



Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings

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Abstract

Invasive plants are often associated with reduced cover of native plants, but rarely has competition between invasives and natives been assessed experimentally. The shrub *Lonicera maackii*, native to northeastern Asia, has invaded forests and old fields in numerous parts of eastern North America, and is associated with reduced tree seedling density in Ohio forests. A field experiment was conducted to test the effects of established *L. maackii* on the survival and growth of transplanted native tree species. The experiment examined above-ground competition (by removing *L. maackii* shoots) and below-ground competition (by trenching around transplanted seedlings). The effects of above-ground competition with *L. maackii* were generally more important than below-ground competition, though both were detected. Shoot treatment was the key determinant for the survival of all species except *P. serotina*, whereas trenching only enhanced survival for *A. saccharum* caged and *P. serotina*, and only in the shoot removal treatment. For the surviving seedlings, *L. maackii* shoot removal increased growth of *A. saccharum* seedlings protected with cages, but actually reduced the growth of unprotected *Q. rubra* and *A. saccharum* seedlings, indicating that *L. maackii* shoots confer some protection from deer browsing. Significant interactions between root and shoot treatment on *Q. rubra* growth parameters, specifically greatest growth in the shoot present & trenched treatment, is attributed to protection from deer browsing combined with release from below-ground competition. Despite this protective function of *L. maackii* shoots, the overall effect of this invasive shrub is increased mortality of native tree seedlings, suggesting it impacts the natural regeneration of secondary forests.

Introduction

The impact that invasive species (novel, invasive colonizers sensu Davis and Thompson (2000)) have on native species, communities, and ecosystems has received increased attention in recent years (e.g., Usher (1988); Lodge (1993); Office of Technology Assessment (1993); Vitousek et al. (1996); Ewel et al. (1999)). In the case of invasive plants, most studies have investigated the characteristics of invasive species or native communities associated with successful invasions (e.g., Brothers and Spingarn (1992); Williamson and Fitter (1996); Mack (1996); Rejmánek

(1996); Rejmánek and Richardson (1996); Reichard and Hamilton (1997); Stohlgren et al. (1999)). While invasive plants are often considered responsible for declines of native species richness, this is largely based on correlations among sites that have been invaded for a long period of time. These correlations do not determine the causality of current patterns; they do not account for historic events such as disturbance (Hobbs and Huenneke 1992) that have not only led to the establishment of exotics, but also negatively affected native plant populations. Also, they do not separate 1) the effects of the invasive species in suppressing native species from 2) any tendency of

invasives to become abundant in sites where species richness or densities of native species are lower. There is a need for experimental research to determine direct ecological effects of specific invasive plant species on native plants. Manipulative experiments such as these have been rare in invasion ecology and are needed to advance this field (Kareiva 1996).

A handful of studies have experimentally tested the effects of invasive plants on native plant populations and communities. The growth rate of the native tree *Liquidambar styraciflua* was reduced by above- and belowground competition from the invasive vine *Lonicera japonica* (Dillenburg et al. 1993). The invasive shrub *Acacia cyclops* had a negative effect on the native shrubs *Rhus glauca* and *R. lucida* (Midgley et al. 1992), and seedlings of the invasive *Acacia saligna* reduced growth rates of seedlings of the native shrub *Protea repens* (Witkowski 1991). The germination and growth of *Cirsium vinaceum*, a threatened endemic thistle of New Mexico, were reduced by the invasive *Dipsacus sylvestris* (Huenneke and Thomson 1995). Seedlings of the invasive biennial *Alliaria petiolata* negatively affected seedlings of *Quercus prinus*, but its effects on two other native species was lower than intraspecific competition in those species (Meekins and McCarthy 1999).

We used field experiments to test whether the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), negatively affects the seedling survival and growth of trees native to Ohio, USA. *Lonicera maackii* is a "novel, invasive colonizer" (Davis and Thompson 2000) as it has been dispersed a long distance, is currently expanding its range in North America, and has a large impact on its environment. Native to northeastern China, Korea, and parts of Siberia and Japan (Luken and Thieret 1996), *L. maackii* was introduced to North America in 1896 and subsequently promoted for landscaping and wildlife habitat improvement, and the subject of a cultivar improvement program at USDA Soil Conservation Service (Luken and Thieret 1995). Its ability to escape from cultivation and naturalize was noted by 1924 and it is now recognized as a problem at numerous arboreta (Luken and Thieret 1995). It is naturalized in Ontario (Pringle 1973) and ≥ 24 eastern states in USA (Trisel and Gorchov 1994). The first report of naturalized *L. maackii* in Ohio was for Hamilton County (Braun 1961), but it is now naturalized in 34 other counties (Trisel 1997). It is now by far the commonest shrub, native or alien, in Greater Cincinnati

(Luken and Thieret 1995) and is one of only 12 plant species that can not be planted on Department of Conservation property in Illinois (Harty 1993). It thrives in both open habitats and forests with a history of cattle grazing or other human disturbance (Luken 1988; Luken and Thieret 1995). It has invaded most forest stands near Oxford, Ohio, growing at densities of up to 6800 shrubs ha⁻¹ (Trisel and Gorchov 1994). The density of this shrub is negatively correlated with stand basal area (Hutchinson and Vankat 1997) and it may be excluded from the interior of large, mature forests (Luken and Thieret 1995).

An upright shrub, *L. maackii* sprouts readily from the burl and has plastic stem growth that allows it to both tolerate shade and take advantage of high light levels (Luken et al. 1995, 1997). Seedlings establish under a wide range of light levels (Luken and Goessling 1995). *Lonicera maackii* has bird-dispersed fruits (Ingold and Craycraft 1983) and experiences less herbivory than most native woody species (Trisel and Gorchov 1994). It expands leaves much earlier in the spring, and retains them later in the fall than native woody plants (Trisel and Gorchov 1994); similar phenologies enabled two exotic shrubs in Wisconsin to accomplish much of their annual carbon gain while native shrubs and trees were leafless (Harrington et al. 1989).

To date, no definitive study has been undertaken to determine if *L. maackii* has caused changes in native floras (Luken and Thieret 1995), although there is correlational evidence. *Lonicera maackii* density was negatively correlated with cover of herbs and density and species richness of tree seedlings among forest stands in southwest Ohio (Hutchinson and Vankat 1997). Within a single woodlot, *L. maackii* basal area was negatively correlated with species richness and basal area of native shrubs and sapling density of *Acer saccharum*, the canopy dominant (Medley 1997). Within stands, the richness and abundance of herbs and tree seedlings was lower under *L. maackii* shrubs than away from them (Collier et al. 2002). Similarly, negative correlations were found between density of the congener *L. tatarica* and native herb species richness and cover, and tree seedling density (Woods 1993). *Lonicera X bella* is negatively associated with *Cornus racemosa*, an important shrub in Wisconsin forests (Barnes 1972).

These observations support the hypothesis that *L. maackii* reduces native plants via allelopathy and/or competition, but the pattern could also be due to successful invasion only in the most disturbed, species-

poor stands and sites within stands. Few field experiments have been done to investigate the effects of any invasive *Lonicera* shrub on the survival or growth of native species. Removal of *L. maackii* from 5 m diameter plots in a 40-yr-old stand increased the density of other plants, and of one of the most common species (*Vitis vulpina*), but most of the species were generalists rather than taxa of mature forests (Luken et al. 1997). The reproduction of three native annual herbs was enhanced in small plots where *L. maackii* was removed, as was the survival of the two species with earlier leaf phenologies (Gould and Gorchov 2000). Growth and fecundity, but not adult survival, of three perennial herbs was also enhanced in *L. maackii* removal plots (Miller 2001).

We investigated the effect of *L. maackii* on survival and growth of seedlings of four native tree species. If canopy tree recruitment is reduced under *L. maackii*, then forest succession is changed. Using transplanted seedlings, we tested two hypotheses for how *L. maackii* may negatively effect seedlings of native trees: 1) above-ground competition and 2) below-ground competition.

Methods

The field experiments were carried out in Gregg's Woodlot, an isolated 7 ha anthropogenically disturbed woodlot 1.8 miles south of Oxford, Ohio (30°28'30" N, 84°43'30" W) on the glaciated Till Plain where the natural vegetation was primarily mesophytic beech-sugar maple forest. This stand has a tree (≥ 10 cm diameter at breast height) density of 576 ha⁻¹, and a basal area (BA) of 21.4 m² ha⁻¹. The most important species in the canopy, based on relative density and BA, are *Carya ovata*, *Fraxinus* spp., *Carya laciniata*, and *Quercus rubra* (nomenclature followed Gleason and Cronquist (1991)). Trees were selectively cut in approximately 1900, the woodlot was regularly grazed by cattle and burned into the 1950s, but has been unmanaged since then (T. Gregg, pers. comm.). The shrub layer in this stand is dominated by *L. maackii* (0.7 shrubs m⁻²) of relatively uniform size; other shrubs are very sparse.

We used a 2 × 2 factorial experiment to evaluate survival and growth of transplanted seedlings of four tree species in plots subjected to one of two levels of *L. maackii* shoot treatment and one of two levels of root treatment.

In May 1992, we selected 160 individual *L. maackii* shrubs ≥ 1.5 m tall with no large (> 15 cm DBH) tree boles within 2 m or large canopy gaps within 10 m. Canopy cover, measured 14 July 1994 2 m above each of these shrubs with a spherical densiometer (Lemmon 1956), averaged 95.5% (range 84–99%). Within a 2 m radius of these shrubs, *L. maackii* dominated the understory, with a shrub (genet) density 0.72 m⁻² (± 0.03 SE), a stem (≥ 8 mm basal diameter) density of 1.52 m⁻² (± 0.06), and a BA of 3.36 (± 0.16) m² ha⁻¹.

We established 1.5 m × 1.5 m experimental plots centered on each *L. maackii* shrub, with all plots ≥ 10 m apart. No shrubs of other species were within the plots. Forty plots were randomly assigned to each of the following treatments:

1. *L. maackii* shoots removed (shoot competition removed)
2. Soil around planted seedlings trenched to remove roots of *L. maackii* and other forest plants (root competition removed)
3. *L. maackii* shoots removed and soil trenched around planted seedlings (both shoot and root competition removed)
4. unmanipulated, control.

In May 1992, the stems of the central *L. maackii* shrub in each shoot removal plot were cut 25 cm above ground level and stems of nearby *L. maackii* were pruned so that no branches remained within a 45° projection from the outside edge of the plot.

One seedling of each of four native canopy tree species (*Acer saccharum*, *Fraxinus americana*, *Prunus serotina*, and *Quercus rubra*) was planted in each plot using a planting bar. Seedlings were planted 60 cm from the base of the shrub in each of four cardinal directions, with species randomly assigned to positions. Seeds of *Q. rubra* were collected from trees along the Marcum Trail, Miami University Natural Areas (Oxford, OH) in the fall of 1991, placed in moist sand, and stratified for 3 months at 4 °C. The seeds were then planted in Metro-Mix 250 in "containers" and grown in a greenhouse. Seedlings of *A. saccharum*, *F. americana*, and *P. serotina* were purchased in a bare-root and dormant condition from Musser Forests (PA) and Keeling Nurseries (MO) in May of 1992, and were kept refrigerated until planted. Seedlings of *P. serotina* were planted first (29 May–4 June) because the leaves of these seedlings had already expanded upon arrival. Seedlings of *A. saccha-*

rum were planted 11–15 June, *F. americana* 16–23 June, and *Q. rubra* 28 June–2 July. In treatments 2 and 3 each seedling was planted in the center of an area 30 cm × 30 cm trenched to a depth of 30 cm deep using a spade (*L. maackii* roots are largely confined to the top 15 cm). Several seedlings died, apparently from transplant shock; these were replaced 13–15 July 1992. Also at this time, any shoots of *L. maackii* that had grown beyond the 45° limits (detailed above) were cut.

On 24 May 1993 the trenched plots of 4 dead seedlings were excavated and examined for *L. maackii* root growth. The original trenches were still present and almost no roots grew across them, so the plots were not retrenched.

Because of high mortality and high rates of deer browsing during the first year of the study, a second cohort of *A. saccharum* seedlings, referred to as “*A. saccharum* caged,” was planted 24–28 May 1993. This second cohort was protected by cylindrical enclosures 30 cm in diameter by 40 cm tall made of chicken wire stapled to a wooden stake hammered into the ground. Seedlings were randomly assigned to one of the cardinal directions available at each plot because of mortality. In plots where all 1992 seedlings had survived, the randomly chosen cardinal direction plus 45° was selected as the planting location.

Seedlings were censused and *L. maackii* sprouts cut 12 October 1992, 24 June 1993, 25 September 1993, and 11 July 1994.

Leaves from all seedlings were harvested 21–22 September 1994 and leaf area was determined with a LiCor leaf area meter. Seedling stems and roots were excavated 20–26 October 1994. Roots, leaves, and stems were dried for 4 days at 50 °C and weighed to obtain total biomass and shoot (stem + leaf): root ratio. Analyses of leaf biomass showed the same patterns as those of leaf area (Trisel 1997), so only the latter are reported here. Total stem length (includes main shoot axis and all lateral branches) was measured for each seedling.

To determine the significance of shoot treatment (S), root treatment (R), and their interaction on seedling survival (V) of each species we used three-way log-linear models (Sokal and Rohlf 1995). If the three-way interaction (SRV) for a species was significant, then separate two-way tests of independence were conducted. If the three-way interaction was not significant, then simpler models were used to test the significance of individual interaction terms. For each term, significance ($P = 0.05$) was tested by calculat-

ing the G -statistic for goodness of fit for the model with that term and for the model without that term, then subtracting the former from the latter, and comparing this difference to the Chi-squared ($df = 1$) distribution. PROC CATMOD using SAS version 6.2 was used for these analyses.

For each species, the effect of treatments on each growth response was tested using 2-way ANOVA ($P = 0.05$, using Statview 4.02) with the main effects being shoot treatment (removed vs. present) and root treatment (trenched vs. not trenched). These main effects were considered fixed effects, so the F for each effect and the interaction was obtained by dividing the within-group MS by the error MS (Sokal and Rohlf 1995).

Results

The number of seedlings surviving, of the 160 planted, varied by species as follows: *A. saccharum*, 39 (24.4%); *A. saccharum* caged, 75 (46.9%); *F. americana*, 62 (38.8%), *P. serotina*, 17 (10.6%), and *Q. rubra*, 24 (15%). The apical meristems of all but 12 seedlings (11 *A. saccharum* caged and one *F. americana*) were damaged or removed.

Acer saccharum

The three-way interaction between survival, shoot treatment, and root treatment was not significant ($G = 0.9$). Root treatment did not significantly affect survival ($G = 2.8$) but shoot removal of *L. maackii* significantly increased survival ($G = 4.2$) (Figure 1).

For the 39 surviving seedlings, total biomass was significantly lower where *L. maackii* shoots were removed (Figure 2a and Table 1), but there was no significant effect of root treatment. The interaction between root and shoot treatments approached significance ($P = 0.06$); trenching increased biomass only where shoots were removed. Shoot/root ratio was significantly lower where *L. maackii* shoots were removed, but there was no significant effect of root treatment or interaction (Table 1).

Although the effects of shoot and root treatments did not significantly affect total stem length, there was a significant interaction between the treatments (Table 1). When the soil was trenched stems were longer with *L. maackii* shoots removed, but with no trenching, stems were longer with the shoots present (Figure 3a).

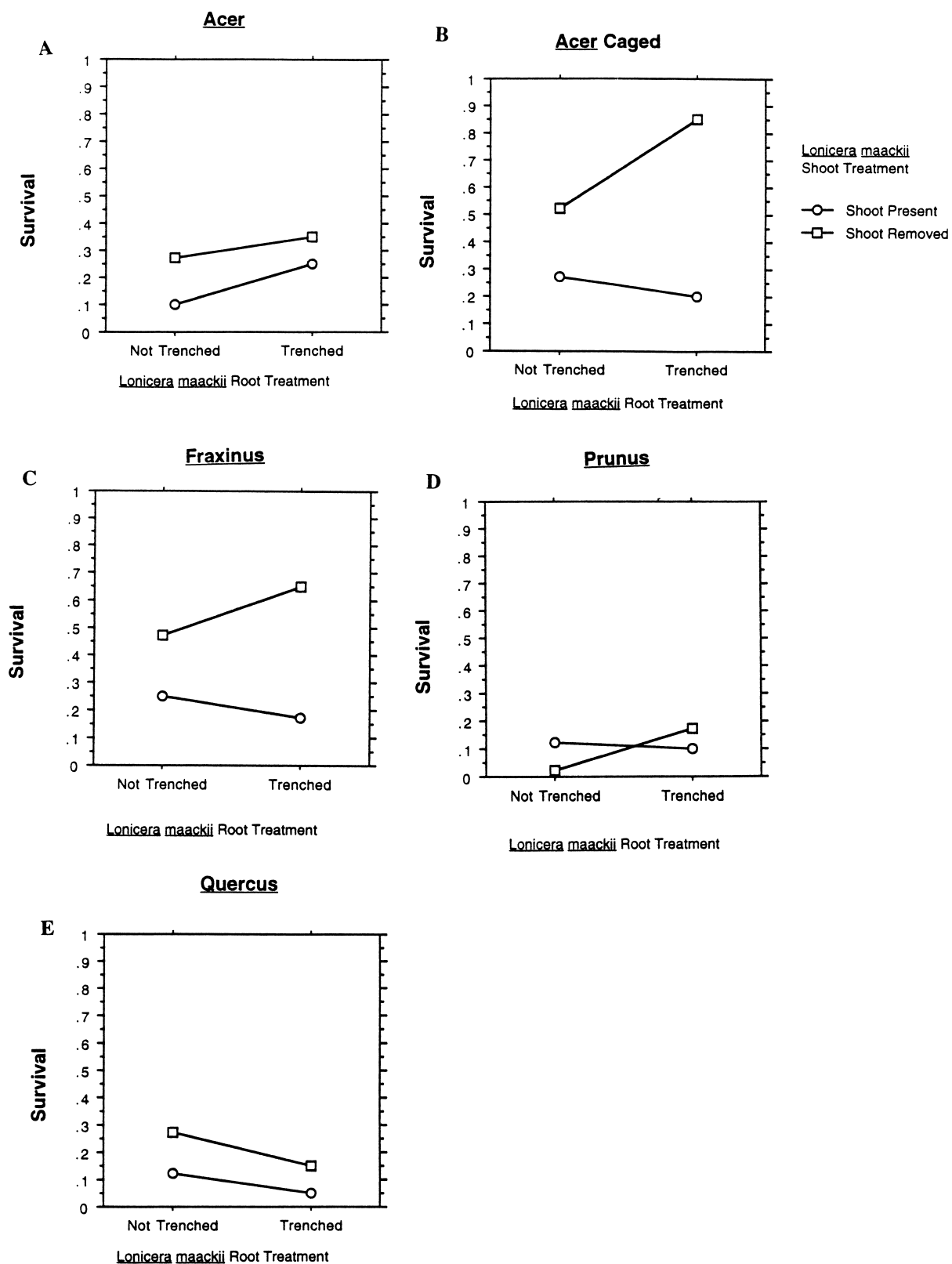


Figure 1. Effects of trenching and *L. maackii* shoot removal on survival of tree seedlings. N = 160 seedlings per species (40 per treatment). A. *Acer saccharum*. B. *Acer saccharum* caged. C. *Fraxinus americana*. D. *Prunus serotina*. E. *Quercus rubra*.

Table 1. Summary of 2-way ANOVAs of the growth responses of seedlings of *Acer saccharum*, *Fraxinus americana*, *Prunus serotina*, and *Quercus rubra* to shoot treatment (removal v. present), root treatment (trenched v. not trenched), and the interaction of treatments. For all effects, $df = 1$, so Sum of Squares (SS) = Mean Squares (MS). Since effects were fixed, F 's were obtained by dividing by the Error MS.

Species	Dependent Variable	Effect	SS	F	P
<i>Acer</i>	Total Biomass	Shoot treatment	23.4	4.90	.033
		Root treatment	0.4	0.09	ns
		Shoot $\times$ Root	17.5	3.65	.064
	Shoot/Root Ratio	Shoot treatment	0.255	6.60	.015
		Root treatment	0.087	2.24	ns
		Shoot $\times$ Root	0.020	0.52	ns
	Stem Lengths	Shoot treatment	91.4	1.67	ns
		Root treatment	3.0	0.06	ns
		Shoot $\times$ Root	280.1	5.12	.029
<i>Acer Caged</i>	Leaf Area	Shoot treatment	210343	10.11	.003
		Root treatment	13107	0.63	ns
		Shoot $\times$ Root	45085	2.17	ns
	Total Biomass	Shoot treatment	23.6	3.72	.058
		Root treatment	18.4	2.91	.092
		Shoot $\times$ Root	0.1	0.15	ns
	Shoot/Root Ratio	Shoot treatment	0.026	0.52	ns
		Root treatment	0.072	1.43	ns
		Shoot $\times$ Root	0.025	0.50	ns
<i>Fraxinus</i>	Stem Lengths	Shoot treatment	304.4	5.69	.019
		Root treatment	344.8	6.44	.013
		Shoot $\times$ Root	48.3	0.90	ns
	Leaf Area	Shoot treatment	0.001	0	ns
		Root treatment	29256	1.79	ns
		Shoot $\times$ Root	42174	2.59	ns
	Total Biomass	Shoot treatment	118.8	1.36	ns
		Root treatment	23.4	0.27	ns
		Shoot $\times$ Root	89.6	1.02	ns
<i>Quercus</i>	Shoot/Root Ratio	Shoot treatment	0.17	1.15	ns
		Root treatment	0.18	1.22	ns
		Shoot $\times$ Root	0.06	0.40	ns
	Stem Lengths	Shoot treatment	224.3	0.29	ns
		Root treatment	1912.3	2.44	ns
		Shoot $\times$ Root	390.6	0.50	ns
	Leaf Area	Shoot treatment	460.2	0.02	ns
		Root treatment	10154	0.46	ns
		Shoot $\times$ Root	58541	2.67	ns
<i>Quercus</i>	Total Biomass	Shoot treatment	2.40	1.63	ns
		Root treatment	5.85	3.98	0.060
		Shoot $\times$ Root	8.77	5.96	0.024
	Shoot/Root Ratio	Shoot treatment	0.121	2.44	ns
		Root treatment	0.097	1.95	ns
		Shoot $\times$ Root	0.021	0.41	ns
	Stem Lengths	Shoot treatment	38.84	2.04	ns
		Root treatment	2.80	0.15	ns
		Shoot $\times$ Root	94.28	4.96	0.037
<i>Quercus</i>	Leaf Area	Shoot treatment	64801	8.13	0.011
		Root treatment	19034	2.39	ns
		Shoot $\times$ Root	55517	6.96	0.017

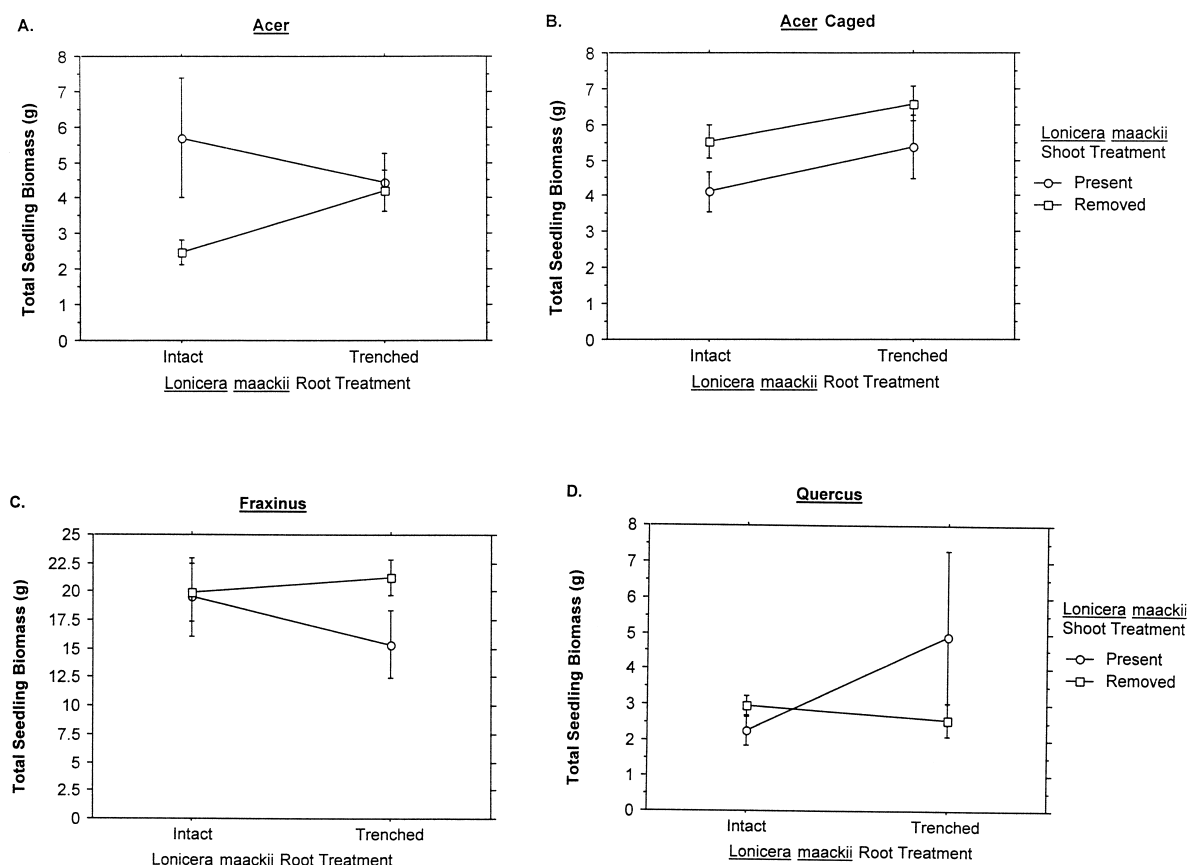


Figure 2. Effects of trenching and *L. maackii* shoot removal on mean (+ SE) total biomass of tree seedlings. A. *Acer saccharum* (N = 39 total seedlings). B. *Acer saccharum* caged (N = 75). C. *Fraxinus americana* (N = 62). D. *Quercus rubra* (N = 24).

Leaf area of *A. saccharum* seedlings was significantly higher in treatments with *L. maackii* shoots present (Figure 4a and Table 1); there was no effect of root or root-shoot treatment interaction.

Acer saccharum caged

The three-way interaction between survival, shoot treatment, and root treatment for *A. saccharum* caged was significant ($G = 7.6$) necessitating separate analyses stratified by treatment. Shoot removal significantly increased survival whether the soil was trenched ($G = 36.8$) or not ($G = 5.3$) (Figure 1b). If the shoots were removed, trenching significantly increased survival ($G = 10.2$). If the shoots were present, root treatment did not significantly affect survival ($G = 0.62$, Figure 1b).

For the 75 surviving seedlings, total biomass tended to be higher where *L. maackii* shoots were removed ($P = 0.058$) and following trenching ($P = 0.092$, Figure 2b and Table 1), but the interaction was

not significant. There were no treatment or interaction effects on shoot/root ratio.

Shoot treatment and root treatment both had significant effects on seedling stem length, but there was no significant interaction. Stems were longer where *L. maackii* shoots had been removed and where the soil was trenched (Figure 3b and Table 1).

There were no significant effects of either treatment or their interaction on leaf area (Figure 4b and Table 1).

Fraxinus

The three-way interaction between survival, shoot treatment, and root treatment for *F. americana* was not significant ($G = 2.69$). Root treatment did not significantly affect survival ($G = 0.5$) but *L. maackii* shoot removal significantly increased survival ($G = 21.3$, Figure 1c).

For the 62 surviving seedlings, there were no significant effects of root treatment, shoot treatment, or

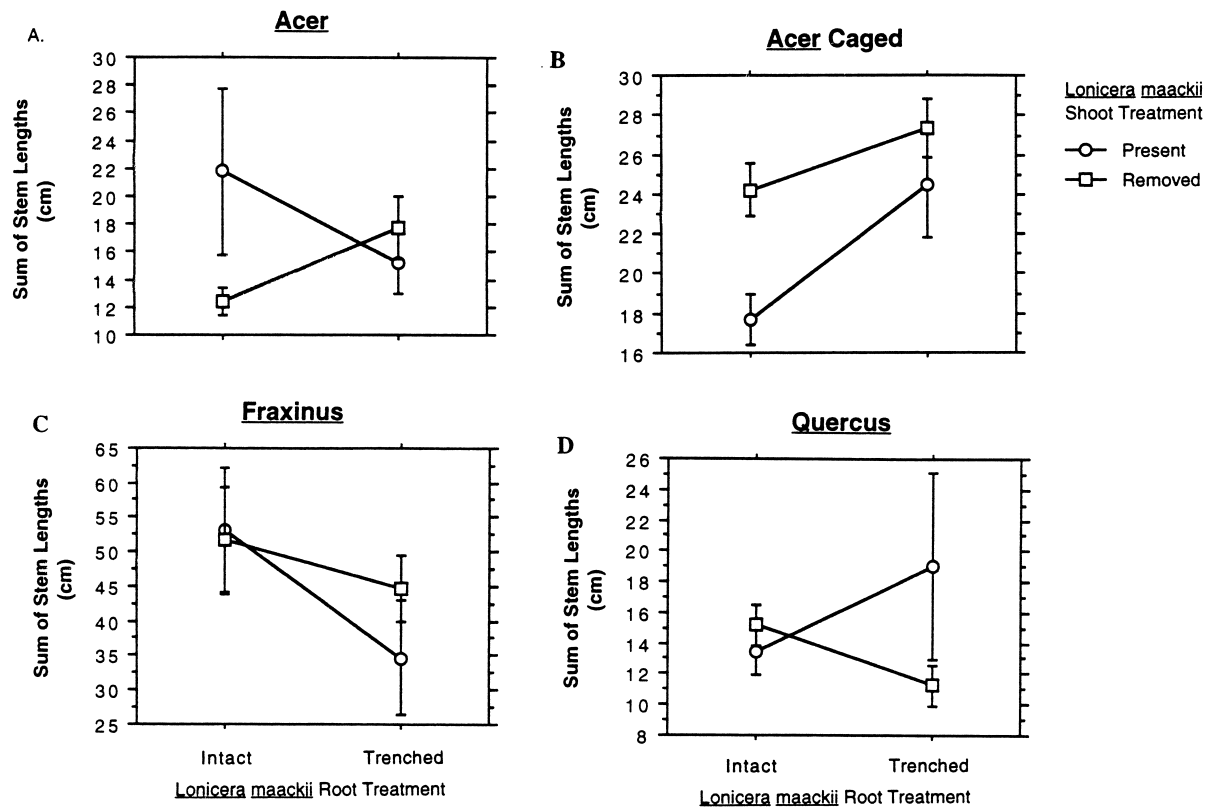


Figure 3. Effects of trenching and *L. maackii* shoot removal on mean (+ SE) total stem length of tree seedlings by treatment. A. *Acer saccharum*. B. *Acer saccharum* caged. C. *Fraxinus americana*. D. *Quercus rubra*. Sample sizes as in Figure 2.

their interaction on total biomass, shoot/root ratio, stem length, or leaf area (Figures 2c, 3c, 4c and Table 1).

Prunus serotina

The three-way interaction between survival, shoot treatment, and root treatment for *P. serotina* was significant ($G = 4.0$). Shoot removal did not significantly affect survival whether the soil was trenched ($G = 0.95$) or not ($G = 3.1$). If the shoots were removed, then trenching significantly increased survival ($G = 5.6$). If the shoots were present, trenching did not significantly affect survival ($G = 0.13$, Figure 1d).

Too few seedlings (17) survived to detect growth responses to the treatments.

Quercus rubra

The three-way interaction between survival, shoot treatment, and root treatment for *Q. rubra* was not significant ($G = 0.05$). Root treatment did not signifi-

cantly affect survival ($G = 3.2$), but shoot removal increased survival ($G = 5.1$, Figure 1e).

For the 24 surviving seedlings, total biomass was not significantly effected by shoot treatment, but was marginally affected by trenching, and significantly affected by the interaction between treatments (Table 1). When the soil was trenched, total biomass was greater in the shoot present treatment, but when not trenched it was greater where shoots were removed (Figure 2d). There were no significant treatment or interaction effects on shoot/root ratio.

There were no significant effects of root or shoot treatment on total stem length, but the interaction was significant (Table 1). Total stem length was greatest in the shoot present/trenched treatment (Figure 3d).

Leaf area was not affected by trenching, but was significantly affected by shoot treatment and the interaction between shoot and root treatments (Table 1); it was highest in the shoot present/trenched treatment (Figure 4d).

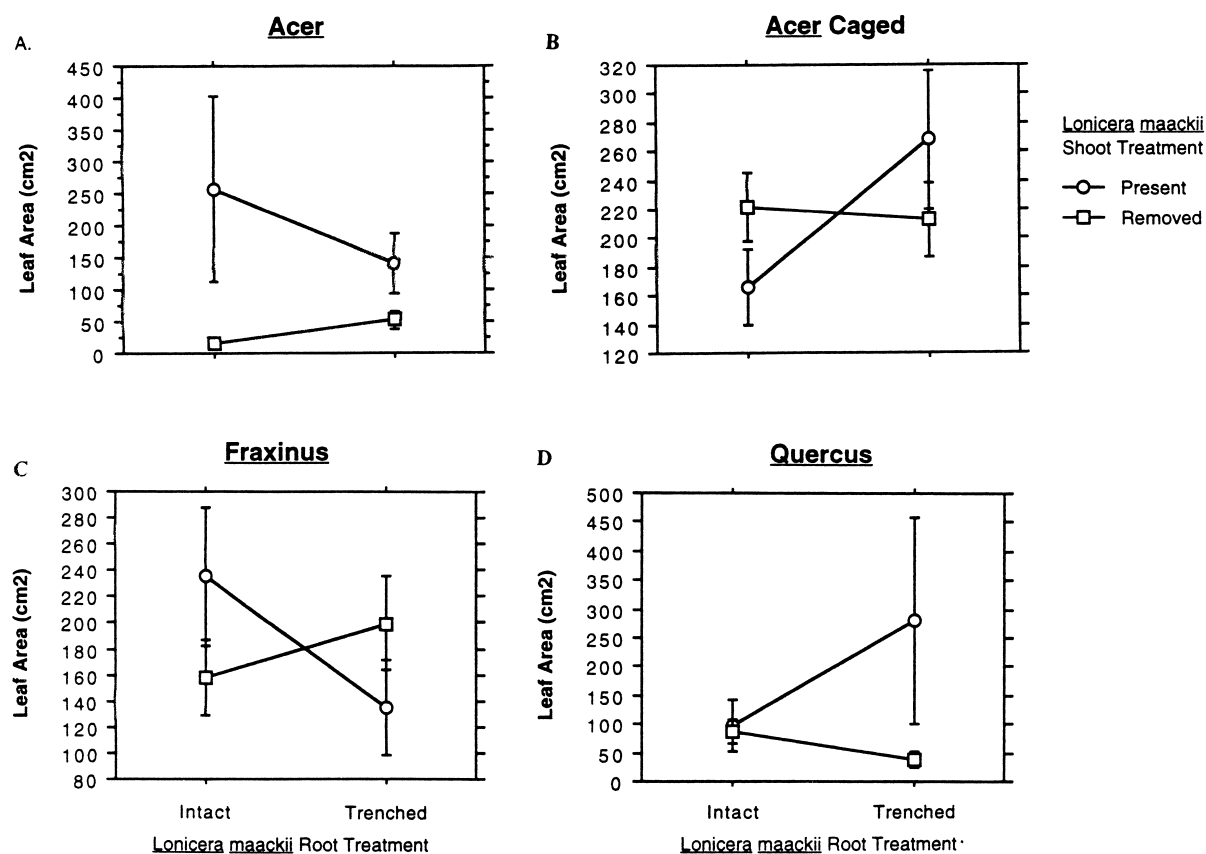


Figure 4. Effects of trenching and *L. maackii* shoot removal on mean (+ SE) leaf area of tree seedlings by treatment. A. *Acer saccharum*. B. *Acer saccharum* caged. C. *Fraxinus americana*. D. *Quercus rubra*. Sample sizes as in Figure 2.

Discussion

The effect of *Lonicera maackii* removal was greatest for *A. saccharum* caged, where survival was increased from 27% in the control to 90% in the shoot removed/root trenched treatment. Effects on survival were also strong for the first *A. saccharum* cohort and *F. americana*, but were less pronounced for *P. serotina* and *Q. rubra*. Although this may reflect species differences in competitive response to *L. maackii*, we think it is more likely due to differences in survival among species related to factors other than competition. The caging of *A. saccharum* minimized mortality due to deer browsing, enhancing our ability to detect treatment effects, whereas the low survival of *P. serotina* and *Q. rubra* across treatments reduced our ability to detect treatment effects on survival and growth.

While trenching reduced competition from all plants rooted outside the planting areas, much of this competition is due to *L. maackii* given its abundance

and the concentration of its roots in the upper 15 cm of the soil. While the shoot effects can be attributed specifically to *L. maackii*, we cannot compare these effects to effects of other shrubs. However, shrubs of other species are very sparse at this site and other secondary forests in this area.

The effects of above-ground competition with *L. maackii* were generally more important than below-ground competition, though both forms of competition were detected. Shoot treatment was the key determinant for the survival of all species except *P. serotina*, whereas trenching only enhanced survival for *A. saccharum* caged and *P. serotina*, and only in the shoot removal treatment.

The above-ground effects are most likely due to competition for light, as there was no mechanical impact on the tree seedlings, nor did we detect any necrosis on seedlings growing under *L. maackii*. However, the above-ground effects might also be due to allelopathy, as it is difficult to distinguish the effects of competition versus allelopathy (Weidenhamer et al.

1989). *Lonicera maackii* appears to have allelopathic properties; its leaves and water extract of its leaves reduced *F. americana* germination and *A. saccharum* seedling growth in greenhouse experiments (Trisel 1997). Seedlings in the shoot removal treatment would be exposed to reduced levels of any allelopathic compounds from *L. maackii* leaves via either throughfall or decomposing *L. maackii* leaves.

Where growth responses to trenching were detected, they were in the expected direction. However, growth responses to *L. maackii* shoot removal were inconsistent: this treatment increased total biomass, and stem length in caged *A. saccharum*, but reduced total biomass, shoot:root ratio, and leaf area of unprotected *A. saccharum*, as well as leaf area of *Q. rubra*. We infer that browsing by deer negatively impacted unprotected tree seedlings, and that *L. maackii* shoots confer some protection from this browsing. Evidence of prevalent browsing includes the fact that 141 of the 142 survivors from the first cohort of seedlings of all species had damage to the apical meristem (Trisel 1997), although insects and winter kill could also cause this damage. While cages prevented consumption of entire seedlings they did not exclude browsing; 63 of the 74 surviving *A. saccharum* caged seedlings had damage to the apical meristem. The dense stands of mature *L. maackii* shrubs apparently limited the movement of deer through the woodlot. Deer trails developed in areas of the woodlot where there were shoot removal treatments in close proximity to one another (DET, personal observation).

Deer browsing can also account for the significant interaction of shoot and root treatment on *Q. rubra* total biomass, stem length, leaf area; these growth responses were all greatest in the shoot present and roots trenched treatment. Where *L. maackii* shoots were present they reduced the incidence of deer browsing, thus permitting trenching to release seedlings from root competition.

The branching strategy of *L. maackii* may give it a competitive advantage over native species in forested environments. Luken et al. (1995) described the production of long shoots by *L. maackii* in response to higher light exposures. This growth form permits the arching branches of *L. maackii* to overtop its neighbors. Height can be a key determinant of success between individuals competing for light (Lovell and Lovell 1985). From the initiation to the completion of this field experiment, *L. maackii* (unpruned) shrubs averaged 1.5–2.5 m tall, while the native tree seedlings were 0.2–0.6 m tall.

The findings of this study were comparable to other studies of plant competition. Survival and growth of Engelmann spruce and lodgepole pine seedlings in British Columbia were significantly reduced by the presence of high herb and shrub cover (Coates et al. 1991). Similarly, Walker and Vitousek (1991) demonstrated that the negative effect of an exotic invader on an important late-successional tree species in Hawaii was due to competitive effects on seed germination, seedling growth, and survival, rather than allelopathy. The invasive vine, *Celastrus orbiculatus*, apparently changed the course of old field succession in southern New England (Fikes and Niering 1999). Similarly, the effects of *L. maackii* on tree seedling survival and growth may result in a modification of forest succession. Because *Acer saccharum* is one of the most important canopy tree species of southwestern Ohio (Vankat et al. 1975) and in eastern deciduous forests in general, the competitive effects of *L. maackii* on this species alone could have very pronounced effects on successional patterns.

Because of *L. maackii* early leaf expansion we expected it would more negatively affect those native species (such as *Aesculus glabra* and *P. serotina*) that expand leaves early and might depend on early-season photosynthesis to remain competitive. High mortality in all treatments for *P. serotina* prevent us from evaluating this prediction, however. Among three species of forest annuals, the effects of *L. maackii* were more negative for species with earlier phenologies, which were also less shade tolerant (Gould and Gorchov 2000). We expected the effect of *L. maackii* shoot competition to positively correlate with shade intolerance. According to Kobe et al. (1995) the relative rank of shade tolerance for the species examined in this study is $A. saccharum > F. americana \approx Q. rubra \approx P. serotina$. Contrary to our prediction, *A. saccharum* showed the most dramatic responses to shoot competition.

A greater sensitivity of *A. saccharum* to *L. maackii* could explain the inverse correlation of *A. saccharum* seedling density to *L. maackii* density among 93 forest stands near Oxford, OH; seedling density of four other species, including *F. americana* and *P. serotina*, were unrelated to *L. maackii* cover (Hutchinson and Vankat 1997). However, Collier et al. (2002) found that within stands the density and cover of seedlings of all tree species were reduced under *L. maackii* shrubs vs. away (≥ 2 m) from *L. maackii* shrubs.

Our findings support the hypothesis that above-ground competition is a major cause of reduced tree

seedling density in forests invaded by *L. maackii*. Additional research is necessary to determine whether this invasive shrub is shifting the species composition of forest stands and redirecting succession.

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