

Separating Above- and Belowground Effects of *Alliaria petiolata* and *Lonicera maackii* on the Performance of *Impatiens capensis*

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ABSTRACT.—Invasive plants can exert their effects on native plants through both above- and belowground mechanisms. In a fully factorial field study, we examined the effects of activated carbon addition and removal of aboveground biomass (*i.e.*, cutting) on the survival, growth and reproduction of transplanted *Impatiens capensis* seedlings in habitats dominated by either *Lonicera maackii* (honeysuckle) or *Alliaria petiolata* (garlic mustard). Activated carbon can adsorb organic molecules, including potential allelochemicals. Cutting of *A. petiolata* increased survival and fruit production of *I. capensis*, while cutting of *L. maackii* increased survival and tended to increase fruit production. Carbon application tended to increase survival of *I. capensis* in *A. petiolata*-dominated plots, but had no effect in *L. maackii*-dominated plots. The effects of carbon application on growth and fruit production of *I. capensis* depended upon the cutting treatment in *A. petiolata* – dominated plots. In plots where *A. petiolata* was not cut, carbon application increased height and fruit production. In plots where *A. petiolata* was cut, carbon application decreased height and tended to decrease fruit production. *Impatiens capensis* tended to survive longer when in competition with *A. petiolata* than with *L. maackii*. While carbon application may benefit native plant growth in the presence of *A. petiolata*, the addition of activated carbon after removal of aboveground biomass, a source of both allelochemicals and light competition, may have little benefit as an understory plant restoration tool.

INTRODUCTION

In recent years, concern regarding invasive species has increased worldwide. In the United States alone, the economic impact of invasive species across taxonomic groups is approximately \$120 billion per year; further, invasive species have been anecdotally identified as a threat, at least in part, for one-half of endangered or threatened species (Pimentel *et al.*, 2005). Plants make up a significant portion of invasive species worldwide. The phenomenal success of invasive plants has been attributed to a variety of traits that provide advantages over native species (Levine *et al.*, 2003). Most generally, invasive plants may negatively impact other species through aboveground competition, especially for light (Braithwaite *et al.*, 1989; Woods, 1993). Invasive plants that are successful competitors for light and reduce its availability to other species are likely to have major impacts in invaded communities.

Invasive plants may also affect other species through belowground mechanisms. In addition to competition for soil resources, most plant species produce some allelopathic compounds, such as monoterpenes or phenols, in their roots and leaves (Ehrenfeld, 2006). Germination, growth and reproduction of neighboring plants can be affected by these compounds as a result of their impacts on various physiological processes (Rice, 1974).

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Allelopathic compounds released by plants may have direct effects through plant-plant interference or may have indirect effects through altering soil chemical ecology (Inderjit and Weiner, 2001). The release of allelopathic compounds appears to contribute to the success of several important invaders of North America (Hierro and Callaway, 2003; Orr *et al.*, 2005). In addition, allelopathic compounds produced by some plants may have greater effects on species that have not been exposed to such compounds in invaded habitats than on adapted species in their native range, a phenomenon known as the novel weapons hypothesis (Callaway and Ridenour, 2004).

The effects of allelopathy may be mitigated through the use of activated carbon, which specifically adsorbs organic molecules from aqueous solutions or soils with little effect on inorganic nutrients. Application of carbon to soils mitigated the phytotoxic effects of *Centaurea maculosa* on both conspecifics and other species (Ridenour and Callaway, 2001; Perry *et al.*, 2005). Further, *Festuca* plants grown with carbon in the absence of *C. maculosa* were actually 20% smaller than those grown in the absence of carbon, suggesting that intrinsic effects of carbon are unlikely to be the cause of increased plant performance in the presence of a competitor (Ridenour and Callaway, 2001). Kulmatiski and Beard (2006) found that in fields that had experienced invasive species dominance for nearly 47 y, activated carbon application to field plots was effective in decreasing the frequency of invasive species, while increasing the abundance of native species. Activated carbon therefore provides a tool to investigate the importance of belowground influences of invaders on native plant individuals and communities, and may be useful in restoration activities.

There are two invasive species prominent in the Midwest that may exhibit allelopathic effects. *Alliaria petiolata* (Bieb.) Cavara & Grande (Brassicaceae), garlic mustard, is a biennial Eurasian herb, which was first introduced to North America for medicinal and culinary purposes (Nuzzo, 1993). This plant is a major herbaceous invader of forest understory and edge communities throughout North America. *Alliaria petiolata* plants have demonstrated negative effects on a wide range of native understory plant species, including *Impatiens capensis* (McCarthy, 1997; Meekins and McCarthy, 1999; Carlson and Gorchoff, 2004; Hochstedler *et al.*, 2007). The primary mechanism driving the success of *A. petiolata* is unknown, but allelopathy and resource competition are both probably important (Meekins and McCarthy, 1999; Vaughn and Berhow, 1999; Prati and Bossdorf, 2004). McCarthy and Hanson (1998) concluded that *A. petiolata* was successful because of its ability as a competitor, and that allelopathy was unlikely to be important. However, Vaughn and Berhow (1999) isolated two major glucosinolates from garlic mustard and suggested that these compounds can inhibit the germination and growth of mycorrhizal fungi, a result corroborated by Roberts and Anderson (2001). Stinson *et al.* (2006) recently demonstrated that *A. petiolata* does in fact negatively impact growth of several tree species through disruption of mycorrhizal mutualisms. Prati and Bossdorf (2004) showed that soil conditioning by *A. petiolata* inhibited germination of *Geum* species, an effect that could be mitigated with activated carbon. In addition to glucosinolates, other allelochemicals that garlic mustard contains include a variety of allyl and flavonoid glycosides and cyanide (Cipollini *et al.*, 2005; Cipollini and Gruner, 2007).

Lonicera maackii (Rupr.) Maxim (Caprifoliaceae), Amur honeysuckle, is native to northeastern China, Korea, Siberia and Japan and was first introduced in North America for landscaping and wildlife habitat (Luken and Thieret, 1995). This shrub is a major woody invader of forest edges, old-fields and disturbed forest understories throughout eastern North America and the Midwest. *Lonicera maackii* is thought to negatively affect herbaceous

plants, tree seedlings and spring ephemerals primarily through competition for light (Hutchinson and Vankat, 1997; Gould and Gorchov, 2000; Miller and Gorchov, 2004). Removal of *L. maackii* has been shown to increase survival and fruit production of *Impatiens pallida* (Gould and Gorchov, 2000). Hartman and McCarthy (2004) associated increased native seedling survival in plots where *L. maackii* had been removed with increased light availability. Gorchov and Trisel (2003) found that aboveground effects (*i.e.*, shading) were more important than belowground effects on native tree seedlings, although the study focused on belowground resource competition rather than allelopathy. The allelopathic effects of leaf extracts of *L. maackii* on several woody and herbaceous species, including *I. capensis*, have been demonstrated (Cipollini and Dorning, 2006; Cipollini *et al.*, 2008a). In addition, Cipollini *et al.* (2008b) demonstrated the allelopathic potential of several phenolic metabolites in methanol extracts of leaves of *L. maackii*.

For these two invaders, debate still exists on the relative importance of aboveground versus belowground influences on native plant performance. In this study, we investigated the effect of removal of aboveground biomass (*i.e.*, cutting) and activated carbon addition to field plots dominated by either *Lonicera maackii* or *Alliaria petiolata* on the performance of the co-occurring native annual herb *Impatiens capensis* Meerb. (Balsaminaceae) jewelweed. *Impatiens capensis* was chosen for this study due to its ready availability, the ability to measure reproduction in a single season and previous evidence that *Impatiens* species are negatively impacted by *A. petiolata* and *L. maackii* (McCarthy, 1997; Gould and Gorchov, 2000). Cutting was intended to primarily ameliorate light competition, but may also remove a source of allelochemicals and may have increased soil moisture availability through a reduction in transpiration. Activated carbon addition was intended to mitigate the effects of putative allelochemicals in the soil, but may have other unknown effects on soil characteristics. We expected that *I. capensis* growing with uncut invasive species in the absence of activated carbon would exhibit the lowest seedling survival and growth, while treatments with cut invasive species and added activated carbon would exhibit the highest rates. The outcome of the other two treatment combinations would elucidate the extent to which each of these factors affected plant performance. We expected that cutting would be particularly beneficial for *I. capensis* in *L. maackii*-dominated plots, while activated carbon addition would particularly benefit performance of *I. capensis* in *A. petiolata*-dominated plots. The basis for this expectation is that *L. maackii* produces dense shade with an extended leaf phenology and has been shown to have strong aboveground effects (Gould and Gorchov, 2000; Gorchov and Trisel, 2003; Miller and Gorchov, 2004), which may be more important than the allelochemicals that it produces (Trisel, 1997; Dorning and Cipollini, 2006; Cipollini *et al.*, 2008a). In addition, research has demonstrated that *A. petiolata* affects soil composition and native plants through the release of allelochemicals (Prati and Bossdorf, 2004; Stinson *et al.*, 2006), and it is unlikely to influence light availability for *I. capensis* as much as *L. maackii* due to its smaller stature.

METHODS

We performed the study in a natural area adjacent to the Frank O. Hazard Arboretum of Wilmington College in Wilmington, Ohio, in 2006. The study area is found along Lytle Creek and contains a second-growth maple-beech-oak forest. The soil types in the study area are either Sloan silt loam or Sligo silt loam, which are considered floodplain soils (Garner and Meeker, 1962). For each invasive species, we used a fully factorial blocked design with the main factors of activated carbon (+ or -) and removal of aboveground biomass (+ or -). Treatments were replicated in four sites (or blocks) for each invasive species. The

four sites per invasive species were independently selected based on the visually-even distribution of either second-year *Alliaria petiolata* or mature *Lonicera maackii*, taking care to avoid sites with both species. Sites were separated by no more than 0.5 km. There were very few other species present in the chosen invaded sites. We selected and prepared the sites on 28 Apr. and 5 May. Within each of the four main sites per invasive species, we established four 1-m² main plots, with six 100-cm² subplots, where *Impatiens capensis* would be subsequently transplanted. The treatment combinations were haphazardly assigned to each main plot in each site. For activated carbon treatments, we added 10 mile of activated carbon (Aquarium Pharmaceuticals Black Magic Activated Carbon, Chalfont, Penn.) and mixed it into the first 8 cm of soil in each of the 100-cm² subplots. This ratio of activated carbon to soil volume has been shown to ameliorate allelopathic effects in other studies (Ridenour and Callaway, 2001; Prati and Bossdorf, 2004). We disturbed an equivalent area of soil at every subplot, regardless of whether carbon was applied, to control for soil disturbance effects. At the same time, for removal treatments, we cut and removed the aboveground biomass of each invasive species at the soil surface. For *L. maackii*-dominated areas, plots were located directly adjacent to the stem of the *L. maackii* plants. For *A. petiolata*-dominated areas, plots were located in the midst of several *A. petiolata* individuals. Although removing aboveground biomass also certainly affected belowground competition, we did not kill the roots of either species, which remained alive and resprouted throughout the growing season. On 13 May we planted one *I. capensis* seedling, all of similar height and obtained locally within the natural area, in each subplot in each main plot, yielding 96 experimental plants per invasive species (4 sites \times 2 cutting treatments \times 2 carbon treatments \times 6 plants). On 17 May we constructed cages using grade stakes and chicken wire and placed them over each of the main plots to protect the seedlings from herbivory and trampling by deer or other animals.

We measured height, number of fruits and survival of the seedlings on a bi-weekly basis after the transplants had been allowed sufficient time to establish in their new areas. Measurements began on 18 Jun. and ended on 13 Aug. Because the exact day of death of experimental plants could not be determined, survival was determined by noting the sampling time period during which mortality occurred and assigning the interval a number from one to five. The maximum height and fruit number were determined for each plant that was not affected by vandalism or transplant stress. Plants that died prior to 16 Jul. were excluded from the analysis of maximum height and fruit number, as it was assumed that they were unable to successfully reproduce in this time period. A total of 23 plants were destroyed by vandalism in the *Lonicera maackii*-dominated plots. For the *Alliaria petiolata* experiment, there were 70 plants included in the height and fruit analysis, while for the *L. maackii* experiment, there were 38 plants included in the height and fruit analysis.

For each invasive species, the maximum fruit number, maximum height and interval of death for *Impatiens capensis* were analyzed using a three-way mixed model nested Analysis of Variance (ANOVA), with the main random factor of site and the two fixed main factors of cutting and carbon application (Ryan *et al.*, 2005). In the ANOVA model, each *I. capensis* plant was nested in the interaction of cutting and carbon application which accounts for the non-independence of the *I. capensis* plants in each main plot (Neter *et al.*, 1996). The only interaction investigated in the ANOVA model was the interaction of cutting and carbon application, which was the primary interaction of interest. Data for the *Alliaria petiolata* and *Lonicera maackii* plots were analyzed separately. For *L. maackii* plots, the site factor was removed from the model because there were fewer data points due to vandalism and lower survival. The

low sample size did not allow us to include this source of variation and this factor was not of primary interest. There was an outlier in the *L. maackii* plots that was excluded from the height and fruit data analysis in order to meet the model assumption of normality, which was tested using the Ryan-Joiner Method for all analyses (Ryan *et al.*, 2005). A failure-time analysis was not used for the survival data due to the non-independence of *I. capensis* plants within each plot, an important assumption of this statistical method (Fox, 1993). The relationship between fruit number and height was investigated using simple linear regression separately for data from the *A. petiolata* and *L. maackii* plots. To examine differences between *L. maackii* and *A. petiolata* plots, the average *I. capensis* height, fruit number and survival was determined for each site and then a simple *t*-test was performed using these four site averages per invasive species. The alpha level to determine significance was set at 0.05 for all tests.

RESULTS

For the *Alliaria petiolata*-dominated plots, survival was significantly affected by site ($F_{3, 49} = 9.30$, $P < 0.001$) and cutting ($F_{1, 49} = 8.94$, $P = 0.004$; Fig. 1). *Impatiens capensis* plants lived longer where *A. petiolata* was removed. The effect of carbon on survival approached significance ($F_{1, 49} = 3.67$, $P = 0.063$; Fig. 1), with carbon application increasing survival. Plant height was significantly affected by site ($F_{3, 43} = 7.63$, $P < 0.001$) and the interaction of carbon application and cutting ($F_{1, 43} = 9.10$, $P = 0.004$; Fig. 2). In plots where *A. petiolata* was uncut, application of carbon increased height, while in plots where *A. petiolata* was cut, application of carbon decreased height. Fruit number was significantly affected by site ($F_{3, 43} = 8.06$, $P < 0.001$) and cutting ($F_{1, 43} = 10.54$, $P = 0.002$; Fig. 2). Cutting of aboveground biomass of *A. petiolata* increased fruit production in *I. capensis*. The interaction of carbon application and cutting on fruit number was marginally significant ($F_{1, 43} = 3.93$, $P = 0.054$; Fig. 2). In plots where *A. petiolata* was not cut, application of carbon increased fruit production, while in plots where *A. petiolata* was cut, application of carbon had a slight negative effect on fruit production. Maximum height and maximum fruit number were significantly positively related ($F_{1, 58} = 33.63$, $P < 0.001$, $r^2 = 0.367$).

For the *Lonicera maackii*-dominated plots, cutting significantly increased survival ($F_{1, 29} = 40.88$, $P < 0.001$; Fig. 1). There was no effect of carbon application, cutting or their interaction on maximum height (Fig. 3). Cutting nearly significantly increased maximum fruit number ($F_{1, 18} = 3.11$, $P = 0.095$; Fig. 3). Maximum height and maximum fruit number were significantly positively related ($F_{1, 35} = 16.51$, $P < 0.001$, $r^2 = 0.321$).

Impatiens capensis lived longer, achieved greater maximum height and produced more fruits in *Alliaria petiolata* plots compared to *Lonicera maackii* plots, although only the first was marginally significant ($t = 3.00$, $P = 0.058$; Fig. 4).

DISCUSSION

In the *Alliaria petiolata*-dominated plots, *Impatiens capensis* benefited independently from both amelioration of above-ground effects and from application of activated carbon. Past research concerning the success of *A. petiolata* has implicated both light competition and allelopathy independently, and this is the first study to show the importance of the interaction of these factors. McCarthy and Hanson (1998) thought that the negative effects of *A. petiolata* on native species were most likely associated with aboveground competition and not allelopathy. Indeed, Meekins and McCarthy (1999) showed that first year rosettes of *A. petiolata* can compete successfully with some woody plant seedlings, but not with *I. capensis*. Here, we found that cutting of aboveground biomass of second-year *A. petiolata* increased reproduction and survival of *I. capensis* seedlings. Other studies have

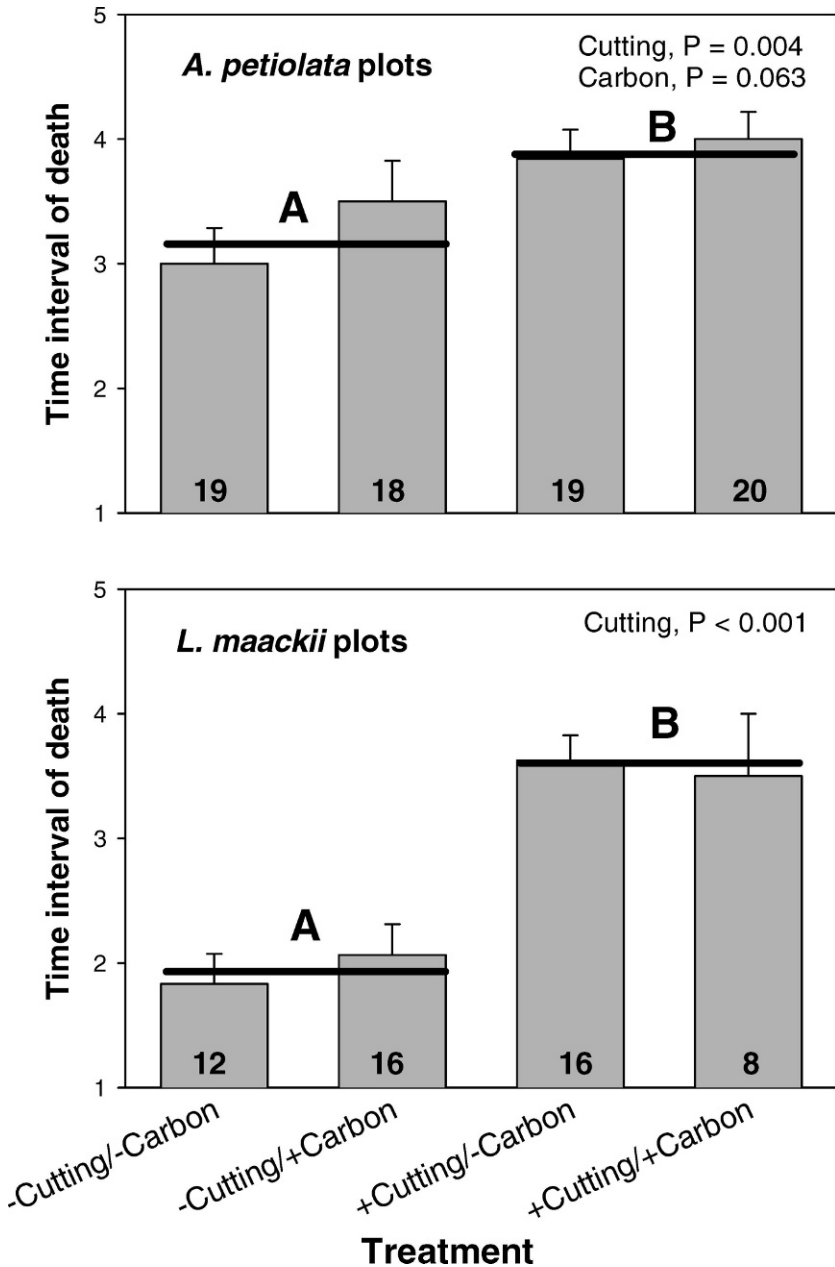


FIG. 1.—Mean \pm SE time interval of death for *Impatiens capensis* plants for the four treatment combinations of aboveground cutting and soil application of activated carbon for both *Lonicera maackii* and *Alliaria petiolata* plots. Horizontal bars indicate means for two levels of main factor of cutting. Horizontal bars with the same letter are not significantly different at P = 0.05. Numbers on each bar indicate the sample size (n) for each treatment combination. Time interval of death was determined by noting the sampling interval during which mortality occurred and assigning the interval a number from 1 to 5

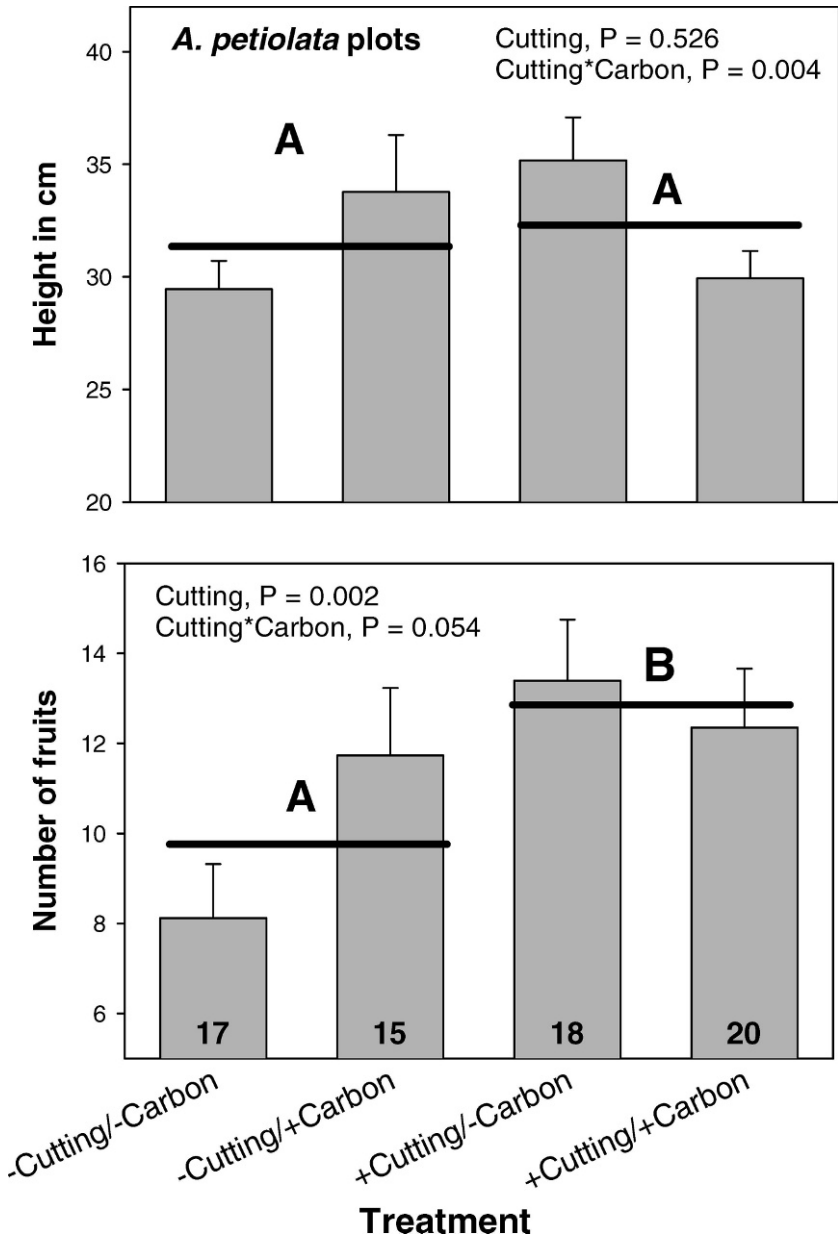


FIG. 2.—Mean \pm SE maximum height and maximum fruit number for *Impatiens capensis* plants found in *Alliaria petiolata* plots for the four treatment combinations of aboveground cutting and soil application of activated carbon. Horizontal bars indicate means for two levels of main factor of cutting (+ and -). Horizontal bars with the same letter are not significantly different at $P = 0.05$. Numbers on each bar indicate the sample size (n) for each treatment combination; sample size is the same for both maximum fruit and maximum height means

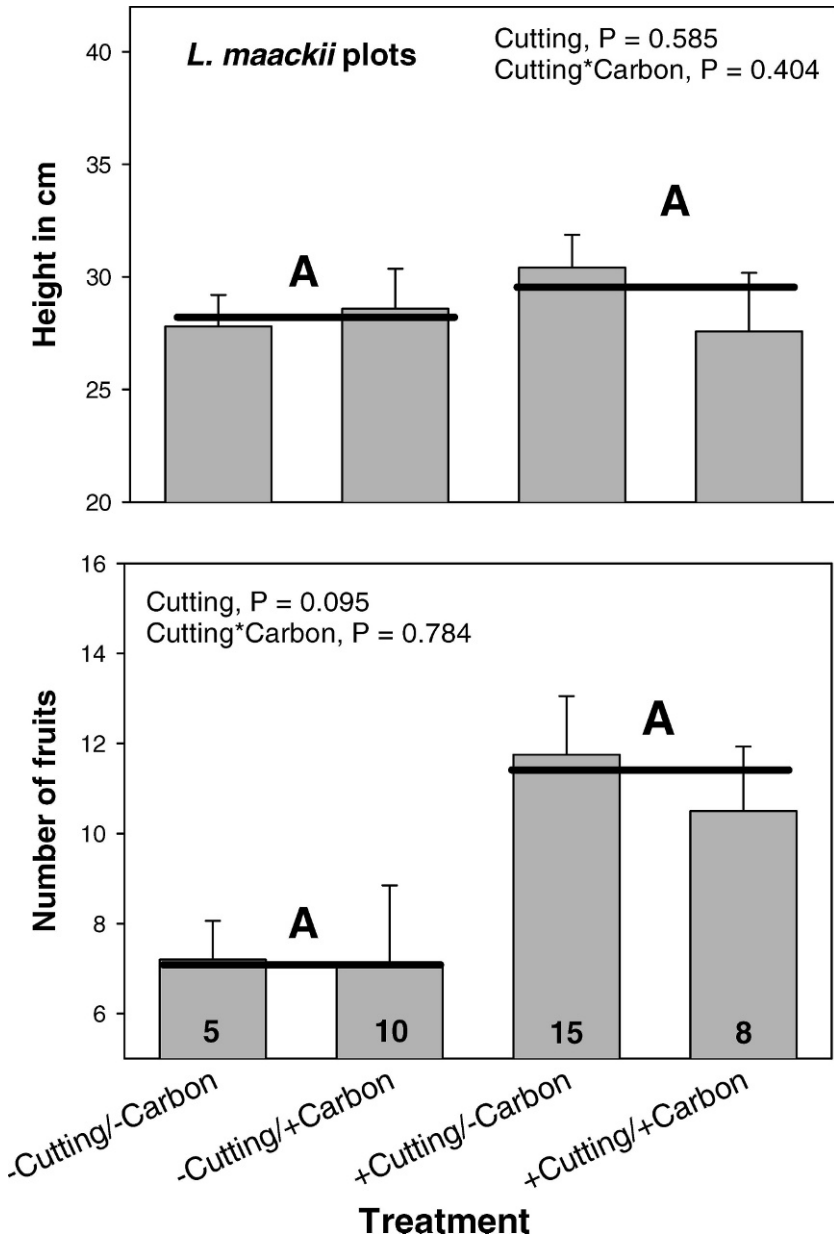


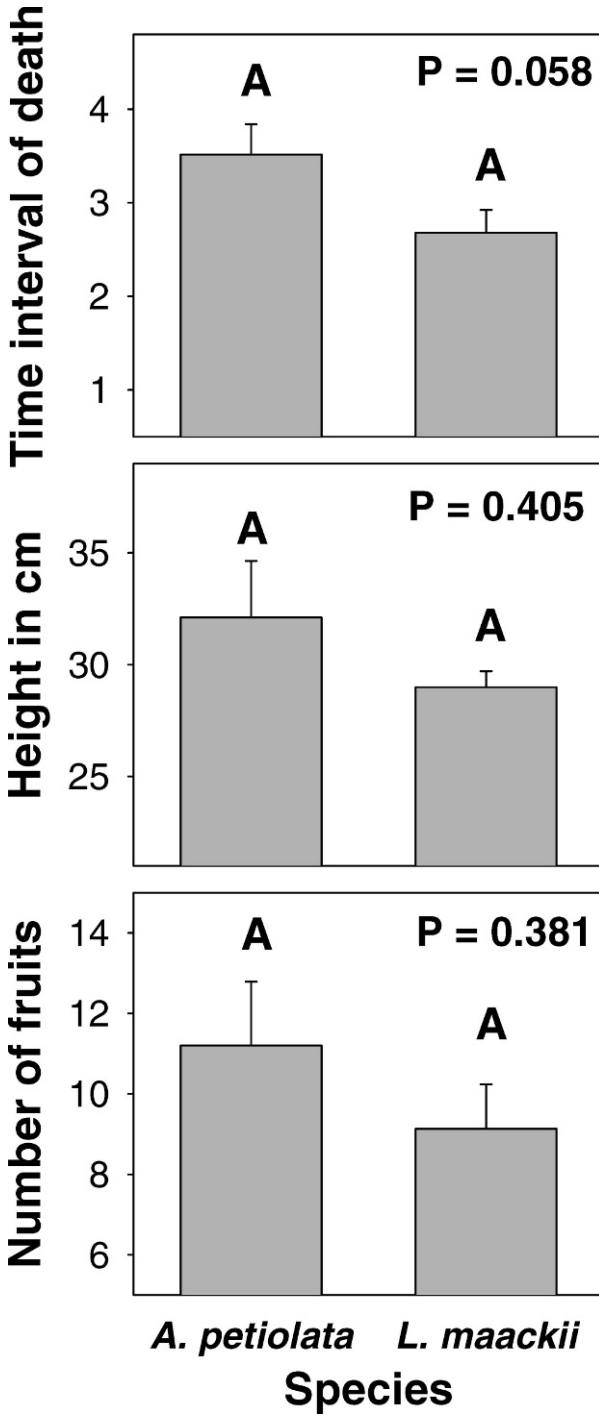
FIG. 3.—Mean \pm se maximum height and maximum fruit number for *Impatiens capensis* plants found in *Lonicera maackii* plots for the four treatment combinations of aboveground cutting and soil application of activated carbon. Horizontal bars indicate means for two levels of main factor of cutting. Horizontal bars with the same letter are not significantly different at $P = 0.05$. Numbers on each bar indicate the sample size (n) for each treatment combination; sample size is the same for both maximum fruit and maximum height means

suggested that the negative effects of *A. petiolata* may be due largely to allelopathy toward native plants or their mycorrhizal mutualists (Vaughn and Berhow, 1999; Roberts and Anderson, 2001; Prati and Bossdorf, 2004; Stinson *et al.*, 2006). It is possible that activated carbon benefited *I. capensis* plants in the presence of *A. petiolata* either directly or indirectly by protecting mycorrhizal symbioses. Further, when carbon was added to plots where *A. petiolata* was intact, growth, reproduction and survival reached levels approaching those found in plots where aboveground biomass was removed, suggesting that amelioration of soil allelopathy and above-ground competition have nearly equivalent effects on *I. capensis*.

Interestingly, carbon application was only significantly beneficial to fruit number and height if aboveground biomass of *Alliaria petiolata* was present and tended to had negative effects where aboveground biomass was removed. We have found that carbon addition to soils in the absence of invasive plant extract negatively impacted growth in *Arabidopsis thaliana* (K. Cipollini and R. Murphy, pers. obs.). It is possible that, in the absence of the aboveground biomass that can be both a source of allelochemicals and a source of photoassimilates required for root allelochemical production, activated carbon adsorbed molecules that were vital to *Impatiens capensis* survival and growth. Activated carbon may also have alternate effects in soils, including decreasing beneficial microbial activity in soil (Bais *et al.*, 2005). This negative effect may have been particularly noticeable in the absence of allelochemicals that the carbon could adsorb.

Our statistical analysis of height and fruit data in the *Lonicera maackii*-dominated plots was constrained by low sample sizes, which limits our results and conclusions. Nonetheless, the results of this study indicate that aboveground competition by *L. maackii* is an important factor suppressing survival and reproduction of *Impatiens capensis*. On the other hand, activated carbon did not significantly improve the performance of *I. capensis* in *L. maackii* plots. Extracts from the roots and leaves of *L. maackii* are known to strongly suppress the germination of *I. capensis* and other species (Trisel, 1997; Dorning and Cipollini, 2006), and the growth of *Arabidopsis thaliana* (Cipollini *et al.*, 2008a), but carbon application was either unable to completely ameliorate allelopathic effects of *L. maackii*, or the potential allelopathic effects of this plant seen in the laboratory (*e.g.*, Dorning and Cipollini, 2006), do not extend to the field. Another explanation is that soil nutrients were too low to see the effects of allelopathy, as allelopathic effects of *L. maackii* can be attenuated by low nutrient levels (Cipollini *et al.*, 2008a). However, the negative effect of carbon in the absence of aboveground biomass seen in the *Alliaria petiolata*-dominated plots was also apparent in the *L. maackii*-dominated plots. This suggests that in the presence of *L. maackii*, activated carbon had enough benefits on the performance of *I. capensis* to counterbalance its negative effects seen in the absence of *L. maackii*. We will conduct future research with increasing levels of carbon to see if allelopathic effects can be alleviated with greater carbon application. *Lonicera maackii* had a greater impact on *I. capensis* survival than *A. petiolata* and is likely a larger threat to understory plants in general.

To our knowledge, this is the first study to attempt to separate the effects of aboveground competition and allelopathy of these two species on a native species in the field. While removal of aboveground competition of both *Alliaria petiolata* and *Lonicera maackii* enhanced the performance of *Impatiens capensis* as expected, the application of activated carbon benefited target plants in the presence of intact invasive plants. This both confirms that these species exert some of their negative effects through allelopathy and suggests that activated carbon may be an important restoration tool in sites where removal of these invasive species is constrained.



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Fig. 4. Mean \pm SE time interval of death, maximum height and maximum fruit number of *Impatiens capensis* in *Alliaria petiolata* and *Lonicera maackii* plots. Bars with the same letter are not significantly different at $P = 0.05$

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