Effects of Leaf Litter on Establishment, Growth and Survival of Invasive Plant Seedlings in a Deciduous Forest

ABSTRACT.—Disturbance often promotes plant invasion. Small disturbances to the forest floor expose bare soil to light which may promote seed germination and establishment. We tested the hypothesis that small disturbances to the litter layer allow invasive species to become established in forest interiors. We found that seedlings of the invasive shrub *Lonicera maackii* were found in sites with significantly lower leaf litter mass than regularly spaced points along a transect. We then investigated establishment and survival of *L. maackii* and the invasive biennial *Alliaria petiolata* in plots randomly assigned to three treatments: litter removed, litter added and control. Significantly more *L. maackii* seedlings established in the litter removed and control plots than the litter added treatments, but there was no effect on survival. Significantly more *A. petiolata* seedlings established in the litter removed plots than in the control or litter added treatments. Survival of established *A. petiolata* seedlings was significantly greater in control than in litter removed plots, but the final number of *A. petiolata* seedlings was greatest in the litter removed treatment. Our results confirm that bare patches of soil in the forest interior are colonization sites for invasive plant species.

INTRODUCTION

Habitat disturbance is often invoked as a causal reason for the invasion of an exotic plant species (Hobbs and Huenneke, 1992). Generally the focus is on large disturbances that cover many tens of square meters, or even hectares, *e.g.*, grazing, fires and human disturbance (Parker *et al.*, 1993; Gentle and Duggin, 1997; Stohlgren *et al.*, 1999) that enhance light and release nutrients to the soil that can decrease competitive interactions between plant species (Davis *et al.*, 2000). Smaller disturbances are more frequent, however (White, 1979); in forests these include single tree falls and leaf litter movement due to animal foraging (Theimer and Gehring, 1999). Small disturbances to leaf litter open bare patches of soil and allow increased light to reach the forest floor. The small openings in the leaf litter may provide an opportunity for invasive species to become established in a new habitat or facilitate the spread of a previously established population (Meekins and McCarthy, 2001). Furthermore, the greater litter depth of old growth forests compared to second growth stands (Bray and Gorham, 1964) may be one explanation for the lower invasibility of those forests (Brothers and Spingarn, 1992).

A meta-analysis of the effects of leaf litter on plant life history stages found that germination was the stage most negatively affected by the presence of leaf litter, although leaf litter had a generally negative effect on all life history stages (Xiong and Nilsson, 1999). Litter can act to reduce establishment through several mechanisms: shading, mechanical impedance, reduced thermal amplitude in the soil and biochemical effects (Facelli and Pickett, 1991). Few studies have investigated the effect of leaf litter on forest invasions. Increased leaf litter reduced the emergence of the invasive *Celastrus orbiculatus* (Oriental bittersweet) and shifted the allocation of seedling growth to longer hypocotyls and smaller radicles and cotyledons (Ellsworth *et al.*, 2004). In wetlands invaded by *Lythrum salicaria* (purple loosestrife) small disturbances that reduced leaf litter reduced the ability of the native *Typha* spp. to compete against the invader (Hager, 2004). The effect of leaf litter is not always negative; McAlpine and Drake (2002) found that leaf litter in tree fall gaps in New Zealand enhanced the growth of one invasive species (*Berberis darwinii*) and did not inhibit the growth of another (*Cytisus scoparius*).

We investigated the role of litter disturbance in the invasion of two non-native species prevalent in forests and successional habitats in eastern U.S. and adjacent Canada, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae) (Amur honeysuckle) and *Alliaria petiolata* (M. Bieb.) Cavara and Grande (garlic mustard). The shrub *L. maackii* is native to northeastern Asia and was introduced into the United States in 1898 as an ornamental plant (Luken and Thieret, 1996). It has since naturalized and become abundant from forest interiors to open disturbed sites (Luken and Thieret, 1996). Its red fruits ripen in the fall and are consumed throughout the winter by several species of birds, some of which disperse the seeds (Bartuszevige and Gorchov, 2006). The seeds of this species do not have dormancy and therefore do not form a seed bank (Hidayati *et al.*, 2000). *Lonicera maackii* negatively affects growth, fecundity and

cover of forest annuals, perennials and tree seedlings (Gould and Gorchov, 2000; Collier *et al.*, 2002; Gorchov and Trisel, 2003; Miller and Gorchov, 2004).

Alliaria petiolata is a fast-growing biennial herb that was introduced to North America from Europe in 1868 (Nuzzo, 1993). Seeds are dispersed in the fall by water (Byers, 1988) or by "hitchhiking" on the feet of mammals (Cavers et al., 1979). Alliaria petiolata forms a persistent seed bank, and seeds are known to be viable in the soil for up to five years (Baskin and Baskin, 1992). Alliaria petiolata has negative effects on forest annuals and tree seedlings (McCarthy, 1997), including Quercus prinus (Meekins and McCarthy, 1999), as well as graminoids and spring perennial forbs (Carlson and Gorchov, 2004).

Leaf litter depth may play a key role in the invasion of both Lonicera maackii and Alliaria petiolata. Hutchinson and Vankat (1997) found L. maackii density correlated negatively with basal area across stands in southwest Ohio, and inferred that greater shade inhibited invasion; however, deeper leaf litter could alternatively or additionally account for the lower invasibility of stands with greater basal area. Hutchinson and Vankat (1997) mention anecdotal evidence that suggests L. maackii invasion is associated with disturbances to the forest floor that decrease leaf litter and the herbaceous layer. Nuzzo (1993) found A. petiolata invasion to be linked to disturbance, with plants commonly invading habitats such as riverbanks, floodplains, trailsides, roadways, forest edges and urban areas. Anderson et al. (1996) proposed that micro-site disturbance facilitates A. petiolata establishment by providing small sites with reduced competition and Nuzzo (1999) found that A. petiolata cover declined in the absence of disturbance. However, experimental removal of leaf litter did not increase A. petiolata germination, growth, or reproduction (Meekins and McCarthy, 2001).

To investigate the effects of small-scale disturbance of leaf litter on these two invasive plant species, we tested whether *Lonicera maackii* seedlings occur in sites with reduced leaf litter and experimentally removed litter from plots in a second-growth forest. To further test whether greater litter depth is responsible for the low invasibility of old-growth forest, we included a treatment where litter depth was doubled. We predicted that *L. maackii* and *Alliaria petiolata* seedling establishment and survival, and *L. maackii* growth, would be enhanced by leaf litter removal and reduced by leaf litter addition.

METHODS

DISTRIBUTION OF LONICERA MAACKII AS A FUNCTION OF LITTER

We tested whether Lonicera maackii seedlings were associated with sites of reduced leaf litter in Gregg's Woodlot in Butler County, southwest Ohio $(39^{\circ}28'30''N, 84^{\circ}43'40''W)$. The canopy was dominated by Carya ovata, Fraxinus spp. and Quercus rubra. A complete description of the site is available in Gould and Gorchov (2000). We sampled leaf litter in May 2003 every 3 m along a 125 m transect by inserting a 5 cm diam circular pipe into the ground, cutting away all leaf litter outside the pipe, and collecting the litter within the pipe. At the same points, we located the nearest (within 1.5 m of transect line) L. maackii seedling ≤ 6 cm in height and took another litter sample from directly around each seedling. The seedling was discarded. The 6 cm height threshold helped ensure that the sampled L. maackii was, in fact, a seedling. Litter samples were dried for 48 h at 100 C and massed. A Wilcoxon 2-sample test was used to test if there were significant differences between transect points and seedling points.

LEAF LITTER MANIPULATION EXPERIMENT

This experiment was carried out in a second growth forest at the Miami University Ecology Research Center ($39^{\circ}30'$ N, $84^{\circ}44'$ W) in Butler County, southwest Ohio. Density of trees >10 cm dbh was 491/ha. The canopy was dominated by *Acer saccharum* and *Fraxinus americana* and the understory by *A. saccharum*. We cleared *Lonicera maackii* shrubs in a flat, 20×16 m area with uniform canopy cover in Sept. 2003 before fruits ripened and fell. We then established 75 circular plots 0.25 m radius (0.196 m²) in a grid centered within this area with 1 m spacing between plots. Each plot was encircled by plastic bird fencing (mesh size = 2.54 cm to prevent litter movement) attached to bamboo poles and secured to the ground using landscape staples.

In Nov. 2003, after all tree leaves had fallen, plots were randomly assigned to three experimental treatments: litter removed (all leaf litter within the plot removed), control (no manipulation) and litter added (litter from a removal plot added). Mass of litter averaged 26.29 ± 2.02 (mean \pm se) g dry weight (range 21.4–34.3 g), based on additional control plots not used in the experiment, so litter added plots

 0.82 ± 0.12^{b}

 $0.56 \pm 0.20^{a,b}$

Litter added

Control

 3.3 ± 0.7^{a}

 1.0 ± 0.5^{b}

of leaves per L. maackii seedling at this date, for each litter treatment. Means within columns with different letters are significantly different (alpha = 0.05 ; corrected for multiple comparisons)					
	Lonicera maackii			Alliaria petiolata	
	# Seedlings	Survival	# Leaves	# Seedlings	Survival
Litter removed	$5.7 \pm 0.8^{\rm a}$	$0.50 \pm 0.06^{\rm a}$	3.7 ± 0.13	4.2 ± 1.0^{b}	$0.60 \pm 0.09^{\rm a}$

 3.5 ± 0.17

 3.6 ± 0.75

 $0.9 \pm 0.3^{\rm a}$

 $0.4 \pm 0.1^{\rm a}$

 0.40 ± 0.10^{a}

 0.50 ± 0.16^{a}

TABLE 1.-Mean (+ sE) number of Lonicera maackii and Alliaria petiolata seedlings established per 0.25 m radius plot, survival of these seedlings (proportion alive at the end of Jun.) and average number

would average twice this mass. After litter manipulation, 50 Lonicera maackii seeds that had been removed from the fruit pulp by hand were added to each experimental plot to mimic natural seed dispersal by birds. Most L. maackii seed dispersal in southwest Ohio occurs during the winter months, after leaves have fallen from the trees (Bartuszevige et al., 2006). Alliaria petiolata was not sown, as this herb was common in this stand, and therefore its seeds were present in the soil. While seed density may vary spatially, by randomly assigning plots to treatments we prevented this variation from biasing seedling emergence.

Plots were monitored every 14 d Mar.-Jun. 2004 for establishment and survival of Lonicera maackii and Alliaria petiolata seedlings. Individual seedlings were marked with colored toothpicks or paper clips. We counted the number of leaves on each L. maackii seedling over the same time period to measure growth. We defined establishment as the time when the first set of true leaves was fully expanded. This stage has been called 'germination' in some other studies (e.g., Xiong and Nilsson, 1999).

We tested treatment effects on the number of Lonicera maackii and Alliaria petiolata seedlings established per plot with Kruskal-Wallis tests. We selected the mid-May census date because the number of seedlings of both species peaked on this date. The proportion of seedlings surviving of each species was calculated by dividing the number of plants alive at the end of Jun. by the mid-May count. Late Jun. was selected because after this date we could not distinguish seedlings that died from survivors that abscised leaves during the late summer. Treatment effects on this proportional survival measure were determined by Kruskal-Wallis tests. To analyze L. maackii size we calculated, for each plot, the mean number of leaves on seedlings alive in late Jun., and compared treatments with a Kruskal-Wallis test. For each test resulting in a significant treatment effect, we compared each pair of treatments with a Kruskal-Wallis test with alpha values corrected for multiple comparisons (alpha = 0.05/3 = 0.017).

RESULTS AND DISCUSSION

Significantly less litter mass was present around Lonicera maackii seedlings (mean \pm se = 4 \pm 1 g/m²) than transect points $(8 \pm 1 \text{ g/m}^2, t = 2.743, \text{df} = 73, P = 0.004)$.

We found significantly more Lonicera maackii seedlings established in the control and litter removed treatments than the litter added treatment ($X^2 = 17.68$, df = 1, P < 0.0001; $X^2 = 33.71$, df = 1, P < 0.0001, respectively, Table 1) and significantly more Alliaria petiolata seedlings established in the litter removed treatment than in either the control or litter added treatments ($X^2 = 9.32$, df = 1, P = 0.0023; $X^2 = 16.2$, df = 1, P < 0.0001, respectively, Table 1). While we do not know the mechanism by which greater litter reduced seedling establishment, possible causes are lower light levels, physical blockage of growth, change in soil pH or leaching of phytotoxins, all of which are associated with litter (Facelli and Pickett, 1991). Additionally, our placement of L. maackii seeds on the top of the leaf litter may have reduced the number of seeds in contact with soil in the spring. We added L. maackii seeds in this manner to mimic natural seed dispersal by birds which occurs during the winter months; seeds subsequently move passively through the litter with precipitation. Not all studies of the effects of leaf litter on germination take into account the timing of dispersal in their experimental design; frequently seeds are planted, in the field or in the greenhouse, beneath leaf litter (Xiong and Nilsson, 1999; McAlpine and Drake, 2002; Ellsworth et al., 2004). If seeds are unable to reach the soil surface they may be unable to germinate because they lack the proper cues from the soil, or may germinate but die rapidly because the young roots are unable to reach the soil, take root and begin collecting nutrients. We did not inspect for seeds imbedded in the litter as we wished to minimize disturbance to the leaf litter. Peterson and Facelli (1992) tested the effect of leaf litter from deciduous trees on germination of *Rhus typhina* seeds and found that seeds placed on top of the leaf litter did not germinate.

Even within a forest patch, litter depth may vary due to movement by wind and water (Orndorff and Lang, 1981) and litter is generally deeper in the interior than near edges (Shure and Phillips, 1987). Bartuszevige and Gorchov (2006) found that *Lonicera maackii* seeds were dispersed preferentially to the edge of woodlots by American Robins. The combination of dispersal to the edge and lower amounts of leaf litter may facilitate invasion of the edges of woodlots. Although we found lower seedling establishment in plots with greater leaf litter, leaf litter itself was unable to prevent germination of these two highly invasive species in southwest Ohio. Meekins and McCarthy (2001) found that *Alliaria petiolata* rosettes were generally larger and had greater survival and reproduction in lowland areas and in forest edge plots, both of which had less litter than the upland area, although they did not find a significant effect of litter removal on *A. petiolata* demography.

Contrary to what we predicted however, we found that leaf litter had no effect on *Lonicera maackii* seedling survival ($X^2 = 1.02$, df = 2, P = 0.60) or growth ($X^2 = 0.53$, df = 2, P = 0.77). Litter removal actually decreased survival of *Alliaria petiolata* compared to the control treatment ($X^2 = 6.76$, df = 1, P = 0.009) (Table 1). Others have found a significant effect of leaf litter on hypocotyls elongation; hypocotyls are longer in seedlings beneath greater amounts of leaf litter (Peterson and Facelli, 1992; Ellsworth *et al.*, 2004). Although hypocotyl length was not measured in our study, we observed longer hypocotyls in litter added treatment plots than in no litter or control plots, suggesting seedlings allocated more to vertical growth or cell elongation and less to photosynthetic tissues (Peterson and Facelli, 1992).

The greater survivorship of Alliaria petiolata seedlings in the control than in the litter removed treatment was opposite of what we had predicted. This may have been due to the mulching effect of leaf litter. According to Facelli and Pickett (1991) leaf litter maintains soil moisture, moderates soil temperature, provides nutrients during litter decomposition and reduces competition from other plants; these may enhance seedling survival after establishment. The lower survival of A. petiolata seedlings in the absence of litter was modest, however, and did not overcome the positive effect of litter removal on establishment. By the end of Jun., the number of seedlings was still greatest in litter removal plots (n = 63), intermediate (n = 18) in control and least (n = 5) in litter addition plots.

This reduced number of Alliaria petiolata seedlings, as well as the reduced Lonicera maackii establishment, in the litter added treatment compared to the control suggest that litter depth may explain the lower incidence of invasion of old-growth, as compared to second-growth forests (Brothers and Spingarn, 1992), as the former typically, though not always, have greater litter depth (Bray and Gorham, 1964). However, old-growth forests also differ from second-growth forest in other ways *e.g.*, increased competition for nutrients, less available light and greater species or functional group diversity. Change in any one of these factors may facilitate invasion by exotic species. For example, McAlpine and Drake (2002) found that increased light availability from tree fall gaps enhanced germination in one species. Even in old-growth forests, small disturbances to the leaf litter due to mammal activity or abiotic forces can open small patches of bare ground that are colonized by exotic plants. Finally, invasive species are often found at the edges of woodlots and in riparian areas both of which are highly disturbed and have low amounts of leaf litter (Shure and Phillips, 1987). The low level of leaf litter in these habitats may be important in facilitating exotic plant invasion.

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LITERATURE CITED

ANDERSON, R. C., S. S. DHILLION AND T. M. KELLEY. 1996. Aspects of the ecology of an invasive plant, garlic mustard (Alliaria petiolata), in central Illinois. Restoration Ecol., 4:181-191.

- BARTUSZEVIGE, A. M. AND D. L. GORCHOV. 2006. Avian seed dispersal of an invasive shrub. *Biol. Invasions*, 8:1013-1022.
- ------, M. R. HUGHES, A. J. BAILER AND D. L. GORCHOV. 2006. Weather-related patterns of fruit abscission mask patterns of frugivory. *Can. J. Bot.*, **84**:869–875.
- BASKIN, J. M. AND C. C. BASKIN. 1992. Seed germination biology of the weedy biennial Alliaria petiolata. Nat. Areas J., 12:191–197.
- BRAY, J. R. AND E. GORHAM. 1964. Litter production in forests of the world. Advances in Ecol. Research, 2:101–187.
- BROTHERS, T. S. AND A. SPINGARN. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Conserv. Biol.*, 6:91–100.
- BYERS, D. L. 1988. Life History variation of *Alliaria petiolata* in a range of habitats in New Jersey. M.S. Thesis, Rutgers University, New Brunswick, NJ. 133 p.
- CARLSON, A. M. AND D. L. GORCHOV. 2004. Effects of herbicide on the invasive biennial Alliaria petiolata (Garlic Mustard) and initial responses of native plants in a southwestern Ohio forest. Restoration Ecol., 12:558–566.
- CAVERS, P. B., M. I. HEAGY AND R. F. KOKRON. 1979. The biology of Canadian weeds. 35. Alliaria petiolata (M.Bieb) Cavara and Grande. Canadian J. Plant Sci., 59:217-229.
- COLLIER, M. H., J. L. VANKAT AND M. R. HUGHES. 2002. Diminished plant richness and abundance below Lonicera maackii, an invasive shrub. Am. Midl. Nat., 147:60-71.
- DAVIS, M. A., J. P. GRIME AND K. THOMPSON. 2000. Fluctuating resources in plant communities: a general theory of invasibility. J. Ecol., 88:528–534.
- ELLSWORTH, J. W., R. A. HARRINGTON AND J. H. FOWNES. 2004. Seedling emergence, growth, and allocation of Oriental bittersweet: effects of seed input, seed bank, and forest floor litter. For. Ecol. Manage., 190:255-264.
- FACELLI, J. M. AND S. T. A. PICKETT. 1991. Plant litter: dynamics and effects on plant community structure and dynamics. *Botanical Review*, 57:1–32.
- GENTLE, C. B. AND J. A. DUGGIN. 1997. *Lantana camara* L. invasions in dry rainforest open forest ecotones: the role of disturbances associated with fire and cattle grazing. *Aust. J. Ecol.*, **22**:298–306.
- GORCHOV, D. L. AND D. E. TRISEL 2003. Competitive effects of the invasive shrub, *Lonicera maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecology*, **166**:13-24.
- GOULD, A. M. A. AND D. L. GORCHOV. 2000. Effects of the exotic invasive shrub Lonicera maackii on the survival and fecundity of three species of native annuals. Am. Midl. Nat., 144:36–50.
- HAGER, H. A. 2004. Differential effects of *Typha* litter and plants on invasive *Lythrum salicaria* seedling survival and growth. *Biol. Invasions*, 6:433-444.
- HIDAYATI, S. N., J. M. BASKIN AND C. C. BASKIN. 2000. Dormancy-breaking and germination requirements of seeds of four *Lonicera* species (Caprifoliaceae) with underdeveloped spatulate embryos. *Seed Sci. Res.*, 10:459–469.
- HOBBS, R. J. AND L. F. HUENNEKE. 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol., 6:324–337.
- HUTCHINSON, T. F. AND J. L. VANKAT. 1997. Invasibility and effects of Amur Honeysuckle in southwestern Ohio forests. Conserv. Biol., 11:117–124.
- LUKEN, J. O. AND J. W. THIERET. 1996. Amur Honeysuckle, its fall from grace. Bioscience, 46:18-24.
- MCALPINE, K. G. AND D. R. DRAKE. 2002. The effects of small-scale environmental heterogeneity on seed germination in experimental treefall gaps in New Zealand. *Plant Ecol.*, **165**:207–215.
- McCARTHY, B. C. 1997. Response of a forest understory community to experimental removal of an invasive nonindigenous plant (*Alliaria petiolata*, Brassicaceae), p. 117–130. In: J. O. Luken and J. W. Thieret (eds.). Assessment and Management of Plant Invasions. Springer-Verlag, New York, New York, USA.
- MEEKINS, J. F. AND B. C. MCCARTHY. 1999. Competitive ability of Alliaria petiolata (garlic mustard, brassicaceae), an invasive, non-indigenous forest herb. International J. Plant Sciences, 160:743-752.
 - AND ———. 2001. Effect of environmental variation on the invasive success of a nonindigenous forest herb. *Ecol. Appl.*, 11:1336–1348.

- MILLER, K. E. AND D. L. GORCHOV. 2004. The invasive shrub, Lonicera maackii, reduces growth and fecundity of perennial forest herbs. Oecologia, 139:359-375.
- Nuzzo, V. A. 1993. Distribution and spread of the invasive biennial, Alliaria petiolata (garlic mustard) in North America, In: B. N. McKnight (ed.). Biological Pollution: The Control and Impact of Invasive Exotic Species. The Illinois Academy of Science, Indianapolis. p. 37-145.
- ORNDORFF, K. A. AND G. E. LANG. 1981. Leaf litter redistribution in a West Virginia hardwood forest. J. Ecol., 69:225-235.
- PARKER, I. M., S. K. MERTENS AND D. W. SCHEMSKE. 1993. Distribution of 7 native and 2 exotic plants in a tallgrass prairie in southeastern Wisconsin – the importance of human disturbance. Am. Midl. Nat., 130:42-55.
- PETERSON, C. J. AND J. M. FACELLI. 1992. Contrasting germination and seedling growth of Betula alleghaniensis and Rhus typhina subjected to various amounts and types of plant litter. Am. J. Bot., 79:1209–1216.
- SHURE, D. J. AND D. L. PHILIPS. 1987. Litterfall patterns within different sized disturbance patches in a southern Appalachian Mountain forest. Am. Midl. Nat., 118:348–357.
- STOHLGREN, T. J., L. D. SCHELL AND B. VANDEN HUEVEL. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecol. Appl.*, 9:45–64.
- THEIMER, T. C. AND C. A. GEHRING. 1999. Effects of a litter-disturbing species on tree seedling germination and survival in an Australian tropical rainforest. J. Trop. Ecol., 15:737-749.
- WHITE, P. S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review, 45:229-299.
- XIONG, S. AND C. NILSSON. 1999. The effects of plant litter on vegetation: a meta-analysis. J. Ecol., 87:984-994.

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