

Soil biota drive expression of genetic variation and development of population-specific feedbacks in an invasive plant

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Abstract. Invasive plant species alter soils in ways that may affect the success of subsequent generations, creating plant–soil feedbacks. *Ailanthus altissima* is an invasive tree introduced two centuries ago to North America. We hypothesized that geographically distinct populations of *A. altissima* have established feedbacks specific to their local environment, due to soil communities cultivated by *A. altissima*. We collected seeds and soils from three populations in the eastern United States, and in the greenhouse reciprocally planted all families in all collected soils as well as in a control mixed soil, and in soils that had been irradiated for sterilization. There were positive plant–soil feedbacks for two populations in the live field-collected soils, but strong negative feedbacks for the third population. There were no population-level performance differences or feedbacks in the sterilized population locale soils, supporting a soil biotic basis for feedbacks and for the expression of genetic differentiation in *A. altissima*. If populations of *Ailanthus altissima* vary in the extent to which they benefit from and promote these plant–soil biota feedbacks, the interaction between invader and invaded community may be more important in determining the course of invasion than are the characteristics of either alone.

Key words: *Ailanthus altissima*; geographic mosaic theory; invasive species; plant–soil feedback; positive feedback.

INTRODUCTION

Invasive plant species defy the ecological assumption that organisms are most successful when they have adapted to local abiotic and biotic factors. A proportion of the plant species introduced to a novel environment do not struggle to survive, reproduce, and maintain a small population, but instead become invasive. Invasives often attain high densities and produce large numbers of offspring, thus increasing their population size to the detriment of native communities. The mechanisms by which invasive plant species successfully recruit sufficient numbers to not only maintain but also aggressively increase their population have been studied in terms of demographics and competitive interactions between plants, such as allelopathy (Inderjit et al. 2008, Jongejans et al. 2008). For example, the ability to expand populations of invasive plant species that depend on wind for seed dispersal or pollination depends in part on density of existing populations (Davis et al. 2004, Marchetto et al. 2010). Interactions between invasive seedlings and the soil communities in which they grow may be an important aspect of invasion, particularly as many invasive plants cause dramatic alterations in soils (Ehrenfield et al. 2001, Ehrenfield 2003).

Invasive plants cultivate soil environments distinct from soils associated with native plant communities, changing soil pH (Gomez-Aparicio and Canham 2008a), rates of soil organic matter accumulation, and rates of nutrient cycling (Stock et al. 1995). Invasives often exude chemicals that disrupt symbioses between native plant species and beneficial microbes (Wardle et al. 1994, Wolfe et al. 2008) or otherwise alter the composition of soil microbial communities (Batten et al. 2008). These distinctive invaded soils may affect the success of subsequent generations of plants growing at that site, creating a feedback loop in which soil conditions promoted by an invasive species promote further invasion (a positive plant–soil feedback; Klironomos 2002, Callaway et al. 2004, Rout and Callaway 2009). Plant–soil feedbacks are abiotic or biotic soil-based mechanisms that account for shifts in plant population size and community composition (van der Putten et al. 1993, Bever 1994). Negative plant–soil feedbacks prevent species from persisting at fixed locations or at high abundances (Klironomos 2002). Positive plant–soil feedbacks are more often suggested as mechanisms of invasion or local adaptation (Johnson et al. 2010). Certain introduced plants benefit from immunity to naïve pathogens in the new range (van Grunsven et al. 2007), reaping the benefits of mutualisms while escaping the costs of attack by pathogens and saprobes. However, soil communities and the population of the introduced plant may vary by geographic location and thus invasive species may experience variation in feedbacks in different parts of their introduced range.

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To explore the impact that invasive-amended soil may have on the establishment and persistence of the invasive species *Ailanthus altissima*, we designed a greenhouse experiment that would allow us to test the effects of plant genetic family (i.e., within-population genetic variation), plant population, soil origin, and soil biota on seedling performance. *Ailanthus altissima* raises soil pH and nutrient availability (Gomez-Aparicio and Canham 2008a), and grows in persistent monocultural stands with no apparent reduction in performance, suggesting the presence of a positive plant–soil feedback (E. Felker-Quinn, *personal observation*). Such a feedback would provide a mechanism that explains how current populations of *A. altissima* are able to expand their ranges, but it does not explain the success of geographically and genetically distinct populations of *A. altissima*, which have managed to establish themselves under different climatic and soil conditions. We collected seeds and soils from three geographically distinct and established populations in the eastern United States (across a 1000-km latitudinal gradient), and reciprocally planted seeds from all populations in sterile and non-sterile soils collected from all locations (using mixed soil from all populations as controls). We hypothesized that (1) *A. altissima* populations have genetically based (as opposed to environmentally based) differences in plant performance, when grown in the control soil; (2) each population produces seeds which will perform best when grown in soil from their parental population (positive plant–soil feedbacks, specific to each population); and (3) the feedbacks are due to the biotic components of the soils rather than the physical characteristics of each soil. The confirmation of these hypotheses would indicate population-level, locally adapted, positive feedbacks between *A. altissima* and soil microbial communities.

METHODS

Study species

Ailanthus altissima (P. Mill.) Swingle, commonly known as tree of heaven, is native to southeast Asia and was planted in North American cities following its introduction to Philadelphia two centuries ago, where its tolerance for pollution made it a popular shade tree (Kowarik and Saumel 2007). Abundant seed production, fast growth rates, and resistance to drought have made *A. altissima* a persistent naturalized presence in American cities, and it has spread along transportation corridors into forested ecosystems. It is a dioecious, wind-pollinated tree species, which also reproduces via clonal growth, as the surface root system can develop into adventitious stems when damaged. *A. altissima* has also been shown to raise the soil pH and increase soil calcium and net nitrogen (N) mineralization rates within the tree's litter shadow (Gomez-Aparicio and Canham 2008a). While *A. altissima* has been shown to possess allelopathic, herbicidal properties, the active compound, aianthone, is not thought to be auto-toxic or to persist in the soil (Heisey and Heisey 2003).

Seed population and soil collections

To address the hypothesis that local feedbacks promote persistence across the landscape (i.e., each population has a soil-based “home-field advantage”), we collected seeds and soils from three populations of *A. altissima* across a latitudinal gradient that stretches along the Blue Ridge of the Appalachian Mountains. We collected seeds (half to full sibling) from 10 females (hereafter referred to as seed families) from a population in Philadelphia, Philadelphia County, Pennsylvania (PA); from five females from a population in New Market, Shenandoah County, Virginia (VA); and from 10 females from a population in Knoxville, Knox County, Tennessee (TN). Female trees were randomly selected at a minimum of 10 m distance from each other, and separated by a tree of another species where possible, to minimize the possibility that two stems were clones. Each population consisted of several stands of *A. altissima* monoculture as well as several *A. altissima* stems growing in isolation (i.e., at least 100 m from any other *A. altissima* stem). We collected seeds by clipping them from each tree in the winter of 2007, and stored them at 4°C until planting.

In April 2008, we collected soils from each of the populations. We collected a shovelful of mineral soil (top 15 cm) in each of the cardinal directions less than 0.5 m from the trunk beneath each selected mother tree. We collected soils exclusively from beneath female trees because we were interested in the specific influence of *A. altissima* on soils and thus on the next generation of *A. altissima* to grow in these soils. Soils from each site were pooled to form a PA, a VA, and a TN field soil. Approximately 8 L of soil was collected from each location; half of each soil was stored as collected, and will be referred to as “field soil.” We also mixed soils from the three populations to create a control “mixed field soil” in order to test for population genetic variance under common conditions. These soils were stored at 4°C within 24 h of being collected, and a subsample taken within 48 h of collection was used in microbial biomass and soil enzyme analyses. To separate the effects of microbial community composition and activity from the effect of soil physical and chemical properties on growth, the remaining 4 L of soil collected at each location was sterilized. Soils were transported to Steris Isomedix Services (Spartanburg, South Carolina, USA) and sterilized using gamma irradiation for 48 h at 30 kGy; these soils are hereafter referred to as “sterile soils,” and include sterile population soils as well as a sterile mixed soil.

We quantified soil pH, texture (i.e., particle size), microbial biomass carbon (C) and N pools, and extracellular enzyme activity for each of the field soils following protocols recently utilized in Stritar et al. (2010; Appendix: Table A1). Air-dried soil from each site was used to determine soil pH using the 0.1 mol/L CaCl₂ method (Hendershot et al. 1993); additionally, we measured particle sizes of the field soils by determining

soil texture using the hydrometer method (Gee and Bauder 1986). We quantified soil microbial C and N pools using the chloroform fumigation extraction method. These samples were digested by a micro-Kjedahl process, and the digests were run using a Shimadzu TOC-V csh TNM-1 multi-carbon, nitrogen analyzer (Shimadzu Scientific Instruments, Columbia, Maryland, USA) in order to determine pool sizes of microbial biomass C and N associated with each population. To determine the activity of microorganisms in soils from each population and their relative limitation by C, N, and phosphorus (P), we measured the potential activity of C-, N-, and P-degrading extracellular enzymes using methylumbelliferone (MUB)-linked substrates in a fluorometric assay (Molecular Devices, Gemini XPS, Sunnyvale, California, USA). We ran assays using three different substrates: 4-MUB- β -D-cellobioside (EC 3.2.1.91), to determine the activity of cellobiohydrolase, which breaks cellulose into cellobiose dimers; 4-MUB-N-acetyl- β -D-glucosaminide (NAGase, EC 3.2.1.14), to determine the activity of NAGase, which acts upon chitin and is involved in nitrogen cycling; and 4-MUB-phosphate (EC 3.1.3.1), which releases phosphate from phosphomonoesters, to quantify acid phosphatases in the soil (Sinsabaugh et al. 2008). Values obtained were recorded in units of $\mu\text{mol enzyme}^{-1}\cdot\text{h}^{-1}$.

Greenhouse study

To determine the effects of plant population and soil origin on seed germination and seedling performance, we planted all seeds reciprocally into all soils. Each soil treatment was established in book-planter-type root trainers (Tinus Roottrainers, Spencer-Lemaire, Edmonton, Alberta, Canada) by filling the root trainers with approximately 15 cm of potting mix (equal ratios of peat, vermiculite, and perlite), and filling the top 3 cm of the cells with the treatment soil. There were eight soil treatments in total: field PA, field VA, field TN, mixed field control, sterile PA, sterile VA, sterile TN, and mixed sterile control soil. Twenty random seeds from all seed families from each population (25 families total) were planted into each soil treatment. A month after planting, seedlings were thinned to five seedlings from each family. We watered every three days, and randomly shifted the planters monthly to minimize the effects of variations in light or moisture. We measured seedling performance to assess phenotypic differences in growth based on seed population origin. From June to August, approximately every three weeks we measured total germination, total number of leaves, stem height (cm, measured from soil to apical meristem), stem width (mm, measured at cotyledon scars), leaf length and width (cm, both measured on the third leaf from the apical meristem). When plants were 16 weeks old the trees were sacrificed to determine the biomass of leaves, stems, and roots. The root mass and leaves were clipped

from the stem, and all were oven dried for 48 h at 70°C and before weighing.

Statistical analyses

Performance metrics showed that the trees were at the peak of their growth on 1 July, and that thereafter they began to decline, so we used the metrics from this date as well as the final biomass data for all analyses. We analyzed the data collected using mixed-effect models and restricted maximum likelihood (REML) using the statistical program JMP 7 (SAS Institute, Cary, North Carolina, USA). All analyses were run separately for field-collected and sterile soils. To determine quantitative genetic differences among our seed populations we constructed mixed models which included seed population as a fixed effect, family nested within seed population as a random effect, and replicate as a random effect based on performance measures in mixed field soil. The test statistic for family-level effects was determined by likelihood ratio tests, in which the difference between the likelihood ratio of the model described above and the likelihood of the same model with the family effect removed was used as a χ^2 value (one-tailed χ^2 distribution, $df = 1$).

To test for seed population \times soil interactions (statistical evidence of feedbacks), we ran mixed models for the seedlings grown in soils collected from each population (the control mixed soil was excluded) that included seed population, soil origin, seed population \times soil origin as fixed effect, and family nested in seed population as a random effect. For the mixed models, we used Tukey's hsd post hoc test to determine how performance means differed by seed population or soil type where appropriate. We did not have sufficient statistical power to use post hoc tests on family-level means nested within population.

We compared the performance of each population when grown in soil collected from underneath its established invasive population (i.e., "home" soils hereafter, even though this does not refer to soils where *A. altissima* is native) to when grown in soils collected from other populations (i.e., "away" soils, hereafter) in order to evaluate plant-soil feedbacks. To assess the magnitude of plant-soil feedbacks, we calculated Hedge's *d* following the methods described in Kulmatiski et al. (2008), which compares the mean performance of each population grown in "home" soil to the mean performance of the seed populations grown in "away" soils while adjusting for variance and sample size. A value of 0 for Hedge's *d* indicates no difference between "home" and "away" and neutral feedback, values between 0.2 and 0.5 indicate weak effects, 0.5 and 0.8 indicate moderate effects, 0.8 and 1.0 indicate strong effects, and a value of *d* over 1.0 indicates a very large effect (Kulmatiski et al. 2008). Positive values indicate positive plant-soil feedbacks, and negative values indicate negative plant-soil feedbacks to plant performance.

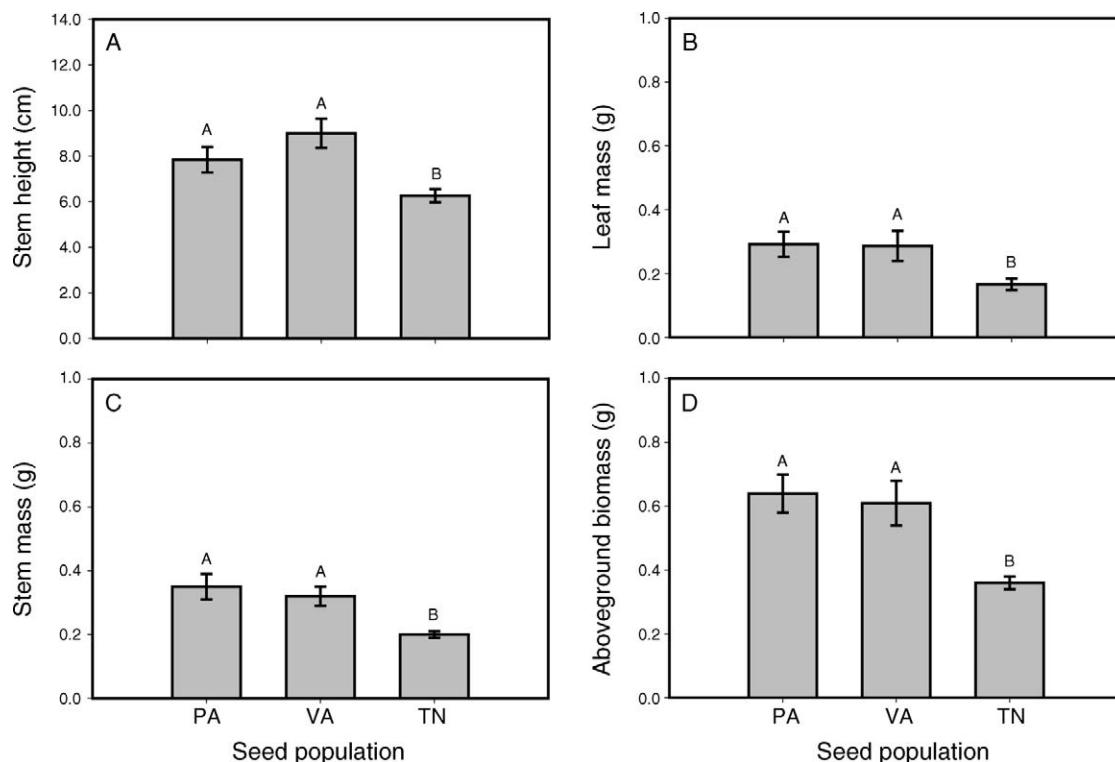


FIG. 1. Seed populations are significantly different when grown in control (mixed field) soil. For the performance metrics of (A) stem height, (B) leaf mass, (C) stem mass, and (D) aboveground mass, Virginia (VA) and Pennsylvania (PA) populations significantly differ from the Tennessee (TN) population (different letters above bars indicate significant differences [$P < 0.05$] indicated by Tukey's *h*sd).

RESULTS

Seed population and soil origin effects on A. altissima performance

In a greenhouse environment, one of the three geographically distinct populations of *A. altissima* displayed genetic differences in performance traits, but not in germination rates. Seeds planted in the common environment of the mixed field control soils differed significantly in performance as measured by stem height, leaf mass, stem mass, and total aboveground biomass (Fig. 1; Appendix: Table A2). PA and VA populations were similar, but TN plants were 20% or 30% shorter than PA and VA plants, respectively, and produced approximately 40% less biomass than the other two populations. Likelihood Ratio Tests show that there was no significant genetic variation among families in mixed field soil. In mixed sterile soil, there were no significant population difference in performance for stem height or stem mass, but there were significant differences by population in leaf mass and aboveground biomass (Appendix: Table A3).

Plant–soil feedbacks

Feedbacks to performance are specific to each population. The four performance traits that showed genetic divergence among populations when seeds were

grown in the mixed control soil all had significant seed population \times soil origin effects in field soils (Appendix: Table A4). In other words, in a common environment plant traits that showed evidence of population-level genetic differentiation changed in their expression when grown in soils collected from different populations, evidence of plant–soil feedback. The Hedge's *d* effect sizes indicate the presence of population-specific feedbacks (Fig. 2). The PA seed population experiences strong to very strong negative feedbacks (Hedge's *d* of -0.90 to -1.16) in their home soil ranging from a 25% decrease in stem height to a 62% decrease in leaf mass. The VA population experiences strong to very strong positive feedbacks (Hedges *d* of 0.94 to 1.40), growing 45% taller and producing up to 200% more biomass (leaf biomass) in VA soils compared to PA and TN soils. TN populations experience mixed positive and negative feedbacks (stem height $d = -0.79$, leaf mass $d = 1.27$, stem mass $d = 0.26$, aboveground mass $d = 0.83$), with TN seedlings 29% shorter but producing 60% more aboveground biomass in their home soils.

Putative mechanisms

We grew seedlings in gamma-irradiated sterile soils from each population to test the hypothesis that plant–soil feedbacks are related to biotic factors in the soil. When we examined the seed population effects on stem

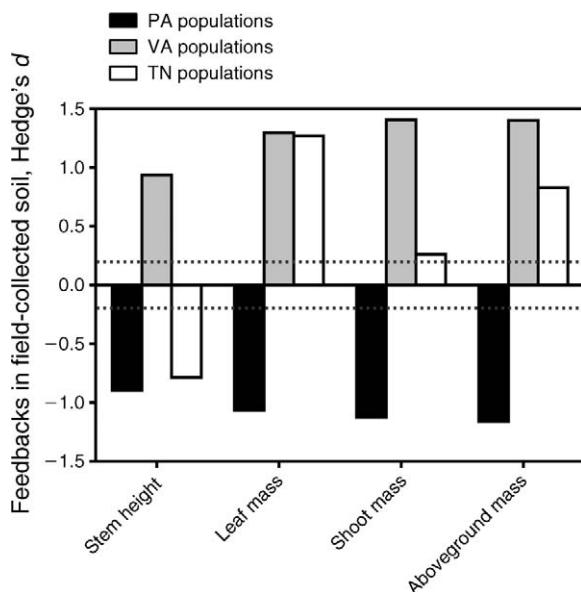


FIG. 2. Population-specific feedbacks to *Ailanthus altissima* performance in field-collected soils. The Hedge's d calculated for each seed population (performance in "home" soils compared to performance in other population soils) is shown for the performance metrics of stem height, leaf mass, stem mass, and aboveground mass. The dotted lines (± 0.20) indicate the minimum value of significant weak plant-soil feedback; values above 0 indicate positive feedback while values below 0 indicate negative feedbacks. PA populations (black bars) experience negative feedbacks grown in their own soils. VA populations (gray bars) experience positive feedbacks. TN populations (white bars) experience negative and positive feedbacks grown in their own soils.

height, leaf mass, stem mass, or aboveground biomass, in the PA, VA, and TN sterilized soils, we found no significant population effects on performance (Appendix: Table A3). There were also no significant interactions of seed population \times soil origin, in other words no statistical evidence for plant-soil feedbacks, in the sterilized soils (Appendix: Table A3). This suggests that any plant-soil feedbacks in the sterilized soils were neutral (no overwhelming negative or positive effects on plants), in contrast to the results in live field soils. There were significant effects of soil origin on seedling performance in sterilized PA, VA, and TN soils, indicating differences in soil nutrient quality. Post-hoc tests (Tukey's hsd) revealed that the traits of stem height, leaf width, and stem mass of all (PA, TN, and VA) seedlings were significantly higher in sterile VA soils and aboveground mass was significantly higher in sterile VA than sterile PA soils. Analysis of the field soils showed differences in microbial biomass pools and the activity of extracellular enzymes, indicating that there may be differences in biologically available nutrients. Virginia soils had the lowest microbial C:N ratio and the lowest potential NAGase activity, indicating that the Virginia soils are likely to have the most biologically available N of the three populations. If the physical

characteristics of each soil were responsible for the feedbacks observed in the field-collected soil, we would have expected to see similar patterns of growth in the sterile soil. Instead, the feedbacks in the sterile soil were neutral, and no expression of genetic variation in performance traits in sterile soil.

DISCUSSION

The results of this experiment demonstrate that (1) the *Ailanthus altissima* populations express genetically based differences in performance traits in mixed and population soils (Fig. 1); (2) there is a geographic mosaic of plant-soil feedbacks of varying direction and magnitude specific to each population in its home soil (the VA population experiences positive feedbacks and the PA population experiences negative feedbacks in their home soils); and (3) the feedbacks are not present in sterile soil, supporting the soil biota as the mechanism for the feedback. These results provide support for the first and third of our original hypotheses, that there is population differentiation in *A. altissima* and that the feedbacks are biotically based, and suggest that plant-soil feedbacks for this invasive species may be more idiosyncratic and soil biota mediate invasion success.

Population-level genetic variance

In mixed field soil, seed populations were genetically distinct for the performance traits of stem height, leaf mass, stem mass, and aboveground biomass, indicating population-level genetic differentiation (Seifert et al. 2009), although phenotypic differences do not allow us to separate selection from genetic drift as possible causal forces in this evolution. There was no family-level variation in the mixed field soil. In contrast, seeds grown in field soils collected from PA, VA, or TN populations displayed different combinations of population and even family-level variation (Appendix: Table A2). The pattern of genetic variation expressed in performance was unique to each field soil type, providing evidence that the soils collected from different parental populations have a strong influence over the expression of varying levels of genetic variation in seedlings.

We were also interested in differentiating between the physical structure of the soil and the soil biota as the causal factor in the observed patterns. Soil type can affect interactions between plants and soil biota such as the strength of the mutualism between coevolving mycorrhiza and plants (Johnson et al. 2010). However, our results suggest that the soil biota play a key role in *A. altissima* expression of population genetic differentiation. The seedlings grown in the sterilized mixed soils showed no population-level differentiation in stem height and stem mass, and the differences in leaf mass and aboveground biomass do not mirror the results of the mixed field soils. In the mixed field soils, VA populations had the highest leaf and aboveground biomass, but in the sterile mixed soils, it was the PA

populations that had the highest biomass (Appendix: Table A3). This suggests that the combined soil biotic communities represented in the mixed field soil enhance the performance of the VA but not the PA population. This evidence of varying interactions across populations between soil biota and *A. altissima* fits into the framework of the geographic mosaic theory of coevolution (Thompson 1997), in which the magnitude and direction of biotic interactions vary across the landscape depending upon the interacting species. Our results show that soil type and communities affect the expression of genetic variation in *A. altissima* grown under greenhouse conditions, and suggest that the expression of genetic variation, and by extension the potential for selection in this species, may be dependent upon the soil and soil biota in which it grows.

Plant–soil feedbacks

The magnitude and direction of the plant–soil feedbacks are unique to each *Ailanthus altissima* population, in contrast to our initial hypothesis. We hypothesized before conducting the experiment that there would be positive plant–soil feedbacks for each of the populations. The VA population was the only population with strong positive feedbacks in its own soil for each performance characteristic considered. There are strong negative feedbacks for the PA population in its own soil, and a mix of feedbacks of varying magnitude and effect for the TN population. These contrasting feedbacks highlight the importance of studying invasive plants within the context of existing plant–soil interactions. When the performance of populations grown in their natal field-collected soils are compared to their performance in soil collected from other populations, it is clear that VA seedlings grew more aggressively in their home soils than do either PA or TN seedlings in their home soils. Based on this result, VA populations might increase in number of individuals and in landscape area invaded faster than other populations. Positive feedbacks may allow VA populations to grow in more dense monocultures, which is of concern for associated native species as allelopathy of *A. altissima* increases as stems grow denser (Gomez-Aparicio and Canham 2008b). Moreover, since this experiment was conducted under the artificial climatic conditions of the greenhouse, it tested only the soil conditions associated with each site, not the different climatic conditions. Much of the previous research on invasive species' plant–soil feedbacks focuses on differences between native and introduced ranges or compares invasive to native species. Comparisons of invasives with conspecifics from their native range (Callaway et al. 2004) or heterospecifics in the invaded range (Klironomos 2002) show that in general, invasive species experience positive plant–soil feedbacks or are simply less dependent on mutualists in the soil (Seifert et al. 2009). In focusing our study on populations within the invaded range rather than on sampling the invasive

range as a homogeneous entity, we have found that in contrast to earlier research and theoretical predictions (Rout and Callaway 2009), invasive populations may experience a range of feedbacks across their invaded range. Different feedbacks may result in varying rates of expansion for different populations.

Biotic mechanisms

The use of sterilized soils allowed us to test our hypothesis that the feedbacks are due to the soil biota present in the field soils, rather than to the physical properties and nutrient levels common to both field and sterilized soils. The results support a biotic feedback, as there were no statistically significant seed population by soil origin (genetic \times environment) effects in sterilized soil, and virtually no difference between populations grown in the sterilized PA, VA, or TN soil (the one exception was for petiole length in sterile PA soil). The positive feedbacks associated with VA (for the traits of stem height, leaf mass, stem mass, and aboveground biomass) and TN (leaf mass, stem mass, and aboveground biomass) populations, and the negative feedbacks associated with PA (stem height, leaf mass, stem mass, and aboveground biomass) and TN (stem height) populations, were associated with a component of the unsterilized soil, an effect consistent with differences in the soil biotic communities or their activities. The population-specific feedbacks may be due to preinvasion soil structure and microbial communities, as suggested by a study of invasive plants across a broad geographic range that shows that the extent to which invasive species alter invaded soils depends in part on preinvaded soil conditions (Dassonville et al. 2008). Plant–soil feedbacks have been associated with the activity of nematodes, bacteria, mutualistic and pathogenic fungi found in the soil (Bever 2003). The pattern of plant–soil feedbacks that we observed could be due to differences in the soil communities associated with each population as well as to the variation in local adaptation that *A. altissima* has made to these conditions. Alternatively, the populations may have been established at different times and are in different stages of accumulating mutualistic or antagonistic biotic interactions (Strayer et al. 2006). However, we were not able to locate introduction records of these populations; therefore conclusions about how these feedbacks change over time are not possible.

Conclusions and implications

The different directions of plant–soil interactions shown by the populations emphasize the importance of understanding how ecological interactions shape population dynamics. Soil-specific feedbacks have been demonstrated with invasive species, in studies in which plants experienced positive feedbacks in their introduced range (e.g., Klironomos 2002). However, this is the first study, to our knowledge, that provides evidence of population-specific plant–soil feedbacks for an invasive

species in its new range. If populations of *Ailanthus altissima* vary in the extent to which they benefit from feedbacks with soil biota as well as in their ability to promote these feedbacks, this suggests that the interaction between invader and invaded community may be far more important in determining the success of invasion than are the characteristics of either component alone. Monitoring these populations over time may allow us to determine how important these feedbacks are in facilitating the further spread of this species, and could focus management plans on populations in locations where the invasive species experiences a significant benefit from its interactions with the soil biota.

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APPENDIX

Population means, feedbacks, and soil properties (*Ecological Archives* E092-100-A1).