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## HABITAT-SPECIFIC RESILIENCE OF THE INVASIVE SHRUB AMUR HONEYSUCKLE (*LONICERA MAACKII*) DURING REPEATED CLIPPING<sup>1</sup>

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**Abstract.** In the development of novel strategies for control of invasive plant species, researchers might first consider plant performance throughout a range of habitats and then concentrate management activities in habitats where plants are least resilient. We determined the relative resilience of forest- and open-grown populations of the invasive shrub *Lonicera maackii* (Caprifoliaceae) growing in northern Kentucky. Resilience was assessed by imposing a clipping regime (once each year from 1986 to 1989) during which shrub resprouting abilities were measured. Habitat-specific population regeneration from seeds in the seed bank was also measured. Forest-grown *L. maackii* shrubs were less resilient than open-grown shrubs when stressed by repeated clipping, due presumably to exhaustion of stored reserves in shrub bases. This suggests that forests are secondary habitats for *L. maackii*. However, resprouting potential and seed production in forests appear sufficient to regenerate populations after most common disturbances. The ability to modify sprouting patterns while maintaining resprouting ability and some seed production over a wide range of habitats is an important adaptation of this invasive shrub. Management suggestions for shrub eradication are provided.

**Key words:** allocation; basal sprouting; Caprifoliaceae; invasive species; *Lonicera maackii*; management recommendations; repeated clipping; reproductive flexibility; resilience; seed bank; shrub eradication.

### INTRODUCTION

Understanding the invasion and eventual domination of established plant communities by exotic plant species is a critical problem now facing ecologists and resource managers (Usher 1988). Recent reviews suggest that two areas of study contribute to an understanding of plant invasions: the characteristics of invading species (Bazzaz 1986, Groves 1986) and the characteristics of invaded communities (Orians 1986). Successful invading species are phenotypically plastic, they have efficient dispersal mechanisms, and they often express both sexual and asexual reproduction (Bazzaz 1986, Groves 1986). Simplified communities with recently accelerated disturbance rates are more susceptible to invasion (Orians 1986). Research attempting to determine the potential spread, reasons for persistence, and ecological limits of invasive species must consider how these species differ from endemic species, how they cope with different environments, and how they respond to common disturbances.

In this study we measured the habitat-specific ability of Amur honeysuckle (*Lonicera maackii* (Rupr.) Maxim., Caprifoliaceae) to regenerate stem and shrub populations when repeatedly stressed by clipping. *Lonicera maackii*, a native plant of northeastern Asia, is an upright deciduous multi-stemmed shrub now naturalized

in many parts of eastern United States and Ontario (Pringle 1973). It is a highly productive shrub that invades forests and also colonizes recently disturbed ground (Luken 1988). It sprouts prolifically from a stout base and also produces numerous red fruits that are eaten by birds in late winter (Ingold and Craycraft 1983). In north-central Kentucky and south-central Ohio much effort, primarily clipping, has been devoted to *L. maackii* eradication because it dominates nature reserves to the exclusion of endemic species.

The purpose of our research was to place shrubs under stress so that habitat-influenced differences in shrub resilience would emerge. Resilience in long-lived shrubs depends on their ability to regenerate new stems, or on their ability to produce seeds successfully. Exotic shrubs are known to be extremely plastic in terms of leaf and stem allocation, particularly in response to light availability (Luken 1988, Harrington et al. 1989, Jones and Mcleod 1989). Such measurements, however, provide neither information on resilience nor information on interactions between production and reproduction. This information can be obtained by examining growth and reproduction under stress (Osmond et al. 1987).

Within an individual plant there is competition for resources among vegetative growth, storage, seed production, and defense (Bazzaz et al. 1987). Productivity and the allocation pattern may ultimately influence resource availability for storage and seed production,

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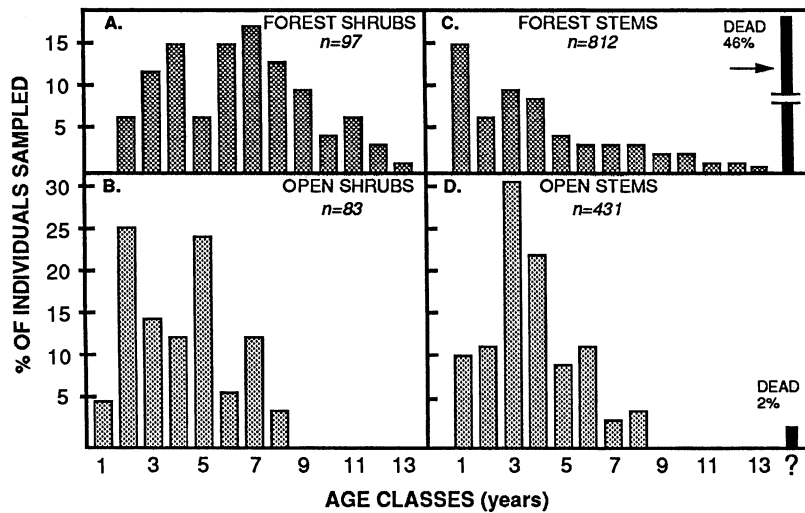


FIG. 1. Age-class distributions for shrubs and stems of *Lonicera maackii* growing in forest and open habitats. Ages were determined in summer 1986 by a destructive sample of shrubs from six forest-grown populations (A and C) and from five open-grown populations (B and D). Standing dead stems were not aged. It was assumed that the oldest stem on a shrub represented maximum shrub age.

two critical factors contributing to shrub resilience. Because *L. maackii* shrubs in forests are less productive than open-grown shrubs (Luken 1988), we hypothesized that forest-grown shrubs, when placed under the stress of repeated clipping, would be less resilient than open-grown shrubs. Results of this research could be of value to resource managers as they develop shrub eradication programs for different habitats.

## METHODS

### Adult shrubs

In mid-July 1986 a rectangular permanent plot (18–120 m<sup>2</sup>) was established in each of five open-grown populations and six forest-grown populations of *L. maackii*. All forest plots were located in preserved forest patches on the Northern Kentucky University campus (39°5' N, 84°40' W). These forest patches (25–40 yr old) are dominated by sugar maple, white ash, and hackberry, and have a history of disturbance from logging and agriculture. All open plots were located on roadside embankments near the campus. Plots were positioned so as to avoid edge effects (>10 m from the forest edge) and trees, and to sample those areas dominated by *L. maackii*. At two open sites plot size was expanded above the standard 18 m<sup>2</sup> primarily to increase the number of shrubs sampled from populations with low shrub densities.

In late July 1986 all stems within the plot boundaries were clipped at the top of shrub bases and their ages were determined by counting annual growth rings. We assumed that the oldest stem on a shrub represented maximum shrub age. Biomass and net primary production (NPP) were estimated by dimension analysis techniques described in Luken (1988). Each shrub base was tagged and numbered with an aluminum tag to

allow comparison of individual shrub growth in pre-clip and post-clip conditions, at least for the first year of the study. Small mammals damaged the aluminum tags during 1988, thus making it impossible to track individual shrubs beyond this time.

In late July of each year (1987 to 1989) plots were rechecked, and all stems originating from the tagged shrub bases were removed. Throughout the study five open-grown populations and six forest-grown populations were sampled, except in 1989 when one of the open-grown populations was accidentally destroyed by mechanical mowing. Shrub death was indicated by failure to resprout. All sprouts were taken to the laboratory, oven-dried at 70°C and then weighed.

Relationships between shrub characteristics in 1987 (resprouts) and 1986 (preclip stems and shrubs) were calculated. Adult shrub- and stem-density as well as NPP measured from 1987 to 1989 were expressed as percentages of the 1986 pre-clip conditions to calculate various indices of resilience. Significant differences between forest- and open-grown populations were determined by rank sum tests with  $P < .05$  established before testing.

### Seeds and seedlings

In February 1988, the time of maximum seed dispersal, a composite of three soil samples 5 cm in depth (totalling 400 cm<sup>2</sup> in area) was taken around individual shrubs. Eight shrubs of similar stem-base size within each of the habitat (open vs. forest) and treatment (clipped vs. undisturbed) combinations were sampled. To avoid edge effects in the plots, samples were taken adjacent to shrub bases in plot centers. Sampling individual shrubs rather than entire plots was done primarily to determine maximum seed-bank sizes. Seed banks are highest directly beneath shrubs and decline

quickly with increasing distance from the shrub (J. O. Luken, *personal observation*).

The soil samples were taken to a heated greenhouse, mixed 1:1 with potting soil (50% well-decomposed peat and 50% vermiculite), spread in flats, and then watered regularly with tapwater. All *L. maackii* seedlings that emerged during the next 8 mo were recorded and removed. After 8 mo the soils were sieved to estimate the number of ungerminated seeds. Seeds that germinated represented 80% of the total *L. maackii* seeds present in the seed bank, while the remaining 20% of the seeds were nonviable.

Untagged shrubs (seedlings) that established in the permanent plots were hand-pulled and weighed in late July 1988 and again in late July 1989.

Rank-sum tests were used to determine differences between habitats in seedling establishment and to determine differences in seed bank size between cut and undisturbed shrubs.

## RESULTS

### Adult shrubs

Forest-grown populations (maximum age  $11.8 \pm 0.6$  yr,  $\bar{X} \pm SE$ ) were significantly ( $P < .05$ ) older than open-grown populations (mean maximum age  $7.2 \pm 0.4$  yr). Because replicate populations from each habitat showed close agreement in age, composite age-class distributions were constructed (Fig. 1). The shrub age-class distributions from both habitats indicated a fairly wide window for shrub establishment. Forest-grown populations had maximum shrub establishment 7 yr after invasion, with gradual increases and decreases of establishment before and after this peak. Open-grown populations established sporadically. Age-class distributions of stems suggested gradually expanding populations in forests, while open-grown populations had a peak of stem release 6 yr into the invasion. No dead shrubs were observed in either forest or open habitats, but large numbers of standing dead stems were found in forest-grown populations.

Regardless of the habitat-specific differences in stem age-class distributions at the time of clipping, shrub bases in both habitats released large numbers of new stems in response to clipping. In 1987 there were no significant ( $P \geq .05$ ) differences between open- and forest-grown populations regarding the ability of shrubs to tolerate clipping or regarding the ability of cut shrub stumps to regenerate new stems (Fig. 2). However, in 1988 and 1989 significant habitat-related differences emerged. Clipping gradually induced much mortality among forest-grown shrubs; stem populations also declined. In contrast, open-grown shrub populations remained stable and stem populations continued to increase. By 1989 there was 30% and 91% of the original shrub density in forest- and open-grown populations, respectively.

In terms of NPP, open-grown populations were sig-

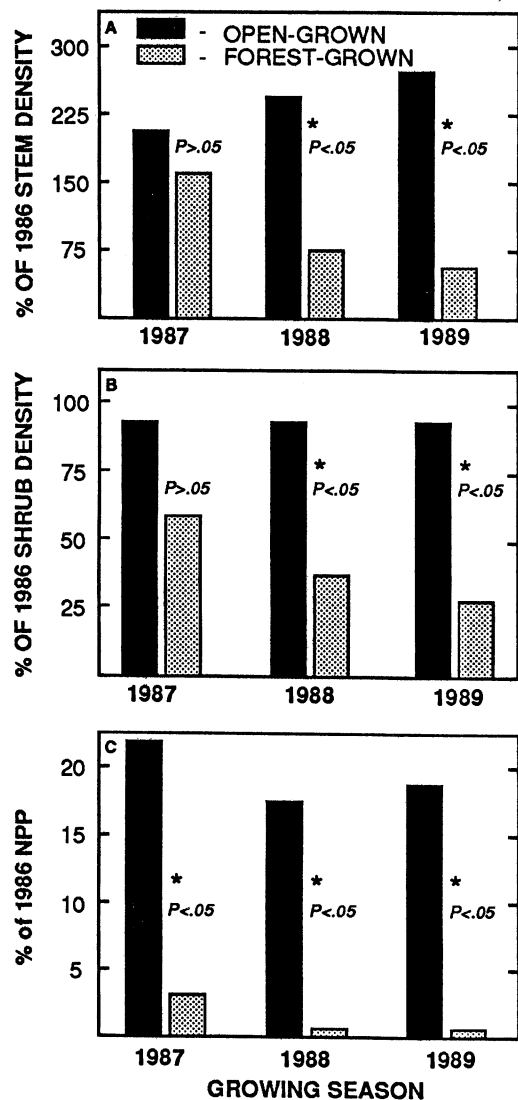


FIG. 2. Numbers of stems resprouting from cut stumps (A), numbers of shrubs persisting during clipping (B), and net primary production between successive clippings (C) of *Lonicera maackii* growing in open and forest habitats during repeated clipping from 1986 to 1989. Only shrubs tagged in 1986 are included; seedlings that established during this time period are not included. Data are expressed as mean percentages of the 1986 measurements, with  $n = 5$  and  $n = 6$  for open and forest sites, respectively, in 1987 and 1988. In 1989  $n = 4$  for open sites. Asterisks indicate significant differences between open and forest sites at  $P < .05$ .

nificantly more resilient than forest-grown populations during all 3 yr of the study (Fig. 2). Net primary production per shrub in both habitats during the growing season following the first clipping (1987) was most highly correlated with NPP or biomass per shrub in the year prior to clipping (1986) (Table 1). Likewise, in both habitats the number of stems per shrub that developed during the first year after clipping was most highly correlated with the number of stems per shrub prior to clipping in 1986. Net primary production per

TABLE 1. Correlation coefficients for relationships established between *Lonicera maackii* shrub characteristics in 1986 (pre-clip) and shrub characteristics in 1987, one year after clipping.

1986	1987	
	Stem mass per shrub	No. stems per shrub
	Open-grown populations†	
NPP‡ per shrub	0.76*	0.46*
Biomass per shrub	0.75*	0.41*
No. stems per shrub	0.15 NS	0.46*
Shrub age (yr)	0.31*	0.23 NS
	Forest-grown populations†	
NPP‡ per shrub	0.81*	0.54*
Biomass per shrub	0.82*	0.53*
No. stems per shrub	0.47*	0.63*
Shrub age (yr)	0.55*	0.36*

\* Significant relationship ( $P < .05$ ) between 1986 and 1987. NS = not significant.

†  $n = 65$  for open-grown populations and  $n = 48$  for forest-grown populations.

‡ Net primary production.

shrub of resprouts in 1987 was more highly correlated with shrub age than was the number of stems per shrub in 1987. This was especially true for forest-grown populations (Table 1).

#### Seeds and seedlings

There were more ( $P < .10$ ) seeds in the soil beneath uncut open-grown shrubs ( $\bar{X} \pm SE$ ,  $1096 \pm 477$  seeds/m<sup>2</sup> vs.  $340 \pm 84$  seeds/m<sup>2</sup> for open sites and forests, respectively). Clipping reduced the soil seed bank around shrubs in both habitats to similar low levels (Fig. 3). Seedling establishment of *L. maackii* was significantly higher in forests (Table 2).

#### DISCUSSION

There is little available information on the ecology or longevity of *Lonicera maackii* in its native north-east-Asia habitat. This species was originally introduced to North America in the late 1850s for landscaping purposes (Dirr 1983). In northern Kentucky, the presence of large shrubs up to 25 yr old in the edges of forests near the study sites (J. O. Luken, *personal observation*) suggests that radiation occurred opportunistically from forest edges into open sites and forest interiors.

#### Resprouting potential

Resprouting in woody plants is a response to biomass removal that depends on the development of stem buds and the availability of stored carbohydrates (Schier and Zasada 1973, Kramer and Kozlowski 1979). Site factors that decrease carbon gain may limit sprouting ability (Mroz et al. 1985). The results of this study indicate that *L. maackii* maintains resprouting potential in both forests and open sites. Furthermore, sprouting ability does not appear to decline with age as in other shrub

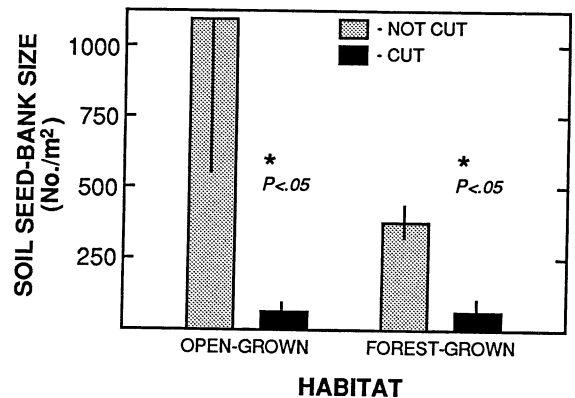


FIG. 3. Estimated soil seed banks adjacent to individual shrubs of *Lonicera maackii* growing in open and forest habitats. Seed banks were measured in February 1988. Shrubs were either clipped in July 1986 or undisturbed. Data are means  $\pm$  SE, with  $n = 8$ . Asterisks indicate significant ( $P < .05$ ) differences between clipped and unclipped shrubs.

species (Miller and Miles 1970, Hobbs and Mooney 1985). Resprouting remains high even in forests where shrubs have lower productivity (Luken 1988) and where large cohorts of stems are annually released from the shrub bases. Thus, within the range of habitats considered in this study *L. maackii* is fully capable of regenerating most shrubs after a single clipping event.

Under repeated clipping habitat-specific differences in shrub resilience emerged. Many forest-grown shrubs died, while open-grown shrubs persisted; the number of stem resprouts in open sites actually increased each year. The stress of repeated clipping apparently drained the carbohydrate reserves of forest-grown shrubs, while open-grown shrubs, because of higher productivity, were able to store carbohydrate between successive clippings. Although direct measurements of carbohydrate reserves in shrub bases were not made in this study, lower correlation coefficients for all relationships between pre-clip and post-clip open-grown shrub characteristics suggest that open-grown resprouts may be less dependent on previous-year shrub performance.

TABLE 2. Density and biomass of *Lonicera maackii* seedlings that established in clipped plots in open and forest habitats. Seedlings were measured in late July 1988 and 1989. For open sites  $n = 5$  in 1988 and  $n = 4$  in 1989; in forests  $n = 6$ .

	Habitat				
	Open		Forest		
	$\bar{X}$	SD	$\bar{X}$	SD	
Density (seedlings/m <sup>2</sup> )					
1988	0.4	0.7	*	5.9	10.0
1989	1.5	0.3	*	3.5	2.9
Biomass (g/m <sup>2</sup> )					
1988	2.2	2.1	NS	1.4	1.2
1989	1.9	3.4	NS	1.1	1.2

\*  $P < .05$ , NS =  $P \geq .05$  (comparisons between habitats).

Greater light availability may allow these resprouts to function as independent units more quickly than do forest-grown resprouts.

Several lines of evidence suggest that light is a critical limiting resource for forest-grown shrubs: a fertilization experiment showed that open-grown shrubs of *L. maackii* were nutrient limited but forest-grown shrubs were not (J. O. Luken, *personal observation*); in other studies, shrub species growing in forests have shown positive growth responses to increased light levels associated with tree death (Huenneke 1983, Dunn 1986, Hicks and Hustin 1989). Therefore, even though exotic shrubs can grow over a wide range of light environments (Harrington et al. 1989, Jones and Macleod 1989), they will be less resilient and easier to control in low-light environments.

#### *Sprouting and seed production*

Vegetative growth and sexual reproduction compete for limited resources within a single plant genet (Wallace and Rundel 1979, Bazzaz et al. 1987, Luken 1987). This is evident in forest-grown *L. maackii* shrubs in which the annual release of large stem cohorts is associated with lower seed production (M. A. Schuler, *unpublished manuscript*) and fewer seeds in the seed bank. (Lower seed availability in forests is somewhat compensated for by better seedling-establishment conditions.) Resources allocated from the shrub bases of *L. maackii* for the release of new stems may not be available for storage, seed production, or defense. Most new stems produced by forest-grown shrubs die during the first year of stem life, and thus the invested energy is largely wasted (Luken 1988).

While there is ample evidence that tradeoffs do occur between sexual and asexual reproduction in *L. maackii*, there is also evidence that dual modes of reproduction are maintained in forest and open habitats. Areas proximal to adult shrubs in both habitats receive large inputs of seeds each year. Such consistency in *L. maackii* seed production may be linked to the fact that seed dispersal in time is precluded by a lack of dormancy mechanisms (C. R. Bierman, *unpublished manuscript*). Persistent seed production coupled with persistent resprouting even in secondary habitats under stressed conditions assure that population regeneration will occur subsequent to a wide variety of disturbances. Clearly, phenotypic plasticity is an important adaptation of exotic shrubs that allows them to dominate forests and open sites (Harrington et al. 1989). Limits on this plasticity that assure the maintenance of asexual and sexual reproduction may be just as important in allowing exotic shrubs to invade and persist.

#### *Management implications*

The results of this study suggest that control of *L. maackii* might best be approached in a habitat-specific manner. Repeated clipping without the use of herbicides will control adult plants of *L. maackii* in forests.

Clipping should occur at least once a year, or even more frequently if possible. When *L. maackii* is cut once and then abandoned, populations develop that are more dense and productive than prior to clipping (J. O. Luken, *personal observation*).

Clipping will not successfully control open-grown shrubs. Here, a combination of clipping and herbicide application may be necessary.

After adult plants in forests and open sites are controlled, seedling populations must be managed. The approach now taken in South African fynbos vegetation to control alien *Acacia* shrubs is to cut or burn the adult plants and then treat the flush of seedlings with herbicide (Holmes et al. 1987, Macdonald et al. 1989). Because the seeds of *L. maackii* are not long-lived in the soil, once adult plants are controlled the seed bank will not be a persistent source of new colonists. We suggest that successful management must first eliminate adult plants followed by a concerted effort to eliminate the subsequent flush of seedlings.

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