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# Effects of English Ivy (*Hedera helix*) on Seed Bank Formation and Germination

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ABSTRACT.—English ivy *Hedera helix* L. is rapidly invading forest ecosystems in the southeastern United States, leading to a decrease in the diversity of native plant species. To determine the underlying mechanism for the loss of diversity and understand the potential for restoration of impacted habitats, we examined whether ivy had a negative effect on seed bank formation and germination. We sampled the seed bank and the summer and fall seed rains in areas with and without ivy. In addition, we determined potential allelopathic effects of ivy on germination of *Coreopsis lanceolata* seeds. The density and species diversity of the seed bank and seed rains were not significantly different between areas with and without ivy. However, ivy led to a marginally significant reduction in the germination rate of *C. lanceolata* seeds. Yet, the effect of ivy on germination only occurred when ivy plants were present. Germination rates did not differ in soil from areas with and without ivy. Our results suggest that native plant communities can regenerate naturally from the seed bank if English ivy were removed.

## INTRODUCTION

Invasive species infestation has been recognized as the second largest threat after habitat loss facing native plant and animal species across the world (Wilcove *et al.*, 1998; Reichard and White, 2001). Invasive species are those species that have spread or are likely to spread into new habitats, develop self-sustaining populations, and become dominant or disruptive to that habitat (Reichard and White, 2001). Changes in community structure by exotics occur because introduced species outcompete native species or modify habitats or key ecosystem processes (Vitousek *et al.*, 1997; Levine *et al.*, 2003).

Although competition often is considered the predominant mechanism by which exotic species overtake native plants (Levine *et al.*, 2003), recent evidence suggests that exotics may invade because they can better exploit disturbed habitats or they are better dispersers than native species (Didham *et al.*, 2005). For example, in a study of garry oak (*Quercus garryana*) meadows, MacDougall and Turkington (2005) found that decreasing the biomass of exotic grasses or removing them completely did not lead to a recovery of the native species, as would be predicted if the exotics were outcompeting the native species. By adding seeds of native species to experimental plots, they determined that low recruitment limited the diversity of native species in disturbed habitats.

Distinguishing among the mechanisms by which exotic species impact native plant communities is important for several reasons. First, understanding of these mechanisms allows us to predict which communities are most likely to be impacted by invasive species (Kolar and Lodge, 2001; Heger and Trepl, 2003; Levine *et al.*, 2003; Minchinton *et al.*, 2006). Second, by determining the primary mechanisms through which invasive species affect native plants in a community, we are better able to make decisions about whether to remove an exotic species or not, and if so which methods would allow native species to be restored successfully (Levine *et al.*, 2003; Ortega and Pearson, 2005; Minchinton *et al.*, 2006).

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English ivy *Hedera helix* L. is an exotic species that is rapidly naturalizing throughout the United States and many other parts of the world. After escaping cultivation, ivy has become common throughout many forests in the southeastern Piedmont and the Pacific Northwest. Currently, it is found in 24 states and is listed as a noxious weed in Oregon and California, even reaching quarantined status in Oregon (USDA, NCRS 2006). Because ivy is more likely to invade disturbed forests, its spread through the southeastern United States has been helped dramatically by the region's history of extensive logging and human habitation (Thomas, 1998). Thomas (1998) suggested that ivy's advantage came from increased light into a forest that had been cut at some point and decreased root competition from trees since they had been cleared for construction projects.

The invasion of ivy into forested areas is facilitated further by its vegetative reproduction and its seed distribution and sprouting. Ivy's rate of vegetative growth can be dramatic. Ivy has been shown to produce as much as 87.1 g/m<sup>2</sup> of biomass a year (Thomas, 1998). The efficiency of its seed germination is just as dramatic. With its pulp removed or ingested by birds, ivy's seed has an almost 100% germination rate and starts to germinate within a couple of weeks of sowing (Clergeau, 1992). Even within its native ecosystem in Europe, ivy can dominate a secondary woodland within 30 y after introduction (Harmer *et al.*, 2001).

Once ivy has invaded, it is able to achieve dominance in a forest ecosystem with its rapid growth, excellent shade tolerance, root sprouting ability, climbing and spreading growth ability and possible allelopathic ability (Hines, 1995). Ivy forms a dense ground cover that prevents the emergence of almost all herbs and dramatically reduces light levels (Thomas, 1980; Harmer *et al.*, 2001).

The general aim of our study was to determine the mechanisms by which English ivy might affect the regeneration of native plant species in a southeastern Piedmont forest after it had been removed. Specifically, we examined if: (1) ivy affects the size or composition of the seed rain or seed bank and (2) ivy has allelopathic effects on seed germination. It is unknown whether ivy has an effect on the size or the composition of the seed rain or seed bank, both of which will contribute to the regeneration of the forest once ivy is pulled (Hyatt and Casper, 2000; Lambers *et al.*, 2005). Hines (1995) found evidence for the allelopathic effects of ivy, but Rice (1976) in a review of the topic did not.

## METHODS

### SEED BANK FORMATION

We examined the existing seed bank and collected the seed rain in a hardwood forest in Oxford, GA (33.5°N, 84.2°W). The study site is a typical secondary Piedmont forest and is dominated by *Liriodendron tulipifera*, *Liquidambar styraciflua* L. and *Nyssa sylvatica*.

To determine the composition of the existing seed bank, 10 141 cm<sup>3</sup> samples to a depth of 10 cm of the seed bank from areas infested with ivy and not infested with ivy were collected on 6 June 2002 on 4 ha plot. We determined sampling locations using random angle measurements and random distances from a single point on a trail along one edge of the plot. Ivy areas were completely covered by ivy, and it has been estimated that ivy has covered those areas for at least thirty years (E. B. Carter, pers. comm.). Areas without ivy have been free of ivy for more than three years and included a mix of areas where ivy had been removed and where ivy had never existed (E. B. Carter, pers. comm.).

The 0.00141 m<sup>2</sup> soil core from each point was spread to a depth of less than 3 mm on 1020 standard flats (54.6 × 28.3 × 6 cm) containing seedless, soilless medium (MetroMix360) and seeds were allowed to germinate in a greenhouse. Flats were alternated for the two site types. The flats were watered three times a day for 5 min from June to

October and for 2 min from October to March. The temperature was maintained at 18 C during the night and 24 C during the day, and the flats were exposed to natural light conditions. The rate of germination was recorded as seeds sprouted and species were determined as plants flowered. Species that never flowered and were unidentifiable to the researchers through leaf or growth characteristics were marked as unknown.

To determine the effects of ivy on spring/early summer seed rain, 10 1020 standard flats (54.6 × 28.3 × 6 cm) flats filled with seedless, soilless medium (MetroMix 360) each were placed flush with soil level in areas where ivy was present and where ivy was not present on 6 June 2002 and allowed to remain there until 5 July 2002, to collect seed rain. In areas with ivy, we placed ivy back over the flat after it was installed. After the flats were removed from the field, they were chilled at 4 C to simulate winter chilling conditions for 2 wk. After cold hardening, seeds were allowed to germinate in same greenhouse conditions as for the seed bank experiment. Seedlings were keyed to species, if possible.

To examine late summer/early fall seed rain, we repeated the above procedure with initial placement of flats in 5 July 2002, and removal on 30 November 2002.

We used unpaired *t*-tests with the presence or absence of ivy in the areas sampled as the grouping variable to examine differences in seedling density, species richness, and diversity for the seed bank and both the seed rain experiments. We used Simpson Index and Shannon-Weaver index as measures of diversity. The results were the same for both indices. As a result, we only present the results for the Shannon-Weaver Index.

#### ALLELOPATHY

Simultaneous with the seed bank experiments, we conducted two allelopathy experiments to examine the effect of English ivy on germination of a perennial native to the piedmont of Georgia. In the first experiment, we examined whether ivy plants have direct allelopathic effects on germination. To do this, 15 ivy plants were grown in a greenhouse in 15 cm diameter pots filled with seedless, soilless medium (MetroMix360) for six weeks to allow roots to establish in the soil. The 15 ivy plants were trained along a trellis after potting to prevent competition for light between ivy and the coreopsis seeds and plants. Fifteen pots without ivy also were placed in the greenhouse at the same time as the pots containing ivy so that they would receive the same watering treatments. Ten seeds of *Coreopsis lanceolata* were sown in each pot. We chose *C. lanceolata* because it is a native perennial with simple growth requirements that might colonize treefall gaps that are common in southeastern forests with English ivy. The pots were arranged in an alternating pattern of ivy and no ivy and the pots were watered and maintained under the same greenhouse conditions as seed bank experiments. Pots were never allowed to dry out between waterings to prevent competition for water between ivy and coreopsis, and fertilizer was given to ivy and no ivy pots every two weeks to prevent competition for nutrients between ivy and no ivy. Germination rates were determined two months after seeds were sown.

In the second experiment, we examined whether there is a residual allelopathic effect of ivy on germination. We collected the top 5 cm of soil without leaf litter from areas where ivy was present and not present at the study site in Oxford, GA, used for the seed bank experiment. Each type of soil was placed in 1020 standard flats (54.6 × 28.3 × 6 cm). Seeds of *Coreopsis lanceolata* were sown in each flat at a rate of 515 seeds/m<sup>2</sup>. This density of seeds was found in a Piedmont forest in Pennsylvania (Hyatt and Casper, 2000). Flats were arranged in an alternating ivy and no ivy pattern and maintained in the same greenhouse conditions as the seed bank experiments. The percent germination was determined two months after planting. Since ivy plants were not present in this experiment, any effects of soil from ivy sites on germination cannot be attributed to physical competition.

TABLE 1.—Effect of English ivy on density and diversity of seed bank and seed rain. Mean  $\pm$  SE

	Seed Bank		Spring/Early Summer Seed Rain		Late Summer/Fall Seed Rain	
	Ivy	No Ivy	Ivy	No Ivy	Ivy	No Ivy
Seedling density (seedlings/m <sup>2</sup> )	2553 $\pm$ 451	2624 $\pm$ 826	6.5 $\pm$ 1.9	11.6 $\pm$ 1.9	78.3 $\pm$ 10.9	59.5 $\pm$ 7.9
Species richness	2.0 $\pm$ 0.3	1.9 $\pm$ 0.4	0.7 $\pm$ 0.2	1.6 $\pm$ 0.4	2.8 $\pm$ 0.4	2.1 $\pm$ 0.4
Shannon-Weaver	1.8 $\pm$ 0.3	1.8 $\pm$ 0.4	0.7 $\pm$ 0.2	1.1 $\pm$ 0.3	1.9 $\pm$ 0.2	1.6 $\pm$ 0.3

To determine whether there were allelopathic effects of ivy, we compared germination rates *Coreopsis* seedlings in pots with and without ivy using unpaired t-tests. We also compared germination rates of seedlings grown in flats with soil from field sites with and without ivy to examine whether there are residual allelopathic effects of ivy even after ivy is removed.

## RESULTS

### SEED BANK FORMATION

For the existing seed bank, the density of seedlings germinated from the seed banks of ivy and no ivy sites did not differ significantly ( $t = -0.075$ , d.f. = 18,  $P = 0.94$ ) (Table 1). In addition, species richness and Shannon-Weaver indexes for sites with and without ivy were very similar (species richness:  $t = 0.18$ , d.f. = 18,  $P = 0.86$ ; Shannon-Weaver:  $t = -0.007$ , d.f. = 18,  $P = 0.99$ ) (Table 1). Tulip poplar, pokeweed (*Phytolacca americana* L.) and goldenrod (*Solidago arguta*) were the most numerous seedlings (see Table 2 for complete listing of seedling species).

For the spring/early summer seed rain, we found patterns of increased seedling density, species richness and diversity in sites without ivy (Table 1). However, the presence of ivy did not have a significant effect on the density of seedlings that germinated ( $t = -1.45$ , d.f. = 18,  $P = 0.17$ ), the species richness of seedlings ( $t = -1.8$ , d.f. = 18, and  $P = 0.09$ ) or the diversity of seedlings ( $t = -1.08$ , d.f. = 18,  $P = 0.30$ ). Of species that germinated from the seed rain (Table 2), the most numerous seedlings were *Gnaphalium purpureum* and *Facelis retusa*.

In contrast to the spring/early summer seed rain, seedling density, species richness and diversity for the late summer/fall seed rain tended to be higher in areas where ivy was growing than in areas where ivy was absent (Table 1). However, there were no significant differences between ivy and no ivy sites for any of the measures ( $P > 0.18$  in all cases). Tulip poplar, blackberry (*Rubus* sp.) and goldenrod were the most abundant species (Table 2).

### ALLELOPATHY

In the first experiment in which seeds were planted in pots with or without ivy, *Coreopsis* germinated  $51.3 \pm 4.7\%$  of the time in pots with ivy and germinated  $64.0 \pm 4.6\%$  of the time in pots without ivy. The decrease in germination in the presence of ivy plants was marginally significant ( $t = -1.94$ , d.f. = 28,  $P = 0.06$ ). However, the power of the test was low (Power = 0.45). Therefore, the decrease in germination in the presence of ivy is most likely a real effect. In contrast to when ivy plants were present, the germination of *Coreopsis* seeds did not differ significantly based on whether the soil in which they were planted was from sites with ivy or sites without ivy ( $t = -1.35$ , d.f. = 18,  $P = 0.20$ ). *Coreopsis* seedlings germinated  $30.5 \pm$

TABLE 2.—List of known species or genus found in seed bank and seed rain experiments

Species	Common Name	Seed Bank		Spring/Early Summer Seed Rain		Late Summer/Fall Seed Rain	
		Ivy	No Ivy	Ivy	No Ivy	Ivy	No Ivy
<i>Facelis retusa</i>	Trampweed			x	x		
<i>Gnaphalium purpurea</i> (N)	Cudweed			x	x		
<i>Liriodendron tulipifera</i> (N)	Tulip Poplar		x			x	x
<i>Morus</i> sp. (N)	Mulberry	x			x		
<i>Nyssa sylvatica</i> (N)	Black Gum		x				
<i>Parthenocissus quinquefolia</i> (N)	Virginia Creeper					x	
<i>Physalis angulata</i> (N)	Ground Cherry		x				
<i>Phytolacca americana</i> (N)	Pokeweed		x				x
<i>Potentilla canadensis</i> (N)	Five Fingers	x	x				x
<i>Pueraria montana</i>	Kudzu	x					
<i>Rubus</i> sp. (N)	Blackberry		x			x	
<i>Solidago arguta</i> (N)	Goldenrod	x	x			x	
<i>Violet</i> sp.	Violet						x

Note: (N)=Native. Scientific names taken from USDA, NRCS (2002)

1.9% of the time in soil where ivy plants had been present while germinating  $35.2 \pm 2.9\%$  of the time in soil where ivy plants had not been present.

#### DISCUSSION

Although English ivy forms a dense ground cover that prevents the emergence of most herbs (Thomas, 1980; Harmer *et al.*, 2001), ivy did not appear to hinder the establishment of a seed bank. Furthermore, ivy only had marginally significant allelopathic effects on seed germination when it was present. Seeds germinated equally well in soil from plots with and without ivy.

#### SEED BANK FORMATION

Sampling of the seed bank indicates that that ivy does not significantly affect the number of seeds or the diversity of seeds in the seed bank. In a similar study in New Zealand, Standish *et al.* (2001) also found that the seed bank and seed rain were not affected by *Tradescantia fluminensis*, an exotic species that also creates a dense ground cover. In contrast, in two previous studies, a single invasive species was able to reduce the diversity and abundance of the seed bank (Holmes and Cowling, 1997; Dunbar and Facelli, 1999). However, in both of those studies the invader was a woody plant that became the tallest species in the area and outcompeted all plants beneath it.

The dynamics of seed banks can be influenced by seed rain, loss of seeds due to germination and loss of seeds due to seed mortality (Baker, 1989). The similarity of the seed bank in areas with and without ivy suggests that these factors are not influenced by the presence of ivy or have little impact on the seed bank at our study site. Indeed, we found that ivy has no significant effect on seed rain. In contrast, areas without ivy should have lost seeds due to germination at a much higher rate than areas with ivy. In a field study at the same site, we found that seeds rapidly germinated in areas from which ivy was removed, whereas no seedlings germinated in areas with complete ivy coverage (Biggerstaff and Beck, in press). Thus, even the plots that had been free of ivy for only three years should have lost

seeds from the seed bank due to germination. However, in the field study, the density of seedlings in plots without ivy was low ( $<6$  seedlings/m<sup>2</sup>) (Biggerstaff and Beck, in press). Therefore, even if the areas that we sampled without ivy have been losing seeds to germination, this loss is small relative to the size of the seed bank and the annual seed rain. Finally, a seed bank can be depleted by seed mortality. Many of the woody species found in the seed bank and seed rain are known to persist in seed banks (Lambers *et al.*, 2005), which suggests that seed mortality is low enough for seeds to survive more than one year. How ivy might influence seed mortality is unknown. However, the lack of an effect of ivy on the size of the seed bank suggests that ivy does not greatly increase seed mortality.

#### ALLELOPATHY

The germination of *Coreopsis* was reduced to a marginally significant degree when exposed to English ivy. While physical competition is still a possibility, our experimental design removed competition for light, water and nutrients. Thus, the reduction in germination of *Coreopsis* suggests a possible allelopathic effect of ivy. Our results coincide with those of Hines (1995), who found decreased germination of radish (*Raphanus* sp.) and pansy (*Viola* sp.) in soil mixed with ivy leaves. The possible allelopathic effects of ivy on germination of native plants suggests a mechanism in addition to decreasing light levels (Thomas, 1980; Harmer *et al.*, 2001) by which ivy may exclude native herbaceous species.

Even though ivy did have a marginally significant effect on germination rates when present, the allelopathic effects of ivy do not appear to remain in the soil after ivy is removed, as we found no significant difference between the germination rates of seeds sown in soil where ivy had and had not been present. In contrast, Wardle *et al.* (1991) used a similar experimental approach and found significant residual allelopathic effects of six species of pasture grass on seedling emergence of nodding thistle (*Carduus nutans*). In many cases, the residual allelopathic effect increased in strength with time since removal of the grasses, perhaps due to the decomposition of exudates from the roots of the grasses (Wardle *et al.*, 1991). Therefore, we might have found a residual allelopathic effect of ivy if we had stored the soil from ivy plots for a period of time before sowing the *Coreopsis* seed. However, in a field study, we found that native seedlings returned rapidly after removal of ivy (Biggerstaff and Beck, in press), which suggests that any allelopathic chemicals produced by ivy degrade rapidly, rather than increase in strength over time.

#### CONCLUSIONS

English ivy may depress the diversity of the local plant community greatly. However, the results of our experiments suggest that the plant community should be able to restore itself naturally after ivy is removed, as ivy does not negatively impact the formation of a seed bank or the germination of those seeds. Yet, the species composition of the community after ivy is removed will depend on nearby seed sources and the persistence of seeds in the seed bank. In sites such as the one that we studied, where the seed bank contains invasive species (*e.g.*, *Pueraria montana*) and where less tolerant native species may have been lost from the community, restoration efforts can be improved by introducing seeds of native species to help restore the site to its previous diversity (Biggerstaff and Beck, in press).

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