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Source: Natural Areas Journal, 37(4) : 540-548

Published By: Natural Areas Association

URL: https://doi.org/10.3375/043.037.0410

RESEARCH ARTICLE

Are Native Tree Seedlings Facilitated by an Invasive Shrub Where White-Tailed Deer Are Abundant?

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Natural Areas Journal 37:540–548

ABSTRACT: Positive interactions (facilitation) between plant species have been documented, particularly in stressful environments. We investigated whether an invasive shrub enhances growth or survival of native tree seedlings in forests where white-tailed deer (*Odocoileus virginianus*) are abundant. Seedlings of four tree species were planted under, or 0.5 m outside of, the canopy of Amur honeysuckle (*Lonicera maackii*) shrubs in plots unfenced or fenced to exclude deer in two stands in southwestern Ohio, USA, and monitored for 1 y. One species succumbed to transplant shock, but browse was extensive on the other three species in unfenced plots. Facilitation was evident on sugar maple (*Acer saccharum*), as seedlings under shrub cover had higher survival and final leaf count in unfenced plots, but not where deer were excluded. However, there was no significant facilitation by *L. maackii* of seedling growth or survival for white oak (*Quercus alba*) or shagbark hickory (*Carya ovata*), indicating this shrub's branches do not deter deer browse on highly preferred species or the effect is too modest to emerge in a one-year study. In at least some cases, the negative effects of *L. maackii* on tree seedlings that have been documented previously are offset by mitigation of the negative effects of deer herbivory. This suggests that where browsing impacts are problematic, deer abundance should be reduced before this, and perhaps other invasive shrubs, are managed.

Index terms: Acer saccharum, browse, herbivory, *Lonicera maackii, Odocoileus virginianus*

INTRODUCTION

Positive interactions between plant species (facilitation) have been reported in several systems, particularly in stressful environments (Bertness and Callaway 1994; Holmgren et al. 1997; Callaway et al. 2002). Intense herbivore browse pressure is a stressor that can prompt facilitation between plant species (Bertness and Callaway 1994; Graff et al. 2007) and several studies have revealed reduced impacts on tree seedlings beneath shrubs or small trees, particularly where the latter are chemically or structurally defended (García and Obeso 2003; Bakker et al. 2004; Smit et al. 2007; Gómez-Aparicio et al. 2008; Vandenberghe et al. 2009; Jensen et al. 2012; Perea and Gil 2014).

Although the competitive, negative effects of various invasive shrub species on tree seedlings have been demonstrated (Woods 1993; Merriam and Feil 2002; Fagan and Peart 2004; Frappier et al. 2004; Webster et al. 2006), there has been minimal investigation of facilitative effects. The high densities of ungulates and invasive plants in many parts of the world (Vavra et al. 2007) provide a setting where browse damage to native plants may be mitigated by invasive plants. In much of the United States, white-tailed deer (*Odocoileus virginianus* Zimmerman) are at densities well above historical levels (McCabe and McCabe 1997; McShea 2012). These high deer densities impact plant composition in forests (Russell et al. 2001; Horsley et al. 2003; Côté et al. 2004; Rooney 2009; Frerker et al. 2014), particularly via browse on tree species (Rossell et al. 2005; Bradshaw and Waller 2016).

There is some evidence that deer browse on understory plants is mitigated by the invasive shrub *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), Amur honeysuckle. *Lonicera maackii* is a large shrub with dense foliage that grows to heights of up to 6 m (Luken and Thieret 1996) and is one of several bush honeysuckle species that are invasive in the eastern United States (Webster et al. 2006). This species is native to northeastern Asia (Luken and Thieret 1996) and its invasive range spans the eastern half of the United States; *L. maackii* is considered invasive and regulated in eight of those states (EDDMapS 2015). Negative impacts of *L. maackii* on native biota have been reviewed by McNeish and McEwan (2016). Specific impacts of *L. maackii* on tree regeneration include reduced density and species richness of tree seedlings in under vs. away plots (Collier et al. 2002), reduced densities of seedlings and saplings in invaded vs. uninvaded stands (Hartman and McCarthy 2008), and greater seedling survival in removal plots (Gorchov and Trisel 2003; Hartman and McCarthy 2004; Loomis et al. 2015).

While the browse preference by deer of *L. maackii* is not well studied, its leaves have low palatability for insects (Lieurance and Cipollini 2012, 2013), and the closely related *L. morrowii* A. Gray, also invasive,

is of moderate preference to deer (Averill et al. 2016). Previous studies have suggested that interactions between *L. maackii* and deer may confer protection from browse to plants under the canopy of *L. maackii*. Cipollini et al. (2009) suggested that standing dead *L. maackii* shrubs may provide protection to native herbs from deer. This structural barrier may prevent them from being browsed. Gorchov and Trisel (2003), while testing the effects of *L. maackii* on sugar maple seedlings, found that where these seedlings were accessible to deer, their mass was much greater where *L. maackii* shoots were present. This finding suggests that *L. maackii* may prevent mass loss of sugar maple seedlings to deer herbivory. We are not aware of any investigations of facilitation of tree seedlings by invasive shrubs, although growth and survival of a highly preferred herb, *Uvularia grandiflora* Sm., was enhanced by cover of the invasive biennial *Alliaria petiolata* (M. Bieb.) Cavara and Grande in the presence of deer (Waller and Maas 2013).

We investigated whether *L. maackii* provides a refuge for native tree species from deer browse, allowing tree seedlings to attain greater height and survival. We hypothesized that facilitation (Figure 1), rather than competition, is the dominant interaction between *L. maackii* and seedlings of native trees where deer are abundant.

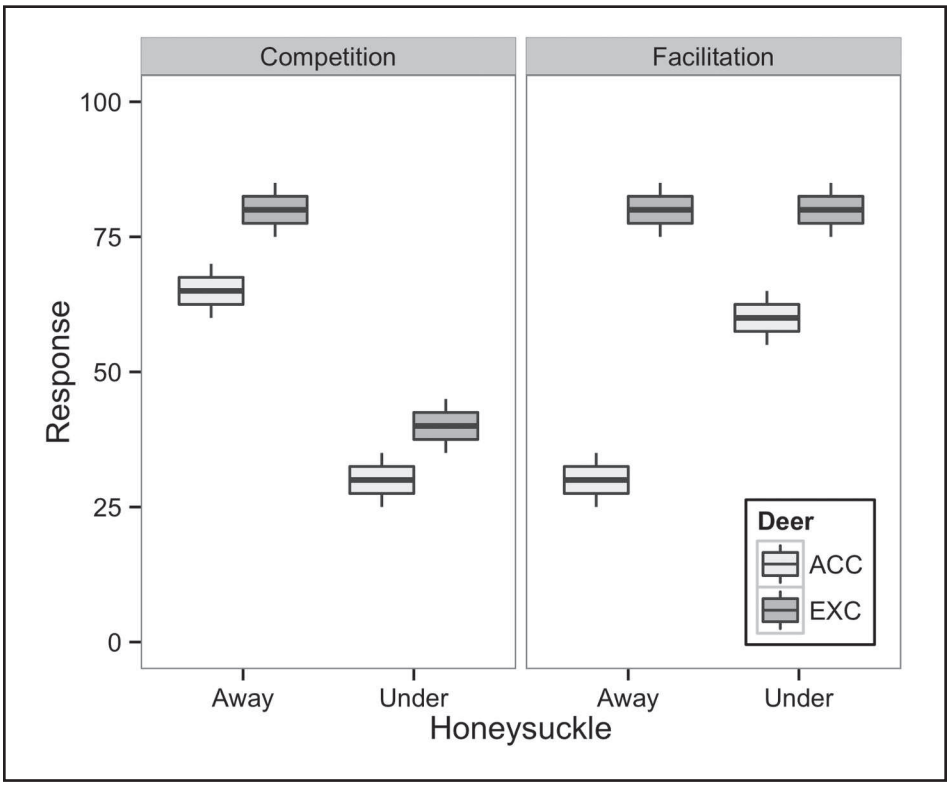

Figure 1. Predictions of tree seedling responses (survival, growth, etc.) based on the hypotheses of competitive or facilitative interactions between *Lonicera maackii* and native tree seedlings under and away from the canopy of *L. maackii* (Honeysuckle) and with (EXC) and without (ACC) fences to exclude deer.

METHODS

Field Methods

We measured the growth and survival of tree seedlings planted under and adjacent to individual *L. maackii* shrubs, with and without deer herbivory (Figure 2). Within the Miami University Natural Areas, in Oxford, Ohio (Butler County), USA (39°29′–39°31′N, 84°42′–84°43′W), we selected two closed-canopy deciduous stands with little anthropogenic disturbance in the past 100 y: Western Woods has tree (≥10 cm dbh) basal area of 24.9 m^2/ha, dominated by *Quercus rubra*, *Fraxinus* spp., *Acer saccharum*, and *Fagus grandifolia* (Gould and Gorchov 2000), while Kramer Woods has 35.1 m^2/ha basal area and is dominated by *A. saccharum*, *Fraxinus americana*,

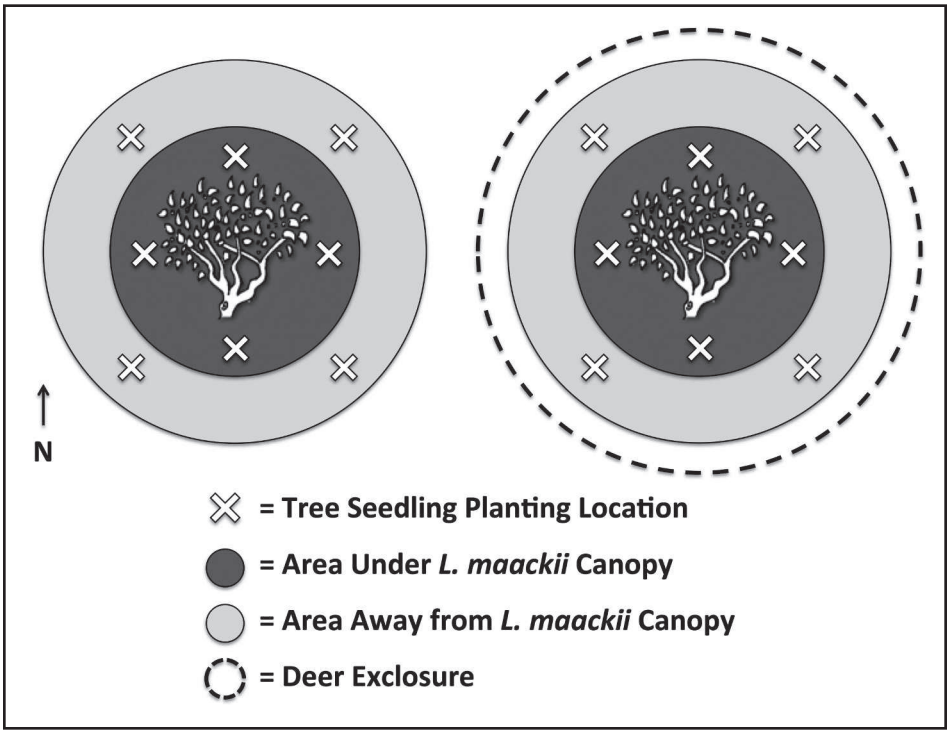

Figure 2. Schematic of study design. Tree seedlings were planted at each of the cardinal directions under the canopy of *Lonicera maackii* and at each of the intercardinal directions 0.5 m outside of the canopy of *L. maackii*. Each *L. maackii* shrub was randomly assigned to have a deer exclosure fence (~1.5 m outside the canopy) or not.

Juglans nigra, and *Liriodendron tulipifera* (Henkin et al. 2013). At each site deer density was higher than the 8 deer/km^2 considered to cause dramatic shifts in forest regeneration (Horsley et al. 2003); it was higher at Western Woods (12.1 deer/km^2 in summer and 23.8 deer/km^2 in winter) than in Kramer Woods (9.9 deer/km^2 in summer and 6.7 deer/km^2 in winter) (estimates by Barrett [2014] based on pellet-based distance sampling [Urbanek et al. 2012]). In each area, we chose ten focal *L. maackii* shrubs that (a) were >2 m tall, (b) had >1 stem, (c) had a canopy that extended down to <2 m from the ground, (d) were isolated from other large *L. maackii* shrubs, (e) were >1 m away from the closest tree, and (f) were >4 m from a trail. Stems of small *L. maackii* plants under the canopy of each focal shrub were cut and painted with Tordon RTU herbicide. In each area, each focal shrub was randomly assigned to be fenced or unfenced. Fenced shrubs were surrounded with 1.25-m tall black plastic mesh fencing, approximately 1 m from the edge of the shrub's canopy (Figure 2). Exclosures were established 5–23 May 2014.

Bare-root tree seedlings of four species were selected; two of very high deer preference (*Quercus alba* L. [white oak] and *Carya ovata* (Mill.) K.Koch [shagbark hickory], hereafter QUAL and CAOV, respectively), one of moderate deer preference (*Acer saccharum* Marshall [sugar maple], hereafter ACSA), and one of low deer preference (*Prunus serotina* Ehrh. [black cherry], hereafter PRSE). These preference rankings were based on Frelich and Lorimer (1985), Strole and Anderson (1992), Horsley et al. (2003), Rooney and Waller (2003), and Wakeland and Swihart (2009). ACSA is considered very shade tolerant (4.76 on a scale of 1–5; Niinemets and Valladares 2006), while the other species are moderately tolerant (QUAL 2.75, CAOV 3.4, PRSE 2.46). CAOV bare-root seedlings were obtained from Musser Forests, Inc. (Indiana, Pennsylvania). PRSE, ACSA, and QUAL bare-root seedlings were obtained from Cold Stream Farm (Free Soil, Michigan). All tree seedlings were 12.5–30.5 cm tall when planted. Tree seedlings were randomly assigned to a cardinal and an intercardinal direction, planting four trees 0.5 m under the canopy of *L. maackii* (cardinal) and four trees 0.5 m outside of the canopy of *L. maackii* (intercardinal; Figure 2). Seedlings were planted 31 May–6 June 2014, and treated with Soil Moist water storing polymer root gel (Musser Forests, Inc.) at the time of planting, to reduce transplant shock.

From June 2014 to June 2015, seedlings were measured monthly during the growing season for survival, height, browse damage, and number of leaves, and once every 2–3 mo during the winter for height and browse. Although some seedlings experienced more than one browse event, we only distinguished "browsed" vs. "unbrowsed" seedlings in analyses. Most, if not all, browse events were attributable to deer, as woody twigs showed the shredding characteristic of deer browse (Swift and Gross 2008), although some browse events consumed only nonwoody tissue. Surviving seedlings were excavated at the end of June 2015, separated into roots and shoots, washed, dried to constant mass at 70 °C, and weighed.

Data Analysis

PRSE seedlings were excluded from all analyses due to high initial mortality (12/40 seedlings were never alive over the course of the study, 30% mortality) and complete mortality by June 2015. In addition, seedlings that were dead at the first census (leafless 2 wk after planting and never leafing out) were excluded from all analyses, as mortality was attributed to transplant shock.

For all other species, tree seedling survival was assessed via survival analysis (Fan et al. 2006). All seedlings surviving at the termination of the study were right-censored. For each species, χ^2 values were calculated from observed deaths and Kaplan–Meier estimates of predicted survival, and differences between treatments and between sites, were calculated using the Peto and Peto modification of the Gehan–Wilcoxon test (Pyke and Thompson 1986; Rich et al. 2010).

Fences were effective in preventing browse, so browse status was only analyzed for seedlings in unfenced plots, using a split-plot, generalized linear mixed-effect logistic regression model. A seedling was scored as "browsed" if it showed evidence of browse, regardless of whether it survived the full year. The model was specified with site and location under or away from the canopy of *L. maackii*as as fixed effects and plot as a random effect. Significance was determined by maximum likelihood (Laplace Approximation).

Final size measurements (leaf count, change in height, root mass, shoot mass, and root:shoot ratio) were analyzed using split-plot, generalized linear mixed-effect models, with fence treatment and location under or away from the canopy of *L. maackii* as fixed effects and site and plot as random effects. Significance was determined by maximum likelihood (Laplace Approximation). These analyses excluded seedlings that died during the one-year experiment. The model for leaf count was a Poisson regression (i.e., leaf count data were fit with a Poisson distribution).

All analyses were completed in R version 3.1.2 (R Core Team 2014) using the nlme (change in height, root mass, shoot mass, and root:shoot ratio; Pinheiro et al. 2014), lme4 (browse status and final leaf count; Bates et al. 2014), and survival (survival analyses; Therneau and Grambsch 2000; Therneau 2015) packages.

RESULTS

For survival and final leaf count of ACSA there were significant interactions of fence treatment and position under shrubs that were consistent with the predictions of facilitation. For the other two tree species, there were no significant treatment effects that provided evidence for facilitation or competition.

Survival

Survival of ACSA seedlings was higher where deer were excluded (Table 1, Figure 3). There was no direct effect of site (Kramer Woods or Western Woods) or position (under or away from the canopy of *L. maackii*), but there was a significant

Table 1. Results of survival analysis for seedlings of *A. saccharum* (ACSA), *Carya ovata* (CAOV), and *Quercus alba* (QUAL). "Deer" refers to fence treatment (deer access or excluded), "Honeysuckle" refers to position under or away from the *L. maackii* shrub. χ^2 values were calculated from observed survival and Kaplan–Meier estimates of predicted survival, and differences between treatments were calculated using the Peto and Peto modification of the Gehan–Wilcoxon test. Significant effects are bolded.

Species	Treatment	χ^2	df	*P*
ACSA	**Deer**	**4.2**	**1**	**0.041**
	Honeysuckle	0.7	1	0.409
	Deer:Honeysuckle	**12.7**	**3**	**0.005**
	Site	1.1	1	0.289
CAOV	Deer	2.2	1	0.137
	Honeysuckle	0.7	1	0.405
	Deer:Honeysuckle	3.2	3	0.365
	Site	0.1	1	0.751
QUAL	Deer	0	1	0.971
	Honeysuckle	2.1	1	0.152
	Deer:Honeysuckle	2.1	3	0.561
	Site	2.1	1	0.152

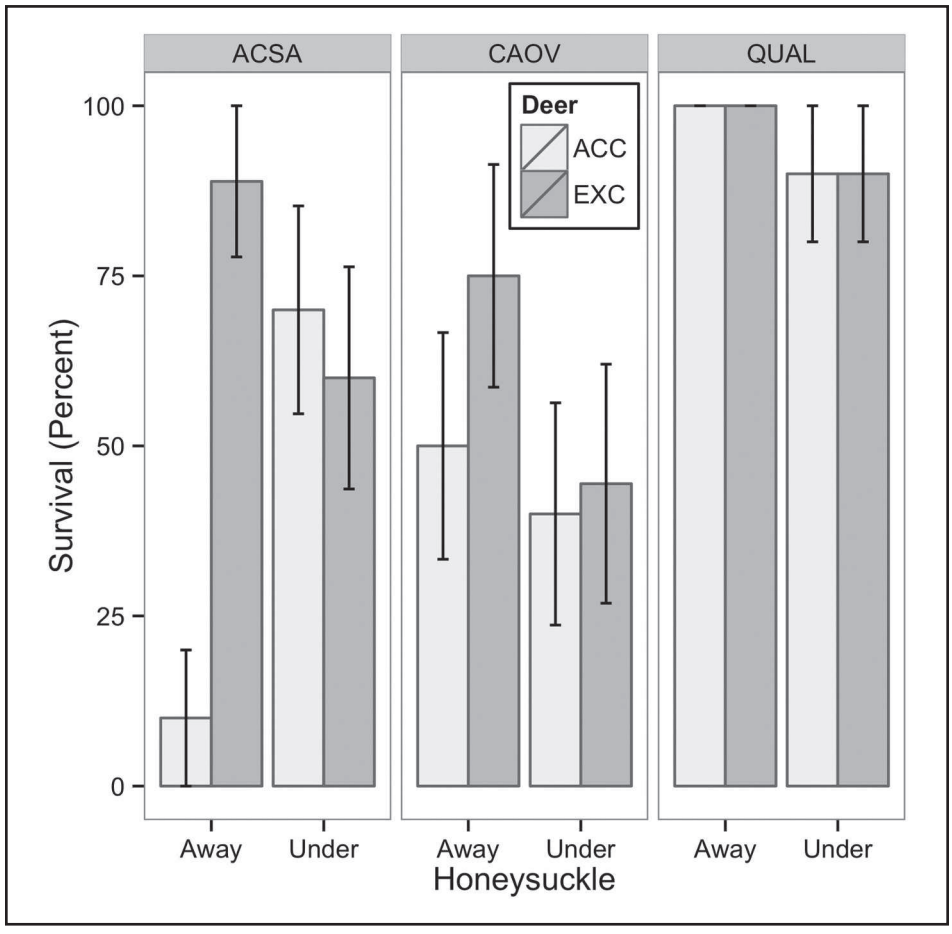

Figure 3. Percent survival (± SE) of *Acer saccharum* (ACSA), *Carya ovata* (CAOV), and *Quercus alba* (QUAL) seedlings planted under or away from the canopy of *L. maackii* and with (EXC) and without (ACC) fences to exclude deer.

interaction of fence treatment and position (Table 1): in unfenced plots, survival was much higher under, rather than away from, the canopy of *L. maackii* (Figure 3). Survival of CAOV and QUAL seedlings was not affected by deer exclosure, position, or site and there were no interactive effects (Table 1, Figure 3).

Browse Status

Exclosures were effective in preventing browse. Considering all seedlings planted in areas accessible to deer, browse was evident on 90% of QUAL, 65% of ACSA, and 55% of CAOV seedlings. There were no significant effects of site or position under or away from *L. maackii* on browse status of ACSA or CAOV seedlings (Peebles-Spencer 2016 table 3A). The effects of site and position on browse status was not tested for QUAL, as all but two of the seedlings were browsed.

Growth, Size, and Root:Shoot Ratio

The number of leaves on surviving ACSA seedlings was higher under *L. maackii* compared to away from *L. maackii* and higher in fenced than unfenced plots (Figure 4, Table 2). There was an interaction between position and fence treatment: ACSA seedlings planted away from *L. maackii* had fewer leaves in areas accessible to deer compared to fenced areas, but for seedlings planted under honeysuckle there was no difference in leaf count between areas of deer access and deer exclosure (Figure 4, Table 2). In addition, there was a significant effect of site on ACSA leaf count ($z = 3.769$, $P = 0.0002$), with seedlings in Western Woods averaging more leaves than seedlings in Kramer Woods. Final leaf count of CAOV and QUAL seedlings did not respond to deer exclosure, position under or away from *L. maackii*, or site, and there were no interactive effects (Table 2, Figure 4).

Mean height of surviving QUAL seedlings declined over the one-year study, with greater loss of height in areas accessible to deer (−6.8 ± 2.0 cm) than areas inside exclosures (−0.2 ± 1.7 cm; mean ± SE) ($F_{1,17} = 6.3315$, $P = 0.022$; Table 3). Deer exclosure had no effect on the change

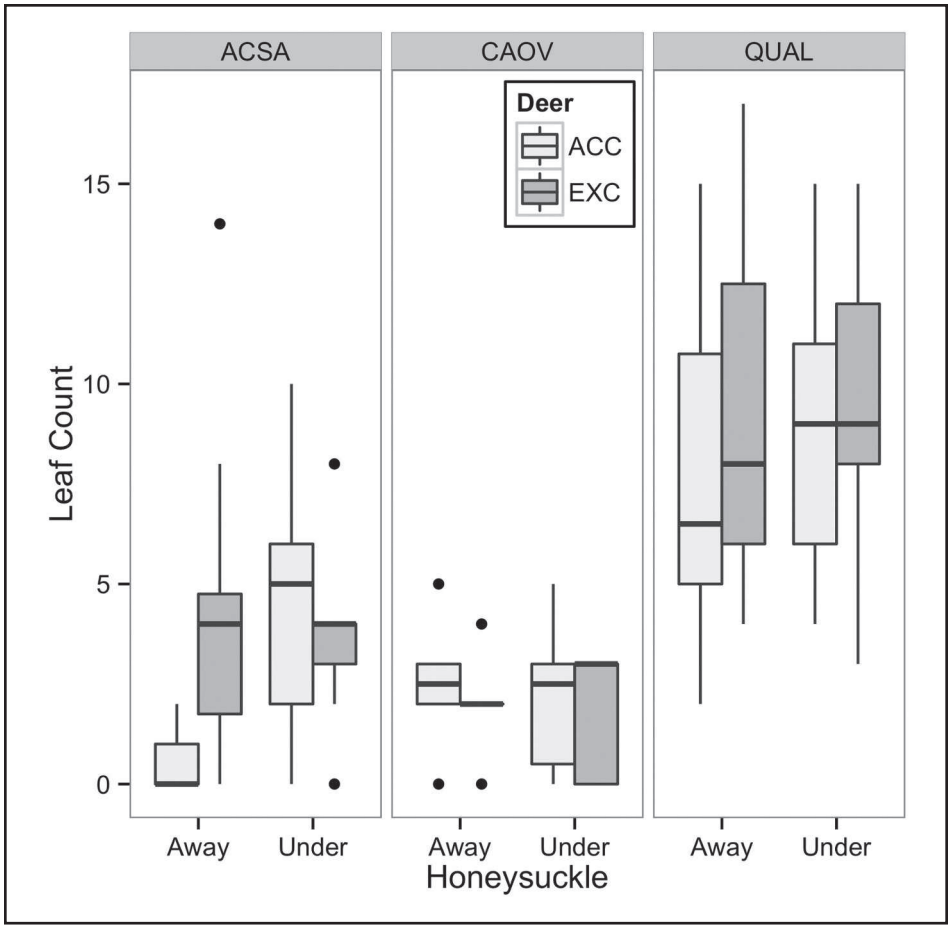

Figure 4. Final leaf count of surviving *Acer saccharum* (ACSA), *Carya ovata* (CAOV), and *Quercus alba* (QUAL) seedlings planted under or away from the canopy of *L. maackii* and with (EXC) and without (ACC) fences to exclude deer.

in height of surviving ACSA or CAOV seedlings. Additionally, there was no significant effect of position under or away from *L. maackii*, site, or the interaction between deer exclosure and *L. maackii,* on the change in height of QUAL, ACSA, or CAOV seedlings (Table 3).

Root mass and shoot mass of ACSA, CAOV, and QUAL seedlings did not respond to deer exclosures or position, and there were no significant interactive effects (Table 3). There was an effect of site on ACSA root mass ($F_{1,16}$ = 5.7486, P = 0.029) and shoot mass ($F_{1,16}$ = 4.8638, P = 0.042), with greater root and shoot mass in Western Woods than in Kramer Woods. There were no site effects on CAOV or QUAL root or shoot mass.

Root:shoot ratio of QUAL seedlings was affected by deer exclosure ($F_{1,17}$ = 4.5570, P = 0.048), with greater root:shoot ratio in areas accessible to deer (4.19 ± 0.55, mean ± SE) than areas inside exclosures (2.84 ± 0.21; Table 3). There was also a trend for greater root:shoot ratio away from *L. maackii* (4.02 ± 0.55) compared to under *L. maackii* (2.96 ± 0.19). However, there was no interaction between deer and *L. maackii* treatments, nor of site, on QUAL root:shoot ratio. Root:shoot ratio of ACSA and CAOV seedlings did not respond to site, deer exclosure, or position under or away from *L. maackii*, and there were no interactive effects (Table 3).

Table 2. Significance of treatment effects on leaf count of surviving seedlings of each species. Significance based on a split-plot, generalized linear mixed-effect model, modified for count data with a Poisson distribution. Treatments as in Table 1. Significance of effects were determined by maximum likelihood (Laplace Approximation). Significant effects are bolded.

Response	Species	Treatment	Estimate	SE	z	Pr(>|z|)
Leaf Count	ACSA					
		Site	**1.035**	**0.275**	**3.7690**	**0.0002**
		Deer	**1.620**	**0.752**	**2.1560**	**0.0311**
		Honeysuckle	**1.527**	**0.747**	**2.0440**	**0.0409**
		Deer*Honeysuckle	**−1.671**	**0.796**	**−2.1000**	**0.0357**
	CAOV					
		Site	−0.243	0.302	−0.8040	0.4214
		Deer	−0.229	0.300	−0.7640	0.4446
		Honeysuckle	−0.117	0.281	−0.4170	0.6766
	QUAL					
		Site	0.216	0.161	1.3420	0.1800
		Deer	0.173	0.160	1.0810	0.2790
		Honeysuckle	0.061	0.111	0.5490	0.5830

Table 3. Results of split-plot, generalized linear mixed-effects models of treatment effects on four size responses of surviving seedlings of each species. Treatments as in Table 1. Significant effects are bolded.

Response	Species	Treatment	df	den df	*F*	*P*
Change in height	ACSA					
		Site	1	16	1.4470	0.246
		Deer	1	16	0.3228	0.578
		Honeysuckle	1	8	0.1190	0.739
	CAOV					
		Site	1	15	3.2739	0.090
		Deer	1	15	0.0182	0.894
		Honeysuckle	1	7	0.1388	0.720
	QUAL					
		Site	1	17	0.6607	0.428
		Deer	**1**	**17**	**6.3314**	**0.022**
		Honeysuckle	1	17	1.0680	0.316
Root mass	ACSA					
		Site	**1**	**16**	**5.7486**	**0.029**
		Deer	1	16	2.2045	0.157
		Honeysuckle	1	8	1.0127	0.344
	CAOV					
		Site	1	15	1.1387	0.303
		Deer	1	15	3.0003	0.104
		Honeysuckle	1	7	3.2736	0.113
	QUAL					
		Site	1	17	0.5638	0.463
		Deer	1	17	0.1000	0.756
		Honeysuckle	1	17	0.0453	0.834
Shoot mass	ACSA					
		Site	**1**	**16**	**4.8638**	**0.042**
		Deer	1	16	2.1826	0.159
		Honeysuckle	1	8	0.0584	0.815
	CAOV					
		Site	1	15	4.2326	0.058
		Deer	1	15	2.3264	0.148
		Honeysuckle	1	7	0.0036	0.954
	QUAL					
		Site	1	17	1.8758	0.189
		Deer	1	17	1.0574	0.318
		Honeysuckle	1	17	1.3003	0.270
Root:shoot ratio	ACSA					
		Site	1	16	1.4318	0.249
		Deer	1	16	0.0634	0.804
		Honeysuckle	1	8	0.7902	0.400
	CAOV					
		Site	1	15	2.5214	0.133
		Deer	1	15	0.0798	0.781
		Honeysuckle	1	7	3.8168	0.092
	QUAL					
		Site	1	17	0.0413	0.841
		Deer	**1**	**17**	**4.5570**	**0.048**
		Honeysuckle	1	17	3.7448	0.070

DISCUSSION

Facilitation

Evidence for facilitation of tree seedlings by *L. maackii* would be an interaction between the effects of position under or away from this shrub's canopy and exposure to deer on tree seedling responses, where in the presence of deer, seedlings performed better under shrubs (Figure 1). Both survival and leaf count of ACSA seedlings showed this pattern. ACSA seedlings planted away from *L. maackii* had much lower survival, and lower final leaf counts on survivors, in areas accessible to deer compared to areas inside exclosures, but seedlings planted under *L. maackii* showed no difference in survival or leaf count between areas of deer access and deer exclosure. Thus, for ACSA, location under the canopy of *L. maackii* mitigates the large, negative effect of exposure to deer browse, facilitating survival and growth. This facilitative effect was not evident in our analysis of browse incidence—in unfenced plots, 80% of ACSA seedlings under shrubs were browsed, compared to only 50% of those away from shrubs. We suspect that seedlings under shrubs were browsed fewer times, on average, and this accounted for their greater survival and final size.

Facilitation was not evident for either of the other two tree species, for which we found no evidence that *L. maackii* deterred deer browse in unfenced plots. While the proportion of CAOV seedlings with evidence of browse was similar to that for ACSA, it was similar under *L. maackii* (50%) as outside of this shrub's canopy (60%). For QUAL, nearly all seedlings in plots exposed to deer were browsed, regardless of position. This was likely due to the high preference for QUAL by deer (Strole and Anderson 1992; Wakeland and Swihart 2009). Despite this high browse, 90% of QUAL seedlings in unfenced plots survived the year. High, but nonlethal, browse on QUAL seedlings was presumably the cause of greater height loss for seedlings exposed to deer, and *L. maackii* branches failed to mitigate this impact. This shoot loss partly accounts for the higher root:shoot ratio of QUAL seedlings exposed to deer, as these seedlings tended to have less shoot mass than those planted where deer were excluded (1.19 ± 0.14 g vs. 1.44 ± 0.14 g). However, QUAL seedlings accessible to deer also tended to have greater root mass (4.39 ± 0.49 g vs. 4.06 ± 0.48 g) than seedlings inside exclosures.

Others have also found this pattern of very high survival of *Quercus* species in response to browse (Jensen et al. 2012; Kern et al. 2012). Our study may have been limited in its ability to detect changes in QUAL survival by its one-year duration, as Jensen et al. (2012) found that effects of deer browse on survival of *Quercus* species was not manifest until the third year of browse exposure.

Competition

Competition would be indicated by a significant negative effect on tree seedling responses where seedlings were planted under *L. maackii* (Figure 1), a result we did not obtain for any growth response for any species. The significant effect of *L. maackii* on ACSA leaf number was in the opposite direction, indicating a growth response to shading. Similarly, QUAL seedlings under the canopy of *L. maackii* tended to have lower root:shoot ratio, indicating greater relative allocation to shoot growth, a typical response to light limitation. Our power to detect competition may have been hampered by our removal of small *L. maackii* individuals in the experimental set-up or our exclusion of size measurements from seedlings that died. Additionally, the duration of our study (1 y) may have been too short to reveal competitive effects of *L. maackii* that have been documented in previous studies. Hartman and McCarthy (2004) found removal of *L. maackii* enhanced seedling survival over 3 y for all six tree species planted, regardless of deer access. Similarly, Gorchov and Trisel (2003) found removal of *L. maackii* shoots resulted in greater survival of *Acer saccharum* and *Fraxinus americana* L. seedlings and a trend for increased survival of *Quercus rubra* after 2 y. Loomis et al. (2015) found higher survival over 2 y of naturally occurring *A. saccharum* seedlings in plots where *L. maackii* was removed.

The only significant effects of site were on size (leaf count, root mass, and shoot mass) of ACSA. All were higher at Western Woods, which we suggest was due not to the higher deer density at this site, but to less light interception by the canopy, as this site had lower canopy basal area.

CONCLUSIONS

Our hypothesis that facilitation, rather than competition, dominates the interaction between *L. maackii* and tree seedlings where deer are abundant, was supported for the one very shade-tolerant tree species (ACSA), but not for the two species with moderate tolerance. This facilitation by *L. maackii* on ACSA growth and survival was observed after only 1 y, suggesting that ACSA may benefit greatly over several years. We expect this benefit would result in greater regeneration and recruitment into the canopy, as differential survivorship of canopy tree seedlings, even at low deer densities, may affect the future composition of the forest canopy (Aronson and Handel 2011). However, our study was limited to two sites and a single year, and the relative importance of competition and facilitation could shift over time or vary among sites. The facilitation by *L. maackii* that we documented provides evidence that, at least for some shade-tolerant species, the competitive effects on tree seedling growth documented in other studies (reviewed above) is ameliorated by mitigation of the negative effects of browse in sites of high deer density.

It is compelling to investigate whether other invasive shrub species similarly protect seedlings from deer browse. In forests with dense deer populations, removal of *L. maackii* or other invasive shrubs that have a protective effect would be expected to reduce regeneration of ACSA and other shade-tolerant trees of moderate browse preference, while not greatly impacting other species, if their response is similar to those found for QUAL and CAOV. If substantiated further, these findings indicate that for natural areas impacted by both overabundant deer and invasive

shrubs, deer density should be reduced first, followed by removal of invasive shrubs, at least if regeneration of trees such as ACSA is a management goal. However, in sites where invasive shrubs are not yet abundant, there is no reason to postpone their removal.

ACKNOWLEDGMENTS

We thank Miami University Natural Areas Committee for permission to carry out the field work and R. Spencer, D. Peebles, G. Peebles, P. Peebles, B. Hoven, G. Dienno, P. Garrett, A. Bowen, K. Martinod, A. (Klinczar) Driscoll, P. Guiden, M. Hassett, J. Samu, and C. Haffey for assistance in the field. We thank Hank Stevens and Mike Hughes for assistance with statistical analyses, and Tom Crist, Hank Stevens, Melany Fisk, Jim Hickey, and four anonymous reviewers for valuable input on earlier drafts of this manuscript. This study was funded by grants from Sigma Xi and Miami University (Academic Challenge program, Botany Department).

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