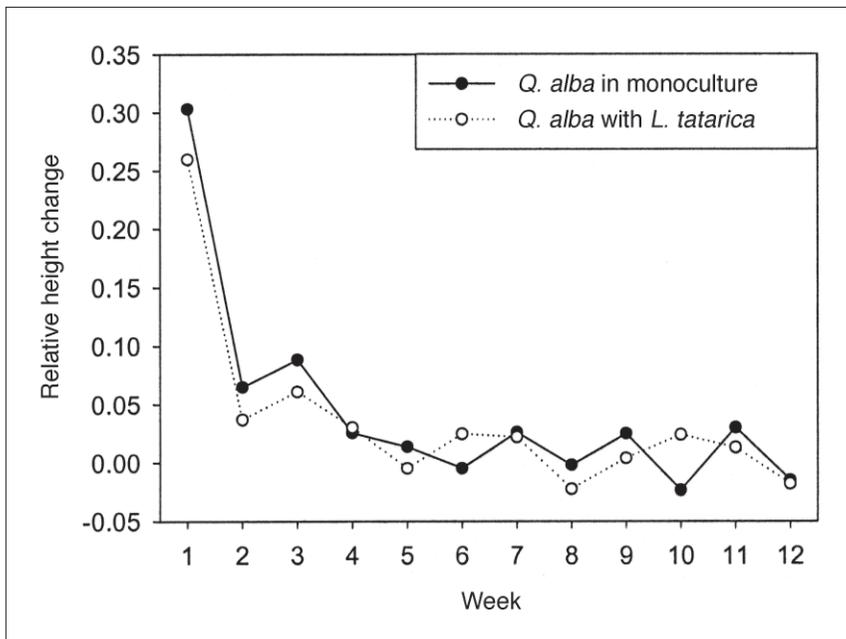


Figure 2. Week-by-week incremental relative height changes for *Quercus alba* in monoculture and when potted with *Lonicera tatarica* (across all density combinations). Following initially high rates, *Quercus alba* growth during subsequent weeks was minimal. No differences exist between treatment groups.

study rejects deleterious seedling-stage effects as a further impact of *Lonicera* invasion, despite past suggestion that *L. tatarica* may suppress other species through the production of allelopathic chemicals (Uesato et al. 1986). We supply indirect evidence that this does not occur during *L. tatarica*/*Q. alba* seedling interactions. These findings demonstrate that the competitive effects of *L. tatarica* on *Q. alba* may differ between the stages

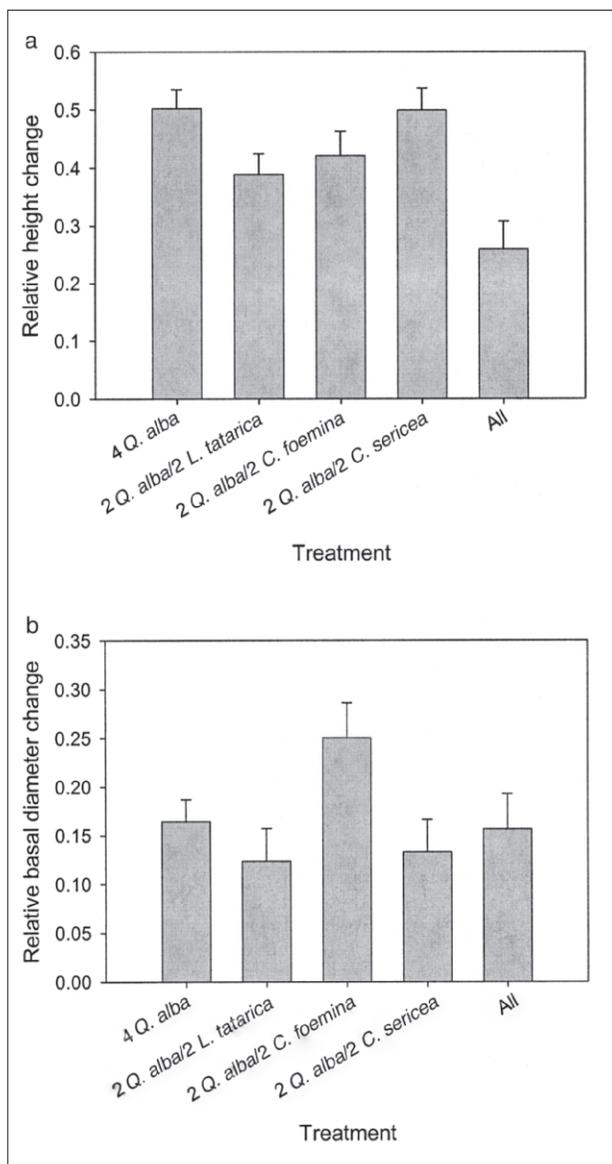


Figure 3. (a) Changes in relative height + 1 standard error for *Quercus alba* seedlings in monoculture, with *Lonicera tatarica* seedlings, with native *Cornus foemina* and *Cornus sericea* seedlings, and when all four species were grown together (All). Seedlings in the All treatment displayed lower increases than seedlings in the 4 *Q. alba* ($p = 0.0007$), 2 *Q. alba*/2 *C. foemina* ($p = 0.0348$), and 2 *Q. alba*/2 *C. sericea* ($p = 0.0019$) treatments.

(b) Changes in relative basal diameter + 1 standard error for *Quercus alba* seedlings in monoculture, with *Lonicera tatarica* seedlings, with native *Cornus foemina* and *Cornus sericea* seedlings, and when all four species were grown together (All). Seedlings in the 2 *Q. alba*/2 *C. foemina* treatment displayed greater increases ($p < 0.05$) than those in the 4 *Q. alba*, 2 *Q. alba*/2 *L. tatarica*, and 2 *Q. alba*/2 *C. sericea* treatments.

increases ($p < 0.05$) than those in the 4 *Q. alba*, 2 *Q. alba*/2 *L. tatarica*, and 2 *Q. alba*/2 *C. sericea* treatments.

of exotic species establishment (where seedling-to-seedling competition is important) and after establishment has occurred (Vilà and Weiner 2004).

The incremental growth for *Q. alba* in monoculture and with *L. tatarica* reveals that a majority of growth occurred during the first three weeks of the experiment (Fig. 2). Following week three, growth was minimal, suggesting that this initial period is critical to seasonal growth of *Q. alba* seedlings. Since no significant differences existed between seedlings in monoculture and with *L. tatarica* during this initial period or during any point in the study, we conclude that *L. tatarica* does not impact seedling performance even during the most active growth period.

In most performance comparison studies, one native and one exotic species are paired (Daehler 2003). In our study, we included a treatment where the two native shrubs were added to pots along with *L. tatarica* and *Q. alba*, to increase pot species richness to four. This approach provides additional data on *Q. alba* performance in simulated natural settings, where more than one other seedling species is likely to co-occur. The apparent effect of increased species richness on *Q. alba* growth suggests that cumulative competitive effects of multiple species (native and exotic) are more important than competition between individual species. This may have serious consequences on *Q. alba* regeneration, which is already minimal in many areas (Cho and Boerner 1991, Lorimer et al. 1994). Additional research on *Q. alba* performance in multispecies cultures is needed to determine *L. tatarica*'s role in this decline.

Although the replacement series experiment showed few differences between *Q. alba* growth in monoculture and with *L. tatarica*, it did reveal that *L. tatarica* increased more in basal diameter, while *Q. alba* seedlings grew more in height. These differences may be a result of differing growth strategies between shrubs and trees (Wilson 1995); however, how this might influence *L. tatarica*/*Q. alba* interactions during invasion is unclear.

This work constitutes an attempt to determine impacts of an exotic shrub invader on the native Northeastern tree, *Quercus alba*. We suggest that seedling-to-seedling competition is not an overwhelming impact of invasion; however, we acknowledge that the duration of this study and its setting necessitate that these results be viewed somewhat cautiously. Our conclusions hinge on the assumption that potted plants were indeed interacting and that greenhouse conditions adequately represented field conditions. We observed morphological changes in above-ground growth and intricately interwoven root systems (observed during biomass sampling), which suggest that interactions occurred both above and below ground. It is unclear as to how our greenhouse-based findings apply to more natural conditions over longer durations. Future work should continue to investigate the impacts of *L. tatarica* on *Q. alba* and other species of eastern deciduous forests, so that informed management and restoration decisions can be made.

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Literature Cited

- Abrams, M.D. 2003. Where has all the white oak gone? *BioScience* 53:927–939.
- Cho, D.S., and R.E.J. Boerner. 1991. Canopy disturbance patterns and regeneration of *Quercus* species in two Ohio old-growth forests. *Vegetatio* 93:9–18.
- Collier, M.H., J.L. Vankat, and M.R. Hughes. 2002. Diminished plant richness and abundance below *Lonicera maackii*, an invasive shrub. *American Midland Naturalist* 147:60–71.
- Daehler, C.C. 2003. Performance comparisons of co-occurring native and alien invasive plants: Implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics* 34:183–211.
- de Wit, C.T. 1960. On competition. *Verslagen van Landbouwkundige Onderzoekingen* 66:1–82.
- Diamond, J.M. 1983. Laboratory, field, and natural experiments. *Nature* 304:586–587.
- Gibson, D.J., J. Connolly, D.C. Hartnett, and J.D. Weidenhamer. 1999. Designs for greenhouse studies of interactions between plants. *Journal of Ecology* 87:1–16.
- 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 Ecology* 166:13–24.
- Gould, A.M.A., and D.L. Gorchov. 2000. Effects of the exotic invasive shrub *Lonicera maackii* on the survival and fecundity of three species of native annuals. *American Midland Naturalist* 144:36–50.
- Grotkopp, E., M. Rejmánek, and T.L. Rost. 2002. Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* 159:396–419.
- Hulme, P.E. 2003. Biological invasions: Winning the science battles but losing the conservation war. *Oryx* 37:178–93.
- Hutchinson, T.F., and J.L. Vankat. 1997. Invasibility and effects of Amur honeysuckle in southwestern Ohio forests. *Conservation Biology* 11:1117–1124.
- Jolliffe, P.A. 2000. The replacement series. *Journal of Ecology* 88:371–385.
- Kareiva, P. 1996. Developing a predictive ecology for non-indigenous species and ecological invasions. *Ecology* 77:1651–1652.
- Lorimer, C.G., J.W. Chapman, and W.D. Lambert. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *Journal of Ecology* 82:227–237.
- Pimental, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:53–65.

- Rehder, A. 1927. *Manual of Cultivated Trees and Shrubs Hardy in North America*. MacMillan, New York, NY. 996 pp.
- Uesato, S., S. Kanomi, A. Iida, H. Inouye, and M.H. Zenk. 1986. Mechanism for iridane skeleton formation in the biosynthesis of secologanin and indole alkaloids in *Lonicera tatarica*. *Phytochemistry* 25:839–842.
- Vilà, M., and J. Weiner. 2004. Are invasive plant species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* 105:229–238.
- Vitousek, P.M., C.M. D'Antonio, L.L. Loope, and R. Westbrooks. 1996. Biological invasions as global environmental change. *American Scientist* 84:470–478.
- Wilcove, D.S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. *Bioscience* 48:607–615.
- Wilson, B.F. 1995. Shrub stems: Form and function. Pp. 91–102, *In* B.L. Gartner (Ed.). *Plant Stems: Physiology and Functional Morphology*. Academic Press, San Diego, CA. 440 pp.
- Woods, K.D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. *American Midland Naturalist* 130:62–74.