Effects of the Exotic Invasive Shrub Lonicera maackii on the Survival and Fecundity of Three Species of Native Annuals

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ABSTRACT.—Negative effects on native plant populations are often attributed to invasions by exotic plants, but experimental evidence is lacking to support many of these claims. Lonicera maackii, an exotic shrub with long leaf phenology, has become naturalized throughout the eastern United States. This study investigated the effects of L. maackii on demography of Galium aparine, Impatiens pallida and Pilea pumila, native annual herbs in differing phenological categories. These interactions were examined in two Ohio forest stands. One stand has a history of logging, burning and grazing and a higher L. maackii density, whereas the other stand has little anthropogenic disturbance and a lower L. maackii density. Three types of experimental plots were established: L. maackii removal, L. maackii present and, at the less disturbed stand, L. maackii absent. Seedlings of the annuals were transplanted and monitored for 1 y for survival to reproductive age and fecundity.

In the more disturbed stand, survival of *Galium aparine* and *Impatiens pallida* and fecundity of all three species were significantly greater in the removal treatment than where *Lonicera maackii* was present. In the less disturbed stand there was no treatment effect on survival, but fecundity of all annuals was greater in the removal treatment than where *L. maackii* was present. Also, fecundity of *I. pallida* and *Pilea pumila* was greater where *L. maackii* was absent than where it was present. At both sites fitness (estimated as the product of survival and fecundity) was highest for each species in the removal treatment and lowest where *L. maackii* was present.

These results demonstrate direct effects of the invasive shrub *Lonicera maackii* on populations of annuals. They suggest that other annuals, particularly those that are shade-intolerant or photosynthesize only in the early spring, will decline in the presence of shrubs with early leaf expansion.

INTRODUCTION

Previous studies have described impacts of exotic plant species on native plant populations (Midgley et al., 1992; Dillenburg et al., 1993; Equihua and Usher, 1993), communities (Braithwaite et al., 1989; Hobbs and Atkins, 1991; Myster and Pickett, 1992; Webb and Kaunzinger, 1993), ecosystems (Vitousek, 1990), landscapes (Bock and Bock, 1992) and the global environment (Vitousek et al., 1996). However, much evidence of these effects is based on correlations observed within 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 that have not only led to the establishment of exotics, but also have negatively affected native plant populations. Also, they do not separate: (1) the effects of the invasive species in suppressing native species from (2) the occupation by invasives of sites from which native species are absent. There is a need for experimental research to determine direct ecological effects of specific invasive plant species on native plant populations.

We used field experiments to test the hypothesis that *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), Amur honeysuckle, has a negative effect on the demography of native

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herbs. Lonicera maackii was introduced from northeast Asia to North America in 1896 for ornamental uses (Luken and Thieret, 1995) and has subsequently escaped into native pastures and forests (Luken, 1988). It is naturalized in at least 24 eastern states in the U.S. and in Ontario, Canada (Trisel and Gorchov, 1994). In Ohio, *L. maackii* spread from Hamilton County (Braun, 1961) to 34 other counties (Trisel, 1997) and has invaded most of the secondary forests near Oxford, Ohio (Hutchinson and Vankat, 1997). Lonicera maackii has low levels of herbivory (Trisel and Gorchov, 1994), bird-dispersed fruits (Ingold and Craycraft, 1983) and long leaf phenology (Trisel and Gorchov, 1994) which are common characteristics of highly invasive species.

Lonicera maackii density was negatively correlated with herb cover, tree seedling density and species richness of tree seedlings among woodlots in southwest Ohio (Hutchinson and Vankat, 1997). Within a single woodlot, L. maackii basal area was negatively correlated with native shrub species richness, native shrub basal area and sapling density of Acer saccharum, the canopy dominant (Medley, 1997). Similarly, negative correlations were found between density of the congener Lonicera tatarica and native herb species richness and cover and tree seedling density (Woods, 1993). The removal of L. maackii was correlated with an increase in herb density in Northern Kentucky (Luken et al., 1997).

Based on these studies we predicted that the presence of Lonicera maackii would reduce the survival and fecundity of three native forest annuals, Galium aparine L. (Rubiaceae), Impatiens pallida Nutt. (Balsaminaceae) and Pilea pumila L. Gray. (Urticaceae). These demographic parameters were measured at two sites, with contrasting anthropogenic disturbance histories and L. maackii densities, over one field season. The annuals have different leaf phenologies and levels of shade tolerance. We predicted that annuals that are more shade intolerant or with early phenology would have greatest reductions in survival and fecundity in the presence of L. maackii, due to its early leaf expansion (Trisel and Gorchov, 1994). We predicted that annuals in the more disturbed site would have greatest reductions in survival and fecundity in the presence of L. maackii. At one site, we also tested whether reductions were due to residual effects of past occupancy by L. maackii or only to effects in the current growing season.

METHODS

Sites.—This study was conducted at two sites, located near Oxford, in SW Ohio (39°30'N, 84°45'W). Gregg's Woodlot, an isolated 7 ha anthropogenically disturbed woodlot, has a Lonicera maackii density of 0.7 shrubs/m² and tree (≥10 cm dbh) density of 576/ha and basal area (BA) of 21.4/m². Trees with the highest importance value (relative density + relative BA) are Carya ovata, C. laciniosa, Fraxinus spp. and Quercus rubra. Trees were selectively cut in approximately 1900, the woodlot was regularly burned and grazed by cattle into the 1950s, but has been unmanaged since then (T. Gregg, pers. comm.). Western Woods (Miami University Natural Areas) is a 40 ha deciduous forest preserve with relatively little anthropogenic disturbance over the past 80 y. It has a L. maackii density of 0.3 shrubs/m² and tree (≥10 cm dbh) density of 383/ha and BA of 24.9 m²/ha. Trees with the highest importance value (relative density + relative BA) are Quercus rubra, Fraxinus spp., Acer saccharum and Fagus grandifolia. This BA is close to the 32.0 m²/ha reported for old-growth beech-maple forest at nearby Hueston Woods Nature Preserve (Runkle *et al.*, 1984). At both sites there was very low density of shrubs other than L. maackii (pers. obs.).

Experimental methods.—Three treatments were used in this experiment to test the effects of Lonicera maackii on the survival and fecundity of native annuals. The L. maackii present treatment was the reference used to study the effects of removing the shrub in the L. maackii removal treatment. The L. maackii absent treatment, which contained no L. maackii

shrubs before to and throughout the experiment, was another reference treatment. Comparing the demography of the annuals in this treatment with that in the *L. maackii* present treatment provided a second measure of the effect of *L. maackii*; however, site factors could also contribute to differences. Comparing the *L. maackii* removal treatment to the *L. maackii* absent treatment enabled us to make inferences on the residual effects due to past occupancy by *L. maackii*, via mechanisms such as allelopathy, alteration of soil nutrients and suppression of native perennial herbs. No shrubs other than *L. maackii* were present in any of the plots.

At Gregg's Woodlot we established 30 blocks (replicates), each consisting of one plot where *Lonicera maackii* was present and one plot from which it had been removed. The circular plots (radius = 2 m) were selected in November 1994, from 60 *L. maackii* present plots and 60 *L. maackii* stem removal plots established in 1992. At that time each was centered on a *L. maackii* shrub at least 1.5 m tall and >2 m from any tree >15 cm dbh (Trisel, 1997). The plots in each block were selected to maximize proximity (2–10 m apart), similarity of tree canopy cover, slope and drainage. All *L. maackii* stems rooted inside the removal plots were cut to 25 cm height in May 1992 and branches of *L. maackii* overhanging these plots were trimmed during the 1992–1995 growing seasons, whereas *L. maackii* present plots were untreated. The absent treatment was not used at Gregg's Woodlot because the three additional years of stem removal reduced possible residual effects of past *L. maackii* occupancy and there were few areas in which *L. maackii* was not present.

At Western Woods in November 1994, we established 20 blocks (replicates), each consisting of one plot in which Lonicera maackii was present, one plot from which L. maackii was removed and one plot in which L. maackii was absent. We used smaller radius plots (1.5 m), due to the difficulty of finding 2 m radius plots without L. maackii in close proximity to areas that contained the shrub. The plots within each block were 2–10 m apart to maximize similarity in tree canopy cover, slope and drainage. Within each block two plots with at least two L. maackii shrubs >1 m tall were located and then randomly assigned to the present or removal treatments. Lonicera maackii shrubs within the removal plots were eliminated by excavating their meristematic burls and L. maackii branches overhanging these plots were trimmed throughout the experiment. The plots in the absent treatment were unmodified.

Within each circular plot, annuals were planted in an area 83 cm \times 60 cm (long axis east-west) located to the north of the plot center. This area had the resident herb and seedling competitors removed every 6–10 d through the 1995 field season. Poultry-wire structures (83 cm \times 60 cm \times 60 cm) were constructed around and over the planting area to exclude large mammalian herbivores. A Latin Squares randomization scheme was used to determine the planting locations of each seedling within each planting area.

Three species of annual herbs were selected based on phenology, availability of seeds and seedlings and occurrence at the study sites. Seeds of the shade-intolerant (Bain and Attridge, 1988), early season (Struik, 1965) annual *Galium aparine* were collected from the Bachelor Reserve (Miami University Natural Areas) during the summer of 1994. Although some authors consider *G. aparine* native to Europe and invasive in North America (Hultén and Fries, 1986), others conclude that both native and invasive populations occur in North America, with forest populations likely to be native (Malik and Vanden Born, 1987). Although typically a winter annual in the study area with germination in the autumn (Struik, 1965; Malik and Vanden Born, 1987), spring-germinating cohorts occur in some populations (Kutsch and Kappen 1991). Seeds of the semi-shade-tolerant (Struik, 1965) mid-season (Cid-Benevento and Schaal, 1986) annual *Impatiens pallida* were collected from the Bachelor Reserve during the late summer of 1994. Seeds of the shade-tolerant late season (Cid-

Benevento and Werner, 1986) annual *Pilea pumila* were collected during the early autumn of 1994.

Seeds of *Galium aparine* were germinated following the methods of Sjostedt (1959) in early March of 1995. Seeds of *Impatiens pallida* were germinated following the methods of Nozzolillo and Thie (1983) in late March 1995. Attempts made to germinate seeds of *Pilea pumila* in February of 1995 were unsuccessful.

On 15 April 1995, 480 similar-sized seedlings of *Galium aparine* were selected and transplanted into the 120 treatment plots (4 per plot). A fungal outbreak in growth chambers reduced the number of usable *Impatiens pallida* seedlings to 283, so 120 seedlings (2/plot) were planted at Gregg's Woodlot and 163 seedlings (3/plot for 43 plots and 2/plot for 17 plots) were planted at Western Woods on 13 May 1995. Seedlings of *Pilea pumila* were collected from a natural population in a deciduous forest in the Bachelor Reserve, Oxford, OH. Four similar-sized seedlings were transplanted into each of the 120 treatment plots on 9 June 1995.

Herb seedlings were measured for initial stem length before transplanting. Thereafter, the herbs were surveyed every 6–10 d for survival, presence of flowers and measures of fecundity. An individual of *Galium aparine* or *Impatiens pallida* was considered to have survived to reproduction if it bore any fruits. An individual of *Pilea pumila* was considered to have survived to reproduction if it was alive on day 82 of the experiment (31 August 1995), the date by which most individuals had produced male inflorescences. This date was chosen because survival of *P. pumila* to the infructescence harvest date was fairly low and some individuals produced infructescences and senesced before that date. The number of individuals that flowered, but did not survive to the harvest date, was not significantly different between treatments at Gregg's Woodlot (df = 1, Log-likelihood contingency test G = 0.446, P = 0.504) nor among treatments Western Woods (df = 2, G = 2.969, P = 0.227).

Fecundity was quantified only for individuals surviving to reproduction. For Galium aparine and Impatiens pallida we counted the number of seeds on each plant at each survey, harvested seeds as they matured and recorded the dry mass of seeds of each individual. Since the seeds of Pilea pumila are extremely small and their maturation is relatively synchronous, the number of nodes with infructescences of each individual were counted and then harvested 120 d after planting (8 October 1995) and infructescence mass was determined. Linear regression between the mass of harvested infructescences and the mass of seeds within infructescences demonstrated that infructescence mass was a good predictor of seed mass (seed mass (g) = $0.60 \times infructescence mass (g) - 0.001g$, $R^2 = 0.89$, n =20, P = 0.0001). Here we only present the most reliable of our estimates of individual fecundity. We chose the maximum number of seeds (within one-seeded fruits) observed on a single survey date for G. aparine since some fruits dehisced before harvest. We chose the total number of seeds harvested for I. pallida and the mass of harvested infructescence for P. pumila. Other estimates of fecundity of each species gave quantitatively similar results for all three species (Gould, 1996).

Fitness (expressed as seeds per surviving seedling) of each species in each treatment was estimated by multiplying the proportion of seedlings surviving to reproductive age by the average fecundity of these survivors. Since fecundity of *Pilea pumila* was estimated as the mass of harvested infructescences, we converted this measurement to an estimate of number of seeds for the calculation of fitness. This was accomplished by multiplying the mass of harvested infructescences by the slope of the regression of seed mass on infructescence mass (0.60) and the constant 10,000 seeds per gram (Cid-Benevento, 1986).

Analysis.—These data did not conform to the assumptions of normal theory statistics (*i.e.*, normal distribution, linear response, etc.), so they were analyzed with generalized

linear models (McCullagh and Nelder, 1989; Dobson, 1990) (see Equihua and Usher, 1993) for application in plant ecology) using SAS Version 6.10. Each response variable (*i.e.*, survival and fecundity) for each species at each site was analyzed separately. Generalized linear models use a linear predictor equation to determine the effect of experimental treatments on response variables. For each data set the distribution of the response variable was determined by producing a frequency histogram and the link function (*i.e.*, transformation) was determined by examining the relationship between the mean and the standard deviation, sorted by treatment and block (McCullagh and Nelder, 1989; Dobson, 1990). The binomial distribution and the logit link function were used to create a logistic regression model to test the effect of treatment on survival of each species. This model appropriately tests treatment effects on categorical data. The Poisson distribution and logarithmic link function were used to create a log-linear model to test the effect of treatment on fecundity for Galium aparine and Impatiens pallida. This model appropriately tests treatment effect on these count variables. The normal distribution and the logarithmic link function were used to test treatment effect on fecundity for Pilea pumila. This model appropriately tests treatment effect on this continuous variable (McCullagh and Nelder, 1989; Dobson, 1990).

Our predictor equations included the parameters: initial length of each experimental seedling (continuous), block number (categorical) and treatment (categorical), in that order:

Response \times Link = f(Initial length) + f(Block) + f(Treatment)

Initial length of the seedlings was included to account for possible initial size effects on survival or fecundity and block number was included to account for spatial variability within each site. Hence, the effect of treatment was detected taking into account possible effects of block and initial length. In some models of survival there was not enough variability of response (*i.e.*, survival was high) for the inclusion of block number and that parameter was removed. Also, there was over dispersion (i.e., greater range in response than expected for the model) of the data to specific models, which resulted in underestimation of the standard errors of the parameter estimates. This was corrected by changing the scaling of the variance-covariance matrix of the parameters from one to the square root of the deviance divided by the degrees of freedom, which did not affect parameter estimates but did change the standard error estimates, maximum likelihood ratios and hypothesis tests (McCullagh and Nelder, 1989; Dobson, 1990). Inference of the significance of each parameter in the model (initial length, block and treatment) was made by determining the Likelihood Ratio statistic. This is the difference in deviance between the maximum likelihood estimate of the parameter effect under the null hypothesis, as calculated by asymptotic chi-square tests and presented in an analysis of deviance table (McCullagh and Nelder, 1989; Dobson, 1990). Also, contrast statements were used to determine pair-wise differences among the three treatments at Western Woods using the same asymptotic chi-square test.

RESULTS

Survival.—Survival to reproductive age of Galium aparine was significantly higher in the Lonicera maackii removal treatment (87%) than the L. maackii present treatment (79%) at Gregg's Woodlot, but there was no significant effect at Western Woods (present = 91%, absent = 92%, removal = 94%) (Table 1). Initial length had a significant effect on survival at both sites (Table 1), with survivors being shorter (Gregg's: mean = 11.1 cm, Western: mean = 12.2 cm) than nonsurvivors (Gregg's: = 12.1 cm, Western: mean = 13.7).

Significantly more individuals of *Impatiens pallida* survived to reproductive age in the *Lonicera maackii* removal treatment (72%) than in the *L. maackii* present treatment (43%)

parameter and chi the bottom up. Si significant in the I	l-square and gnificance of presence of tl	Pr > chi each par he effects	are the tes ameter is () of block a	st statistic an detected, wh and initial le	d P-value asso nile adjusting ngth). Param	for the effection of the form	th these me ffects of the P-values le	odels. The ta e parameters es than 0.05	ble for each (that are abo were conside	species at we it (<i>i.e.</i> ered sign	t each site i , treatmen ificant	is read from t effects are
		Galium	aparine			Impatien	is pallida			Pilea	pumila	
			Chi-				Chi-				Chi-	
Source	Deviance	df	square	Pr > chi	Deviance	df	square	$\Pr > chi$	Deviance	df	square	Pr > chi
Gregg's Woodlot												
Intercept	205.33	0	I	I	156.61	0	I	I	318.35	0	ł	ł
Initial length	201.71	1	4.30	0.038	140.67	1	14.91	0.000	318.21	1	0.11	0.741
Block	NA	NA	NA	NA	NA	NA	ΝA	NA	263.58	29	42.94	0.046
Treatment	197.00	1	5.59	0.018	120.84	1	18.54	0.000	260.78	1	2.20	0.138
Western Woods												
Intercept	117.29	0	I	I	152.42	0	I	ļ	254.38	0	1	I
Initial length	113.76	1	7.31	0.007	146.77	I	8.27	0.004	246.15	1	7.75	0.005
Block	NA	NA	NA	NA	NA	NA	ΝA	NA	227.86	19	17.23	0.575
Treatment	112.97	5	1.64	0.440	144.37	2	2.60	0.273	227.18	5	0.64	0.726

TABLE 1.—Analysis of deviance tables of the effects of treatment on survival of all three species at both sites. Analysis of deviance tables are analogous to analysis of variance tables that are used in ANOVAs. Deviance is similar to an ANOVA's sum of squared error, df is the degrees of freedom of each

Treatment

at Gregg's Woodlot, but there was no significant effect at Western Woods (present = 69%, absent = 83%, removal = 87%) (Table 1). Initial length had a significant effect on survival to reproductive age at both sites (Table 1), with survivors being longer (Gregg's: mean =13.1 cm, Western: mean = 11.7 cm) than nonsurvivors (Gregg's: mean = 10.6 cm, Western: mean = 9.5 cm).

There was no significant treatment effect on survival to reproductive age of Pilea pumila at either site (Gregg's: present = 55%, removal = 64%; Western: present = 71%, absent = 76%, removal = 81%) (Table 1). Block effect was included in models at both sites, but was significant only at Gregg's Woodlot (Table 1). Initial length had a significant effect on survival to reproductive age only at Western Woods (Table 1), with survivors being longer (mean = 9.4 cm) than nonsurvivors (mean = 8.5 cm).

Fecundity.—At both sites Galium aparine had significantly higher fecundity in the Lonicera maackii removal treatment than in the L. maackii present treatment (Table 2, Fig. 1). At Western Woods fecundity in the L. maackii absent treatment was significantly lower than in the L. maackii removal treatment, but it did not differ significantly from the L. maackii present treatment (Table 2, Fig. 1). At both sites there was a significant block effect but no effect of initial length on fecundity (Table 2).

At both sites Impatiens pallida had significantly higher fecundity in the Lonicera maackii removal treatment than in the L. maackii present treatment (Table 2, Fig. 2). At Western Woods, fecundity in the L. maackii absent treatment was significantly greater than in the present treatment, but did not significantly differ from the L. maackii removal treatment (Fig. 2). Block number was significant at both sites, but initial length was significant only at Gregg's Woodlot (Table 2) where it was positively correlated to fecundity.

At both sites *Pilea pumila* in the *Lonicera maackii* removal treatment had significantly greater fecundity than in the L. maackii present treatment (Table 2, Fig. 3). At Western Woods, fecundity in the L. maackii absent treatment was significantly greater than in the present treatment and significantly lower than in the L. maackii removal treatment (Fig. 3). Block number and initial length were significant in the models of fecundity at both sites (Table 2). With increasing initial length, fecundity decreased at Gregg's Woodlot and increased at Western Woods.

Fitness.—Fitness of all three species was greater where Lonicera maackii had been removed than where it was present (Table 3). This pattern occurred at both sites, but the magnitude of the difference was consistently greater at Gregg's Woodlot. Species differed in their performance in the absent treatment relative to the other two treatments at Western Woods. For Impatiens pallida and Pilea pumila fitness in the absent treatment was three to four times greater than the present treatment and only slightly lower than the removal treatment. For Galium aparine, however, fitness in the absent treatment was similar to that in the present treatment.

DISCUSSION

Our results demonstrate that the presence of Lonicera maackii shrubs reduced fecundity of Galium aparine, Impatiens pallida and Pilea pumila in both deciduous forest stands and reduced survival of G. aparine and I. pallida only in the more anthropogenically disturbed stand. Also, the presence of this shrub reduced fecundity of I. pallida and P. pumila compared to where it was absent.

The cause of the negative effect of Lonicera maackii on the survival and fecundity of these annuals has not been determined. Reductions in native plants by nonnative invasives are often the result of complex interactions between the plants and their modified environments. The suppression of native plants by exotics is often attributed to competition for

		Galiu	ım aparine			Impatier	ıs pallida			Pilea 1	pumila	
- Source	Deviance	df	Chi-square	Pr > chi	Deviance	df	Chi-square	Pr > chi	Deviance	df	Chi-square	Pr > chi
Gregg's Woodlot												
Intercept	966.35	0	I	I	156.61	0	I	I	318.35	0	I	Ι
Initial length	966.21	1	0.05	0.829	140.67	1	14.91	0.003	318.21	1	0.11	0.000
Block	659.25	29	100.67	0.000	NA	NA	ΝA	0.000	263.58	29	42.94	0.000
Treatment	512.16	1	48.21	0.000	120.84	1	18.54	0.000	260.78	1	2.20	0.000
Western Woods												
Intercept	652.94	0	I	I	1009.08	0	Ι	Ι	0.9015	0	I	Ι
Initial length	652.34	I	0.28	0.599	1006.85	1	0.47	0.495	0.8849	1	10.66	0.001
Block	483.27	19	77.19	0.000	659.84	19	72.60	0.000	0.4300	19	292.51	0.000
Treatment	435.88	6	21.64	0.000	511.43	6	31.05	0.000	0.2146	7	138.46	0.000

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FIG. 1.—Fecundity of *Galium aparine* (+SE) at Gregg's Woodlot and Western Woods (measured as maximum number of seeds observed per surviving individual). The upper P-values are for treatment effects at each site. The lower P-values for the Western Woods data refer to significant pair-wise contrasts; the endpoints of each line signify which treatments were significantly different

light (Vitousek, 1986; Harrington *et al.*, 1989; Webb and Kaunzinger, 1993; Woods, 1993). This is a likely mechanism for the competitive effect documented here since the leaves of *L. maackii* expand in early April and are fully developed by early May, before leaves expand on native woody plants (Trisel and Gorchov, 1994). The multistemmed individuals form dense thickets that can greatly reduce the amount of light reaching the herb layer (Luken, 1988; Luken *et al.*, 1997). Allelopathy is another means by which *L. maackii* may reduce competitors' performance. Leaves (and water extract of leaves) of *L. maackii* have negative effects on *Fraxinus americana* germination and *Acer saccharum* seedling growth (Trisel and Gorchov, 1995) and *G. aparine* germination (M. Myers, pers. comm.). Allelopathic effects of trees and shrubs (Rice, 1984; Heisey, 1990; Lawrence *et al.*, 1991; Hobbs and Atkins, 1991), including the congener *L. tatarica* (Norby and Kozlowski, 1980) have been demonstrated on other herbs. Also, *L. maackii*'s extensive network of shallow roots may more



FIG. 2.—Fecundity of *Impatiens pallida* (+SE) at Gregg's Woodlot and Western Woods (measured as total number of seeds harvested per individual). *See* Figure 1 for explanation of P-values

readily acquire water and mineral nutrients than roots of native plants, giving this exotic shrub another competitive advantage (pers. obs.).

We do not know whether the negative effects documented in this study are due to specific traits of L. maackii or due to a shrub layer in general. Native shrub layers have been shown to suppress native plant populations (Hobbs and Mooney, 1986; Hobbs and Atkins, 1991). However, differences in native shrub densities cannot account for the differences in herb demography among our treatments because native shrubs were absent from the research plots and were sparse in both sites.

Since all three annuals had reduced fecundity in the presence of Lonicera maackii, our prediction that this invasive shrub would most negatively impact annuals with greater shade intolerance or earlier phenology was not realized. However, our results did confirm the prediction that L. maackii most negatively impacts the survival of shade-intolerant or early season annuals. Differences in survival were only detected at Gregg's Woodlot, where Galium aparine and Impatiens pallida but not Pilea pumila, had reduced survival in the presence of L. maackii compared to where it had been removed. Most growth of G. aparine



FIG. 3.—Fecundity of *Pilea pumila* (+SE) at Gregg's Woodlot and Western Woods (measured as mass of harvested infructescences per individual). *See* Figure 1 for explanation of P-values

occurs in the spring, before the leaves of the canopy have expanded (Struik, 1965). Shadeintolerant characteristics have been described for this species (Bain and Attridge, 1988) and continued growth of shaded individuals results from reduced respiration due to lower photosynthesis (Kutsch and Kappen, 1991). Reduced light environments created by a *L. maackii* canopy could be responsible for the lower survival in *G. aparine. Impatiens pallida* germinates in the late spring and continues to grow until late autumn (Cid-Benevento and Schaal, 1986). It is intermediate in shade tolerance; it persists in the dense shade of the forest floor and in large woodland gaps (Struik, 1965) and has highest survival and seed production at intermediate light levels (Cid-Benevento and Werner, 1986). To the extent that *I. pallida* relies on an open canopy early in its life-cycle, the early expansion of *L. maackii* leaves would reduce its survival. In contrast, *Pilea pumila* is considered shade tolerant (Cid-Benevento and Werner, 1986) and germinates synchronously with tree canopy closure. The shade tolerance of *P. pumila*, as predicted, minimized the effect of shading by *L. maackii* on its survival.

Our results also confirm the prediction that reductions in survival and fecundity of an-

Galium aparine

Pilea pumila

Impatiens pallida

4.6

1.8

85.0

e proportion of in	dividuals survi	ving to reproduc	tive age and the	e measure of fe	cundity
	Gregg's	s Woodlot		Western Woods	
-	Present	Removal	Present	Absent	Removal

4.9

1.4

89.0

5.4

5.7

260.0

TABLE 3.—Fitness of all the species in all three treatments at both sites. This estimate is the product of the

9.2

19.7

474.0

nuals in the presence of Lonicera maackii are greater in more anthropogenically disturbed sites. Reduced survival was only detected at Gregg's Woodlot, the more anthropogenically disturbed site, and the reduction in fecundity in the presence of L. maackii was greater at that site for all three annuals (Table 3, Figs. 1-3). This greater response to L. maackii removal could be due to the greater importance of this invasive shrub at this site, as it not only occurs at greater density $(0.7/m^2)$, but there is a lower basal area of trees, hence less shading by the canopy. The greater density of L. maackii is likely due to past disturbance, by either increased light to the shrub layer (lower tree BA) or soil disturbance (from livestock grazing). However, the larger radius of the removal plots at this site may also have contributed to the greater effect of L. maackii removal.

We can make some inferences of the importance of past occupancy by Lonicera maachii by comparing the demography of annuals in plots where this invasive shrub had been removed vs. plots where it had never occurred at Western Woods. Survival did not differ among treatments for any of the annuals and fecundity was never greatest in the L. maackii absent treatment. Fecundity in the absent treatment was equivalent to that in the present treatment for Galium aparine, equivalent to that in the removal treatment for Impatiens pallida and intermediate between the removal treatment and the present treatment for Pilea pumila (Figs. 1-3). These findings suggest that the major mechanism for L. maackii's negative effect on annuals is not the accumulation of allelopathic compounds or depletion of soil nutrients. These results raise the question: Why do the annuals perform better in the removal treatment than in the absent treatment? Soil disturbance during the removal of L. maackii burls may have enhanced fecundity in the removal plots. However, Luken et al., (1997) found no significant effect of turning under the top 15 cm of soil on herb densities in their L. maackii removal experiment. We suspect the lower fecundity in the absent treatment was due to greater competition from herbs within the planting areas and roots from outside the planting areas, as a result of the lack of previous suppression by L. maackii. The weeding conducted every 6-10 d may have been insufficient to preclude this endemic competition and by not trenching around the planting area we did not prevent root competition.

Our results are comparable to the findings of others on the direct effects of invasive plants on native plant populations. 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). Also, Midgley et al., (1992) found that the invasive shrub Acacia cyclops had a negative effect on the native shrubs Rhus glauca and R. lucida.

As is true for any one year study, the patterns reported here may not hold in years with different weather conditions. Nevertheless, we can use the qualitative demographic responses of the three study species to guide further research and make predictions about the effects of Lonicera maackii on other annuals. Survival of shade intolerant or early season annuals is predicted to decline in highly anthropogenically disturbed habitats that have

7.4

7.4

387.0

high densities of *L. maackii*. Fecundity of annuals, regardless of phenology, shade tolerance or site conditions, is predicted to decline in the presence of *L. maackii*. Other invasive shrubs with early leaf expansion are predicted to have similar effects on survival and fecundity of native annuals.

Many plans for eradication of invasive plants from natural systems assume that the removal of the exotic species will favor the growth of native species (Westman, 1990). This experiment has demonstrated this is true in the case of *Lonicera maackii*. It enforces the need for active eradication of *L. maackii* from native habitats, its elimination from horticultural use and its removal from the USDA's list of Conservation Tree and Shrub Cultivars in the United States (U.S.D.A., 1992).

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