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Allelopathic influences of the invasive *Ailanthus altissima* on a native and a non-native herb^{1,2}

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SMALL, C. J., D. C. WHITE and B. HARGBOL (Department of Biology, Radford University, Radford, VA 24142). Allelopathic influences of the invasive *Ailanthus altissima* on a native and a non-native herb. J. Torrey Bot. Soc. 137: 366–372. 2010.—As a highly aggressive non-native invasive and an allelopathic species, *Ailanthus altissima* (tree of heaven) has the capacity to negatively affect native plant communities by suppressing resident species and altering competitive interactions. We examined effects of *A. altissima* on the establishment and growth of two herbaceous species common in invaded natural areas. Soil samples were collected from six replicate *A. altissima*-dominated stands and six control stands (no *A. altissima* present) in the Appalachian Ridge and Valley province of southwestern Virginia. Two target species, *Verbesina occidentalis*, native to the southeastern US, and *Dipsacus fullonum*, non-native and invasive throughout North America, were selected for their high germination success and contrasting native vs. invasive status. Germination and growth of target species were monitored in greenhouse flats for six weeks. We found severe reductions in all measured aspects of *V. occidentalis* when grown in *Ailanthus* versus control soils, including seed germination ($P = 0.002$), seedling height ($P = 0.001$), leaf production ($P < 0.001$), and root:shoot ratio ($P = 0.008$). In contrast, *Dipsacus fullonum* appeared resistant to allelopathic effects, with no significant differences in germination or growth relative to soil type ($P > 0.25$ for all measures). Our results support the role of allelopathy in the invasive success of *A. altissima* and further suggest that *A. altissima* may differentially affect resident native versus non-native species, potentially facilitating the spread of other non-natives in the invaded community.

Key words: allelopathy, invasive species, plant-soil interactions, Virginia.

Non-native invasive species have become an increasing threat to biological diversity and ecosystem integrity, producing such pronounced environmental impacts that they are considered a primary cause of current declines in global biodiversity (Vitousek et al. 1997, Wilcove et al. 1998, Mooney and Hobbs 2000). For example, nearly half of the species currently listed as threatened or endangered under the US Endangered Species Act are considered at risk because of invasive species (Wilcove et al. 1998). Studies of invasives have demonstrated the capacity of a single species to alter community structure and ecosystem function (Vitousek and Walker 1989, Gómez-Aparicio and Canham 2008). As such, it is becoming increasingly recognized that invasive-mediated changes, particularly through altered soil nutrient dynamics (esp. pH and C and N cycling; Vitousek et al. 1987, Vitousek

and Walker 1989, Ehrenfeld et al. 2001) and the release of inhibitory compounds (Heisey 1990a, Lawrence et al. 1991, Bais et al. 2003, Hierro and Callaway 2003, Callaway and Ridenour 2004, Dorning and Cipollini 2006), have the potential for widespread ecosystem impacts and implications for overall ecosystem susceptibility to invasion.

Modification or introduction of novel plant-soil interactions appears to enhance the invasive ability of some non-native species by altering competitive interactions and potentially facilitating the spread of other non-natives (Ehrenfeld 2003, Callaway and Ridenour 2004). Cascading ecosystem effects have been observed in nitrogen-limited forests of Hawaii invaded by *Myrica faya* Aiton, a nitrogen-fixing shrub. Vitousek et al. (1987) found significant increases in biologically available nitrogen, altered competitive interactions, and changes in ecosystem development patterns in response to this invasive. Ehrenfeld et al. (2001) described marked differences in soil pH and nitrification rates in eastern deciduous forests invaded by *Berberis thunbergii* DC. and *Microstegium vimineum* (Trin.) A. Camus and suggest that these changes are likely to promote further spread of these species. Likewise, the success of some particularly aggressive invasive plants

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has been attributed to the production and release of chemical compounds into the surrounding soil, negatively affecting associated species (i.e., "allelopathy" - *sensu* Muller 1969) (Ridenour and Callaway 2001, Hierro and Callaway 2003). Callaway and Ridenour (2004) attribute this success in part to the introduction of novel allelochemicals, as many resident species lack evolved tolerance to these compounds.

Ailanthus altissima (Mill.) Swingle (tree of heaven; Simaroubaceae) is a rapidly growing non-native and invasive tree, introduced from China to the eastern US in 1784 for horticultural uses (Hu 1979). Today, *A. altissima* has become widely naturalized across much of the US and eastern Canada, particularly in forest edges and other disturbed habitats well-suited to its high light demands and exceptional tolerance of dry, nutrient-poor, and compacted soils (Kowarik 1995, Howard 2004). Prolific clonal growth also allows *A. altissima* to expand occasionally into forest interiors (Kowarik 1995, Knapp and Canham 2000). The invasive potential of *A. altissima* is enhanced further by prolific seed production, with one individual producing up to 300,000 seeds in a single growing season (Bory and Clair-Maczulajtys 1980). These wind-dispersed samaras can disperse > 200 m from parent plants, with up to 100% germination in the following year (Wagner 1958, Landenberger et al. 2007).

In addition to these common invasive traits, the ability of *A. altissima* to exclude other canopy and understory species has been attributed to allelopathy (Lawrence et al. 1991, Gómez-Aparicio and Canham 2008). *Ailanthus* produces a variety of allelochemicals (e.g., quasinsoids) with demonstrated inhibitory or toxic effects on neighboring plants. These compounds leach from plant biomass and root exudates, producing appreciable concentrations in the soil beneath and immediately surrounding its stems (Heisey 1990a, Lawrence et al. 1991). Negative effects on associated species have been demonstrated repeatedly in laboratory and greenhouse studies. Mergen (1959) found reduced seedling growth in > 90% of woody angiosperms (10 spp.) and gymnosperms (35 spp.) exposed to *Ailanthus* leaf extract, and apical meristem death in > 50% of tested species. Heisey (1990a) found significant reductions in radicle growth and complete mortality within one week for weed

and crop seedlings (7 spp.) exposed to root bark extract. Lawrence et al. (1991) showed reduced germination, seedling growth, and reproductive output for all test species (1 woody dicot, 4 herbaceous dicots, 2 grasses native to eastern North America) exposed to *A. altissima* stem and leaf extracts. In contrast, extracts from several native woody and herbaceous species produced no significant effects (Lawrence et al. 1991).

While numerous studies have described allelopathic effects of *A. altissima* on tree and crop species (Mergen 1959, Heisey 1990b, Lawrence et al. 1991, Gómez-Aparicio and Canham 2008), few have examined direct ecological effects on associated herbs. We chose herbaceous species because they are a vital component of eastern deciduous forests, typically comprising the largest proportion of forest diversity (Braun 1950) and particularly sensitive to microenvironmental conditions and disturbance (Small and McCarthy 2005, Gilliam 2007). Our primary objective was to examine the effects of *A. altissima* on establishment and growth of herbaceous species that coexist in natural areas of the eastern US. Unlike many earlier studies, we sought to replicate natural conditions by exposing target species to field-collected soils, thus avoiding uncertainties in extract concentrations or exclusion of other potential edaphic effects (Gómez-Aparicio and Canham 2008). Given the potential for species-specific effects (e.g., Callaway and Ridenour 2004, Gómez-Aparicio and Canham 2008), we also were interested in the potential for *A. altissima* to differentially impact the associated native versus non-native species in the invaded community.

Materials and Methods. FIELD SITES. Seeds and soil samples used in this study were collected from Wildwood Park, a ~22 ha natural area in Radford, Virginia. Wildwood Park is located within the Appalachian Ridge and Valley physiographic province of southwestern Virginia, a region that supports exceptional vegetation diversity (Ricketts et al. 1999). Differences in forest composition across this region largely reflect variations in topography and bedrock geology. Following loss of American chestnut (*Castanea dentata* (Marsh.) Borkh.) in the early 1900's, upper slopes and ridges shifted to dominance of mixed oaks (*Quercus* spp. L.) or oaks and hickories (*Carya* spp. Nutt.) above a species-

poor layer of ericaceous shrubs. Lower slopes and valleys, particularly those underlain by limestone and other calcareous bedrock, support diverse suites of mesophytic or calciphilic forest canopy (e.g., *Tilia americana* L., *Q. muehlenbergii* Engelm., *Magnolia acuminata* (L.) L., *Aesculus flava* Aiton, *Liriodendron tulipifera* L., *Acer saccharum* Marsh., *Celtis occidentalis* L.) and herbaceous layer species (Stephenson et al. 1993). Land use impacts at the study site are minimal, aside from maintained and frequently used hiking trails.

At Wildwood Park, six replicate *Ailanthus altissima* stands were identified. *Ailanthus* stands were defined as closed-canopy forest stands composed exclusively of *A. altissima* in the canopy (i.e., no other mature tree species present). Each stand had a minimum area of 10×10 m (100 m^2). In addition, six corresponding non-*Ailanthus* (control) stands were selected at Wildwood Park. Each control stand was located adjacent to one of the replicate *Ailanthus* stands and met the following criteria: dominated by closed-canopy mixed oaks or oaks and hickories and no *A. altissima* stems evident in the canopy, understory, or within 20 m distance in any direction.

SEED COLLECTION AND SELECTION OF TARGET SPECIES. In fall 2007, naturally matured seeds were collected from native and naturalized herbaceous species common in or near both *Ailanthus* and control stands at Wildwood Park. Seeds of the following species were collected and stored in nylon mesh bags beneath forest leaf litter at Wildwood Park to overwinter (November 2007–March 2008) naturally and encourage seed dormancy-breaking conditions: *Daucus carota* L. and *Osmorhiza claytonii* (Michx.) C.B. Clarke (Apiaceae); *Eupatorium rugosum* Houttuyn, *Eurybia divaricata* (L.) G.L. Nesom, *Verbesina alternifolia* (L.) Britton ex Kearney, and *V. occidentalis* (L.) Walter (Asteraceae); *Dipsacus fullonum* L. (Dipsacaceae), and *Galium aparine* L. (Rubiaceae). All collected species are native to the eastern US except *Daucus carota* and *Dipsacus fullonum* (USDA NRCS 2010). Seeds of each species were collected from single populations not immediately adjacent to or beneath *A. altissima* stems, to reduce likelihood of exposure-mediated differences (differences due to parental exposure to *Ailanthus*) in germination and growth, as described by Lawrence et al. (1991).

In March 2008, germination trials were conducted for field-collected and over-wintered seeds of each species, to evaluate viability and germination success under experimental conditions. Lettuce (*Lactuca sativa* L.) seeds, purchased from Parks Seed Company, also were used to assess adequacy of germination conditions. Three petri dishes were prepared for each species (5 seeds per dish; $n = 15$). Petri dishes were saturated with deionized water and subjected to 12 hours of light and 12 hours of darkness for two weeks. Seeds were evaluated daily for evidence of germination. Only two species showed $> 40\%$ germination success in germination trials (aside from *Lactuca sativa*, 100% germination): *Verbesina occidentalis* (yellow crown-beard; 60% germination), a native herbaceous species common in moist woods, bottomlands, thickets, and waste places from Maryland to Ohio and Missouri south to Florida and Texas (Gleason and Cronquist 1991), and *Dipsacus fullonum* (common teasel; 60% germination), a non-native invasive biennial widespread in open disturbed habitats and moist natural areas across much of eastern Canada and the US, including all regions of Virginia (Hefferman et al. 2001, NatureServe 2009). Therefore, based on relatively high germination rates and contrasting native / invasive status, *V. occidentalis* and *D. fullonum* were selected as target species for experimental analyses.

SOIL COLLECTION. In September 2008, soil samples were collected from the six *Ailanthus* and six control stands at Wildwood Park. Within a 10×10 m area in each stand, five discrete 1×1 m quadrats were located based on random coordinates. Within each quadrat, coarse leaf litter was removed and soil samples collected from the upper 15 cm of the A-horizon. Thus, 30 soil samples were collected across replicate stands (6 stands \times 5 quadrats) and compiled to create *Ailanthus* or control soil treatments. Soil was transported to the lab, processed through a 2 mm sieve to remove gravel, large roots, and other coarse materials, and mixed thoroughly to create one composite sample for each treatment.

GERMINATION AND GROWTH IN *AILANTHUS* VS. CONTROL SOILS. Germination and growth experiments were initiated in October 2008. Four 36-celled planting flats were prepared for each soil treatment (*Ailanthus* or control soils). In each cell, two *Verbesina occidentalis* or

Dipsacus fullonum seeds were gently pressed into the soil surface (planting depth ~5 mm; seeds partially exposed). Flats were covered with plastic domes and placed in the Radford University greenhouse where they experienced natural daylength conditions and temperatures 21–28 °C. Each flat was watered as necessary to maintain adequate moisture and rearranged each week to minimize location influence. After germination and adequate growth for identification (typically ~1 week after germination), each cell was thinned to one plant per cell. (Thus, $n = 72$; 18 cells per species per flat \times 4 flats per soil treatment). Any subsequent thinning or removal of non-target seedlings was performed within three days of seedling emergence.

Seed germination success and seedling growth were measured three times per week for six weeks. Growth measures included plant height (measured from soil surface to apical meristem) and number of leaves (exclusive of cotyledons). After six weeks, all plants were harvested. Roots and shoots were washed thoroughly and oven dried to a constant weight at 65 °C for 72 h. Due to low dry root weights (mean for all plants = 0.014 ± 0.003 g) and associated potential for measurement error, root materials and shoot materials each were pooled by species for each flat. Thus, mean *Verbesina occidentalis* or *Dipsacus fullonum* root, shoot, and total biomass values for each flat were used in analyses ($n = 4$ flats per treatment).

DATA ANALYSIS. The effects of soil treatment (*Ailanthus* vs. control; fixed effect) on germination success (binomial data) were compared using Chi-square tests for each target species. Differences in final plant height and number of leaves between soil treatments were analyzed using multivariate analysis of variance (MANOVA) for each species. Variations in root to shoot ratios relative to soil treatment were examined by one-way analysis of variance (ANOVA). Dependent variables were \log_{10} transformed as necessary to meet assumptions of multivariate or univariate normality and equality of variance. All statistical analyses were conducted using NCSS 2000 software (Hintze 2000).

Results. All measures of *Verbesina occidentalis* success were negatively affected by growth in *Ailanthus* soils. Seed germination

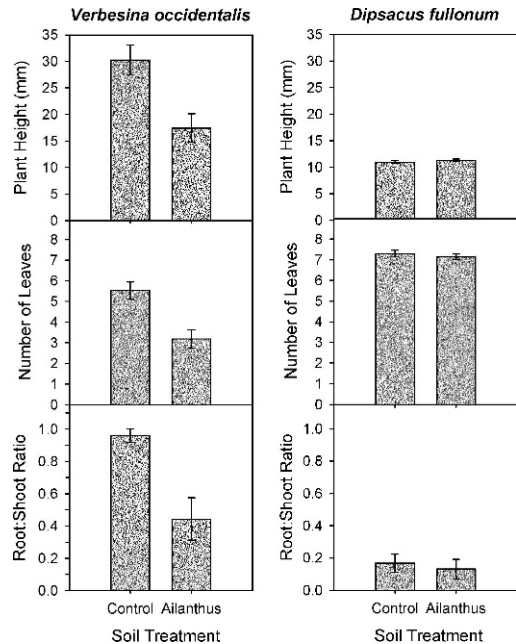


FIG. 1. Mean final plant height, number of leaves per plant, and root:shoot ratio (mean \pm standard error) for *Verbesina occidentalis* (yellow crownbeard) and *Dipsacus fullonum* (common teasel) grown in *Ailanthus* versus control soils (each $n = 72$ for height and # leaves; each $n = 4$ for root:shoot ratio).

was significantly lower in *Ailanthus* soils ($45.8 \pm 5.9\%$) than control soils ($70.8 \pm 5.39\%$, $\chi^2 = 9.26$, $P = 0.002$). MANOVA results (Wilks' $\lambda = 0.907$, $F_{2,141} = 7.25$, $P = 0.001$) also showed *V. occidentalis* seedlings to be significantly shorter (ANOVA, $F_{1,142} = 10.78$, $P = 0.001$) and to produce fewer leaves (ANOVA, $F = 14.60$, $P < 0.001$) when grown in *Ailanthus* versus control soils (Fig. 1). Similarly, *V. occidentalis* allocated less energy to root production in *Ailanthus*-influenced soils, resulting in lower root to shoot ratios (ANOVA, $F_{1,6} = 15.19$, $P = 0.008$) (Fig. 1).

Dipsacus fullonum, in contrast, showed consistently high seed germination regardless of soil type (*Ailanthus* soil = $100 \pm 0\%$ vs. control = $98.6 \pm 1.39\%$, $\chi^2 = 1.01$, $P = 0.316$). The MANOVA test showed no influence of *Ailanthus* soil on *D. fullonum* seedling growth (Wilks' $\lambda = 0.979$, $F_{2,141} = 1.52$, $P = 0.222$), with plants in both treatments similar in height (ANOVA, $F_{1,142} = 0.70$, $P = 0.405$) and leaf production (ANOVA, $F_{1,142} = 1.19$, $P = 0.277$). Root to shoot ratios also did not differ significantly between *Ailanthus* and

control soils (ANOVA, $F_{1,6} = 0.21$, $P = 0.663$) (Fig. 1).

Discussion. We found severe reductions in all measured aspects of *Verbesina occidentalis* when grown in *Ailanthus*-influenced soils, supporting previous work on impacts of *Ailanthus* allelochemicals and their likely importance in its invasive success (Mergen 1959, Heisey 1990a, Lawrence et al. 1991, Gómez-Aparicio and Canham 2008). Root biomass allocation of *V. occidentalis* also was inhibited in *Ailanthus* soils. While changes in biomass allocation in response to allelopathy are often species- or ecosystem-specific, lower root to shoot ratios in *V. occidentalis* suggest a stress response or inhibition of root development (Chapin 1980, Mokany et al. 2006). Similar reductions in root biomass allocation have been reported by Alshahrani (2008) and Vrchotová and Šerá (2008) in studies of allelopathic effects of invasives on native and cultivated species. Rutherford and Powrie (1993), in contrast, found *increased* root:shoot ratios in South African shrubs exposed to allelopathic leachate. They suggest that allelochemical inhibition of roots is most likely early in plant development, whereas inhibition of shoots is more likely later in plant development. Because our seedlings were harvested at six weeks, we were unable to test for allocation changes with plant maturity.

In contrast to *Verbesina occidentalis*, we found no difference in *Dipsacus fullonum* germination or growth in *Ailanthus* versus control soils. Werner (1975) examined germination of *D. sylvestris* (Huds.) (= *D. fullonum* L.) under leaf litter of *Agropyron repens* (L.) P. Beauv., a species with recognized allelochemical effects. She reported reduced germination under *A. repens*, as compared to mixed forb or no leaf litter. While in contrast to our results, Werner notes uncertainty as to the cause of reduced germination – whether due to changes in soil chemistry with litter decomposition or allelochemicals produced by *A. repens*. Further, for *D. sylvestris* seedlings emerging from *A. repens* litter, Werner found significantly higher survival than in any other substrate tested, again suggesting a degree of allelochemical-resistance in this species.

The tendency for some particularly aggressive invaders, including *Ailanthus altissima*, to exclude potential competitors and form nearly pure stands has been attributed largely to

allelopathy (e.g., Lawrence et al. 1991, Callaway and Aschehoug 2000, Bais et al. 2003, Hierro and Callaway 2003, Dorning and Cipollini 2006). Our findings support the capacity for *A. altissima* to alter soil properties and suppress germination and growth of selected associates. It is important to note, however, that without detailed soil assays we cannot conclusively attribute our results to direct chemical inhibition. Differences between *Ailanthus* and control soils seem clearly responsible for observed results, yet changes in soil chemistry, microbes, or other factors also may occur in the presence of *A. altissima* (e.g., Gómez-Aparicio and Canham 2008). While the term allelopathy typically is used to describe negative effects of plant chemical compounds on associated plants, it also has been used more broadly to include indirect effects due to altered soil chemistry (e.g., Whittaker and Feeny 1971, Rice 1984). Given extensive experimental evidence for allelopathic effects of *A. altissima*, our results are discussed largely relative to this concept, considering both narrow and broader definitions.

Differences in allelochemical responses, such as those reported here for *Verbesina occidentalis* and *Dipsacus fullonum*, have been reported frequently in the ecological literature and attributed to individual species susceptibility, previous exposure of individuals or parental plants, nutrient and moisture availability, and other biotic or abiotic triggering factors (Lawrence et al. 1991, Rutherford and Powrie 1993, An et al. 2001, Gómez-Aparicio and Canham 2008). Gómez-Aparicio and Canham (2008) found species-specific responses of native tree seedlings to *Ailanthus altissima*, attributing differences both to allelopathic effects and increases in soil fertility in the presence of *Ailanthus*. Other studies have attributed species-specific resistance to induced biochemical responses, often expressed through the production of secondary compounds in response to soil toxicity or other environmental stimuli (Metlen et al. 2009). For example, *Centaurea maculosa*, non-native and invasive throughout North America, produces phytotoxins effective at excluding most species (Bais et al. 2003, Callaway and Aschehoug 2000). However, *Lupinus sericeus* and *Gaillardia grandiflora*, two associated native species, appear resistant. The mechanism for resistance appears to be increased

production of oxalate, a root exudate effective in reducing damage typically caused by *C. maculosa* phytotoxins (Weir et al. 2006). Like these species, *D. fullonum* may be capable of producing effective biochemical defenses in response to *A. altissima*.

As a final consideration, our contrasting results for a native and a non-native target species are of potential significance. We found pronounced effects of *Ailanthus altissima* on a North American native herb, yet no apparent effect on an associated non-native invasive species. Physical and chemical soil changes, particularly those associated with allelopathy, have been cited as important mechanisms for native species inhibition and the extraordinary success of some invasive plants. Hierro and Callaway (2003) and Callaway and Ridenour (2004), for example, highlight the remarkable success of non-native invasives in new environments, suggesting that increased invasive ability may result from greater allelopathic effects, as resident species lack evolved tolerance to these allelochemicals. Thus, greater invasive species impacts are expected on native residents than on non-natives with which they share a home range. Relative to our study, the extent of *Dipsacus fullonum*'s native range is uncertain, due to early and widespread cultivation (dating back to 12th century France; Andrieu-Ponel et al. 2000). Thus, it is possible (but uncertain) whether *A. altissima* and *D. fullonum* may share a portion of their native ranges in temperate Asia (Howard 2004, Gucker 2009). While an obvious limitation of our study is the comparison of only a single native and non-native species-pair, if this asymmetrical effect – inhibition of a native species and potential facilitation of a non-native species – were to extend to other species co-occurring with *A. altissima*, far-reaching impacts should be expected, particularly relative to overall ecosystem susceptibility to invasion.

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