

Running headline: Neighborhood models of allelopathy

**Neighborhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests**

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## 1 Summary

2 1. Allelopathic interactions between invasive and native species have been suggested to be  
3 an important mechanism for the success of some of the most aggressive plant invaders.  
4 However, field experiments that test the effects of natural levels of allelopathic compounds  
5 on coexisting native species are exceptionally rare.

6 2. In this study, we analyzed the allelopathic effects of the invasive tree *Ailanthus altissima*  
7 on seedling emergence, survival and growth of three native tree species (*Acer rubrum*, *Acer*  
8 *saccharum*, and *Quercus rubra*) in temperate forests of the northeastern US. We used  
9 activated carbon to reduce potential allelopathic interference, and developed neighborhood  
10 models that explain the observed spatial variation in the effects of the activated carbon  
11 treatments on seedling performance as a function of the size, abundance and distribution of  
12 *Ailanthus* trees in the neighborhood.

13 3. Our results showed that the addition of activated carbon to the soil did not affect seedling  
14 emergence or survival, but caused a significant increase in seedling growth of all three  
15 species. Moreover, the activated carbon shifted the overall interaction between *Ailanthus* and  
16 maple seedlings from neutral or slightly positive to very positive for *A. rubrum*, and from  
17 negative to positive for *A. saccharum*, whereas the net interaction between *Ailanthus* and *Q.*  
18 *rubra* was always negative. Since *Ailanthus* has the ability to increase soil fertility, these  
19 species-specific responses are presumably influenced by among-species differences in the  
20 net effects of both allelopathy and changes in resource availability caused by the presence of  
21 *Ailanthus*.

22 4. The cumulative allelopathic effects of *Ailanthus* were proportional to the density of  
23 *Ailanthus* in the neighborhood, regardless of their size. In contrast, *Ailanthus* effects were  
24 strongly influenced by distance from a tree, generally dropping to zero within 5 m from the  
25 trunk.

26 5. **Synthesis:** Taken together, our results indicate that allelopathy is an important  
27 mechanism to take into account when trying to understand the causes and consequences of

1 plant invasions. However, this study also strongly suggests that the real significance of the  
2 allelopathic effects of an invasive species can not be assed independently of its target  
3 community, or in isolation of other resource interactions involving the invader and the native  
4 community.

5  
6 *Key-words:* Acer rubrum; Acer saccharum; *activated carbon*; Ailanthus altissima; *allelopathy*;  
7 *field experiment*; *invasive species*; *neighborhood models*; *plant interactions*; Quercus rubra;  
8 *seedling performance*.

## 10 **Introduction**

11 Biological invasions are recognized as one of the most important causes of ecosystem  
12 degradation and biodiversity loss worldwide (Vitousek *et al.* 1996; Mack *et al.* 2000). As a  
13 result, there has been extensive research to unravel the causes and consequences of the  
14 introduction of new species into natural systems. Ironically, by serving as research tools,  
15 invasive species have contributed enormously to advances in our understanding of the  
16 mechanisms by which individual species can alter community structure and ecosystem  
17 processes (Vitousek 1986; Lodge 1993; Bruno *et al.* 2005). A notable example of how  
18 invasions have stimulated ecological research is in the revitalization of the interest in  
19 biochemical interactions among plants (Callaway & Maron 2006). The ecological  
20 consequences of allelopathy, or the negative effects of one plant on another through the  
21 release of chemical compounds into the environment (*sensu* Muller 1966), has been greeted  
22 with skepticism for decades (Harper 1977; Keeley 1988). As a result, resource-based  
23 interactions such as competition have been usually invoked as the explanation for the effects  
24 of invasive plant species on community structure (Levine *et al.* 2003). However, recent  
25 studies present compelling evidence that allelopathic interactions between invasive and  
26 native species can be one of the mechanisms underlying the remarkable success of some of  
27 the most aggressive plant invaders (Bais *et al.* 2003; Callaway & Ridenour 2004; Prati &

1 Bossdorf 2004; Stinson *et al.* 2006).

2       The skepticism that has characterized the assessment of the role of allelopathy in  
3 nature is at least partially the consequence of the methodological difficulties inherent in  
4 demonstrating the effects of allelopathy under field conditions. Most studies have used  
5 experimental additions of plant extracts under lab conditions, tested on Petri dishes or  
6 sterilized soils on weed species particularly sensitive to chemicals (Hierro & Callaway 2003).  
7 Although there has been significant progress in the use of more realistic and sophisticated  
8 techniques in recent years (mainly in research with invasive species), tests for allelopathic  
9 effects under field conditions are, apart from some remarkable exceptions (e.g., Nilsson  
10 1994; Nilsson *et al.* 2000), still exceptionally rare (Indejit & Callaway 2003). Field  
11 experiments offer the possibility to overcome three main drawbacks of laboratory and  
12 greenhouse tests. First, they test if toxic substances accumulate at sufficient concentrations  
13 or if they persist long enough in natural soils to inhibit the growth of other plants. Second,  
14 toxic effects are tested on coexisting species that can vary in their sensitivity to  
15 allelochemicals. Third, they allow exploring spatio-temporal patterns of variation in  
16 allelochemical effects (e.g., Zackrisson & Nilsson 1992; Jose & Gillespie 1998). The  
17 ecological importance of any given allelochemical compound is likely to be highly dependent  
18 on its spatio-temporal variability in natural communities.

19       In this paper, we test for allelopathic effects under natural conditions of one of the  
20 most important invasive tree species of temperate forests in the northeastern US, *Ailanthus*  
21 *altissima* (Mill.) Swingle (Simaroubaceae). Members of the family Simaroubaceae are known  
22 to produce quassinoid compounds with a wide range of effects on insects, fungi, protozoa,  
23 viruses, and cancer cells (Polonsky 1973, 1985). Several studies have shown that extracts of  
24 all parts of *Ailanthus* (i.e., roots, leaves, trunk) inhibit germination and growth of several plant  
25 species in bioassays or greenhouse experiments (Mergen 1959; Voigt & Mergen 1962;  
26 Heisey 1990a,b; De Feo *et al.* 2003). At least 10 quassinoids, together with alkaloids and  
27 other secondary products, have been isolated from different parts of the plant (see

1 references in Heisey & Heisey 2003). One quassinoids, ailanthone, has been identified as  
2 the major compound responsible for phytotoxic effects (Lin *et al.* 1995; Heisey 1996).  
3 However, ailanthone is rapidly inactivated in non-sterile soils (Heisey 1990b, 1996), so its  
4 actual allelopathic effect under field conditions may be less (if any) than what lab  
5 experiments indicate. *Ailanthus* thus represents an example of a successful invader for  
6 which presumed allelopathical effects are invoked when explaining its invasive success (e.g.,  
7 Kowarik 1995; Vilá *et al.* 2006; Webster *et al.* 2006), but for which no evidence of allelopathic  
8 effects under natural conditions is currently available.

9         We investigated the importance of allelochemical interference by *Ailanthus* on the  
10 emergence, survival and growth of native tree seedlings by using activated carbon (AC) to  
11 reduce potential allelopathic effects in a 2-year field experiment. We used a spatially-explicit,  
12 neighborhood analysis to develop models that explain the observed spatial variation in the  
13 effects of the AC on seedling performance as a function of the size, abundance, and  
14 distribution of *Ailanthus* trees in the immediate neighborhood. A similar neighborhood  
15 approach was successfully used in a parallel study to analyze the impacts of *Ailanthus* on  
16 nutrient cycling in the same study sites (Gómez-Aparicio & Canham, *in press*). Results from  
17 that study showed that *Ailanthus* increases nutrient availability (i.e., pH, exchangeable Ca,  
18 exchangeable K, total N) and cycling rates (i.e., net nitrification) in surface soil, presumably  
19 due to the extraordinarily high nutrient concentration in its leaf litter (as much as 4 times  
20 higher than in native tree species). For example, soil Ca and N pools were twofold higher in  
21 neighborhoods dominated by *Ailanthus* than in neighborhoods dominated by native species  
22 such as *Acer saccharum*, *Fraxinus americana* or *Quercus rubra*. These results imply that  
23 *Ailanthus* could have positive effects on the native seedling community, due to increases in  
24 soil fertility. This highlights the need for an analysis of the relative importance of allelopathy  
25 in a natural setting where other interactions (i.e., facilitation) may also take place. Specifically,  
26 we asked the following questions: 1) Does *Ailanthus* interfere with native tree seedlings via  
27 allelopathic exudates? 2) Are allelopathic effects species-specific? 3) How does the

magnitude of the allelopathic effects vary with the size and spatial distribution of *Ailanthus* in the neighborhood? 4) What role does allelopathy play in the net effect of *Ailanthus* on native seedlings?

## **Material and methods**

### **STUDY SPECIES AND SITES**

*Ailanthus* was introduced from China in 1784, and is now widely naturalized throughout much of the United States (Hu 1979). It produces very large numbers of wind dispersed seeds (Hu 1979), grows quickly in high light (Bazzaz 1979; Feret 1985), and can reproduce asexually via root sprouts (Hu 1979). Although early studies considered it shade-intolerant and unable to invade closed forests, recent studies show that it can establish in intact forests when canopy gaps open (Kowarik 1995; Knapp & Canham 2000). It can reach mature size during a single period of release in a treefall gap, while most native species need several periods (Canham 1989; Knapp & Canham 2000). Although rapid growth and prolific reproduction (both sexually and vegetatively) undoubtedly contribute to its success as invader, the arsenal of biochemical defenses found in all *Ailanthus* tissues suggests allelopathy as another potential mechanism of invasion.

The experiment was conducted in three forest stands in northwestern Connecticut (USA), at elevations from 300 to 500 m. All sites had patchy distributions of *Ailanthus* within the stands. The three sites are approximately 20 km apart, one located near the village of Ameshville (41°58'N, 73°27'W), the second located in the Dark Entry Forest near the village of Kent (41°49'N, 73°23'W), and the third located in the village of New Milford (41°36'N, 73°25'W). Soils at Ameshville (AM) and New Milford (NM) are Dystric Eutrochrepts derived from calcareous glacial outwash over limestone bedrocks, whereas soils at Dark Entry Forest (DEF) are Typic Dystrochrepts derived from glacial till over mica-schist bedrocks (Hill *et al.* 1980). All sites are in second-growth stands (80-130 yr) with a history of logging but no history of agriculture. The species composition of the stands included elements of the oak

forests of southern New England and the northern hardwood forests of the northeastern United States and Canada. The dominant native tree species were *Acer saccharum* Marsh. (sugar maple), *Fraxinus americana* L. (white ash), *Quercus rubra* L. (northern red oak), *Prunus serotina* Ehrh. (black cherry), and *Betula lenta* L. (black birch). The relative basal area of *Ailanthus* was 31.2% in AM, 28.4% in DEF, and 32.3% in NM. The mean DBH of *Ailanthus* trees was ~20 cm in the three sites (19.9 cm in AM, 21.6 cm in DEF, and 24.6 cm in NM), and the maximum DBH ranged from 37.9 cm in DEF to 54.8 cm in AM.

#### SEEDLING TRANSPLANT EXPERIMENT

In June 2005, seedlings of *Acer rubrum* L., *Acer saccharum*, and *Quercus rubra* were collected from the surrounding forests and planted at each of the three study sites. For each species, we selected seedlings of similar age (3-5 years) and height without evident signs of herbivory damage. 20 planting locations were selected per site, stratified along a gradient of distance from and abundance of *Ailanthus* in the immediate neighborhood (defined as a 25-m radius circle around each planting location). We identified and mapped every *Ailanthus* tree with a DBH  $\geq$  2cm within each of the 60 neighborhoods (n = 337 trees), using a laser rangefinder with a digital compass (Laser Technology, Inc., Colorado, USA). Relative basal area of *Ailanthus* in the neighborhoods varied between 0% and 70%.

At each planting location, two 20 x 60 cm plots were established, separated by a distance of 50 cm. The soil of one of the plots was dug to a depth of 20 cm, moved to a bucket where it was hand-mixed with activated carbon (GC Powdered Activated Carbon, General Carbon Corp., Paterson, New Jersey, USA) at a rate of 20 mL/L soil, and put back in the ground (AC treatment). The soil from the second plot was dug to the same depth and moved to a different bucket (to reproduce the disturbance caused to the soil in the AC treatment), and then put back into the ground without adding any chemicals (Control treatment). An additional amount of AC (0.125 L) was applied in May 2006 onto the soil surface of each AC treatment. Activated carbon is frequently used in allelopathy experiments

1 because it acts as an adsorbant for many large organic compounds, therefore minimizing  
2 allelopathic effects while having minor impacts on nutrient dynamics (Cheremisinoff &  
3 Morresi 1978). Activated carbon has been successfully used to test for allelopathic  
4 interactions in a large number of studies (see review in Hierro & Callaway 2003), and has  
5 been recommended as an effective approach for allelopathy studies in the field (Indejit &  
6 Callaway 2003).

7         Three seedlings (one of each of the three native tree species) were planted in each  
8 plot (n = 360 seedlings). We measured the initial stem height, extension growth of the stem,  
9 basal diameter, number of leaves, and diameter of each expanded leaf at the time of planting.  
10 In order to facilitate accurate remeasurement of stem height, a small mark was made on the  
11 stem of each seedling at the ground level. Within the initial pool of seedlings collected for  
12 transplanting, a random subsample (n = 30 per species) was taken to the lab at the  
13 beginning of the experiment for measurement of initial stem height, stem dry biomass, and  
14 dry biomass, area and diameter of all leaves. The objective was to generate, for each  
15 species, regressions of 1) stem dry biomass as a function of stem height, 2) leaf area as a  
16 function of leaf diameter (measured from the base to the tip of the leaves), and 3) leaf dry  
17 biomass as a function of leaf area. These regressions ( $R^2 > 0.9$  in all cases, data not shown)  
18 allowed non-destructive estimations of initial stem biomass, initial leaf area, and initial leaf  
19 biomass for each experimental seedling using field measurements (see below).

20         For each experimental seedling, survival, stem height, stem extension growth,  
21 number of leaves, and diameter of each individual leaf were sampled twice, once at the end  
22 of the first growing season (September 2005) and once at the end of the second growing  
23 season (September 2006). Seedlings alive in September 2006 were harvested and taken to  
24 the lab where leaves were removed and measured for total area using a leaf area meter  
25 (LICOR, Inc.). Roots were rinsed by hand, and the root and shoot systems were separated at  
26 ground level (using the marks on the stems). Roots, stems and leaves were dried for 48h at  
27 60°C and weighed. The extension growth of the stem for the second growing season was



1 separated from the rest of the stem and weighed separately. We considered the biomass of  
2 the extension growth as a more accurate estimation of the effects of AC on biomass  
3 allocation to stems than the total stem biomass. Since some seedlings had finished their  
4 annual growth by the time the experiment started (June 2005), we decided to conduct  
5 statistical analyses using growth data only for the second growing season. Specifically, we  
6 considered 6 response variables: 1) survival after the 2 years of the experiment; 2) extension  
7 growth in 2006; 3) dry biomass of the 2006 extension growth; 4) root dry biomass; 5) leaf dry  
8 biomass in 2006; and 6) leaf area in 2006. Due to the difficulties of excavating *Q. rubra* roots  
9 without losing a significant part of the root system, we decided not to consider root biomass  
10 as a response variable in the analyses for this species.

11 Because variation in light availability was expected to affect seedling growth and  
12 survival, we used fisheye photography to estimate a gap light index (GLI, Canham 1988) for  
13 each seedling plot. GLI is the percentage of “gap” light (Canham 1988; i.e.,  
14 photosynthetically active radiation transmitted through discrete openings in the canopy) that  
15 reaches a point in the understorey over the course of a defined growing season.  
16 Photographs were taken in the middle of each plot by placing the camera (with a fisheye lens)  
17 at approximately 30 cm over the ground. All pictures were taken on cloudy days during  
18 August 2005.

19 The transplant experiment was initially designed including *Ailanthus* as a fourth  
20 seedling species. Given the difficulty of finding natural seedlings of *Ailanthus* in our study  
21 sites, seeds were germinated in the greenhouse in May 2005 and *Ailanthus* seedlings  
22 transplanted to the field at the same time as the native species. *Ailanthus* seedlings were  
23 transplanted to individual 20 x 20 cm plots 30 cm away from the native plots (in order to  
24 avoid potential allelochemical interference among seedlings), using the same soil treatments  
25 used for the plots containing native tree seedlings. However, even though dead *Ailanthus*  
26 seedlings were replaced during the first three weeks of the experiment, no *Ailanthus*

seedlings were alive at the end of the first growing season, and the species had to be excluded from the study.

#### SEED SOWING EXPERIMENT

We conducted a seed sowing experiment at the same locations as the seedling transplant experiment ( $n = 20$  locations per site). Two 30 x 30 cm quadrats were established at each location, one (AC quadrat) next to the seedling plot with AC and the second one (Control quadrat) next to the Control seedling plot. In the AC quadrat, AC was added at a rate of 20 mg/L soil to the first 5 cm of the soil. In the Control quadrat the soil was mixed by hand but no chemicals were added. In each quadrat, 10 seeds of *A. rubrum* and 10 seeds of *Q. rubra* were sown at 1 cm depth in four lines of 5 seeds, each line 2 cm from each other and 5 cm from the border of the quadrat. *Acer saccharum* was not included in the experiment due to the unavailability of seeds during the years of the study. Seeds of *A. rubrum* were obtained commercially from regional seed sources (lot with 98% viability). Seeds of *Q. rubra* were collected in the surrounding forests, and non-viable acorns (empty or depredated by insects), identified by flotation in water, were excluded. To exclude seed predators, we built cages around each quadrat using 24-gauge, 1.5 cm mesh hardware cloth buried to a depth of 5 cm and extending 25 cm aboveground. Seeds were sown in November 2005, and emergence was monitored every two weeks during April-June 2006.

In September 2006, all live seedlings in the seed sowing experiment were harvested and taken to the lab, where they were measured using the same procedures for seedlings in the transplant experiment (see above). Response variables from the sowing experiment were: 1) emergence, estimated as the percentage of seeds with shoots growing beyond the ground surface by the time of the last emergence census (June 2006); 2) survival, estimated as number of emerged seedlings in June that were alive at the end of the experiment in each quadrat; 3) stem dry biomass, estimated as the mean stem biomass of all alive seedlings in each quadrat; 4) leaf dry biomass, estimated as a mean per quadrat; and 5) leaf area, also

estimated as a mean per quadrat. As for the transplant experiment, we decided not to consider root biomass as a response variable in *Q. rubra*.

#### NEIGHBORHOOD ANALYSES OF SEEDLING EMERGENCE, SURVIVAL AND GROWTH

We used a neighborhood approach to the study of allelopathy in which seed emergence, seedling survival, and seedling growth were analyzed as a function of: 1) the study site; 2) the initial size of the seedling (only in the case of transplanted seedlings); and 3) the size, abundance, and spatial distribution of *Ailanthus* in the neighborhood. The models were run separately for each of the study species and response variables in each of the two experiments. For each response variable (Y), our *basic allelopathy model* takes the form:

$$Y = \text{Site}_j * \text{Size}^\lambda * X \quad \text{eqn 1}$$

The first term in the model,  $\text{Site}_j$ , is an estimated parameter that represents the average potential seedling performance (i.e., survival, root biomass, leaf area etc per unit effect of plant size) in the absence of neighboring *Ailanthus* for  $j = 1 \dots 3$  study sites. The second term,  $\text{Size}^\lambda$ , controls for the effects of initial plant size on seedling performance in the transplant experiment, as a function of the parameter  $\lambda$ , which scales the response variable to size as a power function. We used different measures of plant size depending on the response variable analyzed in the model: 1) initial stem height was used as the size estimator for survival and extension growth; 2) initial stem biomass (calculated indirectly using regressions, see above) as the size estimator for extension biomass and root biomass; 3) initial leaf biomass (calculated using regressions) as the size estimator for (final) leaf biomass; and 4) initial leaf area (calculated using regressions) as the size estimator for (final) leaf area. The range of variation among individuals was relatively small because of their similar age.

The third term in the model,  $X$ , captures the neighborhood effects of *Ailanthus* on individual seedling performance. If *Ailanthus* has no effect on seedling performance then  $X = 1$ , if the effect is negative then  $0 \leq X < 1$ , and if the effect is positive then  $X > 1$ . We assumed

1 that the neighborhood effects vary monotonically as a function of an *Ailanthus* neighborhood  
 2 index (ANI):

$$3 \quad X = \exp^{\gamma \left( \frac{ANI_i}{ANI_{max}} \right)} \quad \text{eqn 2}$$

4  $ANI_i$  is the *Ailanthus* neighborhood index for seedling  $i$  of the target species (equation  
 5 below), and  $ANI_{max}$  is the maximum value of ANI for all seedlings of the target species. The  
 6 use of  $ANI_{max}$  standardizes the neighborhood effects term ( $0 \leq ANI_i/ANI_{max} \leq 1$ ) and facilitates  
 7 comparisons across seedling species. To compute ANI we used a simple additive index of  
 8 the abundance of *Ailanthus* within the immediate neighborhood, as a function of the size and  
 9 the distance to *Ailanthus* neighbors. Thus, for  $i=1 \dots n$  *Ailanthus* trees  $\geq 2\text{cm}$  DBH within a 25-  
 10 m radius around the target seedling, the *Ailanthus* neighborhood index (ANI) is given by:

$$11 \quad ANI = \sum_{i=1}^n DBH_i^{\alpha} \exp(-\beta \text{ distance}_i) \quad \text{eqn 3}$$

12 In order to keep the number of parameters manageable and to avoid parameter  
 13 trade-offs, we allowed  $\beta$  to vary and be estimated by the analyses but tried alternative  
 14 models setting the value of  $\alpha$  either to  $\alpha = 2$  or  $\alpha = 0$ . A value of  $\alpha = 2$  indicates that the  
 15 influence of *Ailanthus* scales approximately with tree biomass (i.e.,  $DBH^2$ ), whereas a value  
 16 of  $\alpha = 0$  means that the influence of *Ailanthus* varies as a function of density, regardless of  
 17 size.

18 We estimated a separate  $\gamma$  parameter in equation 2 for each of the two treatments  
 19 (i.e., for activated carbon (AC) vs the control). The parameter  $\gamma$  is an exponential decay  
 20 coefficient, and defines the sign and steepness of the variation in the neighborhood effects  
 21 (X), and therefore in seedling performance (Y), due to an increment in ANI. Positive values of  
 22  $\gamma$  would indicate a positive effect of the presence of *Ailanthus* neighbors relative to the mean  
 23 effects of the native neighbors, whereas negative  $\gamma$  values would indicate a negative effect of  
 24 the presence of *Ailanthus* relative to the presence of native neighbors. The difference in the  $\gamma$

values among the AC and Control treatments measures the magnitude of the allelopathic effects of *Ailanthus* on seedling performance.

In order to test for the possibility of any AC effects, independent of the presence of *Ailanthus*, we ran a modified version of the *basic allelopathy model* in which the average potential seedling performance in the absence of neighboring *Ailanthus* at each site (i.e. term  $Site_j$  in equation 1) was estimated separately for AC and Control seedlings. Different  $Site_j$  terms for the two groups of seedlings would indicate that AC affected seedling performance even in the absence of *Ailanthus*. This could reflect either the presence of other allelopathic species or some other unintended effect of the addition of AC. However, the *modified basic allelopathy model* was never a better fit to the data than the simpler *basic allelopathy model* (see Appendix S1 in Supplementary Material), indicating that effects in AC treatments were directly linked to the presence of *Ailanthus*. The absence of side-effects (i.e. not related to the presence of *Ailanthus*) of the AC is also supported by the lack of significant differences in seedling performance among treatments (AC vs. Control) when only seedlings without *Ailanthus* neighbors were considered in the analyses (see Appendix S2 in Supplementary Material).

We also explored the effect of light on seedling performance by adding a fourth term ( $GLI^{\delta}$ ) to the *basic allelopathy model* (equation 1). However, since the resulting models were never a better fit to the data, this term was dropped from the analyses (results not shown for simplicity). The absence of a light effect on seedling performance was probably a consequence of the limited variation in light levels experienced by seedlings in the understorey ( $GLI = 3-6\%$  in 90% of the cases).

In order to analyze whether the allelopathic effects of *Ailanthus* varied among sites, we tested a modified version of the *basic allelopathy model* in which the value of  $\gamma$  (equation 2) for the AC treatment was allowed to vary as a function of the site (*Site-specific allelopathy model*). The value of  $\gamma$  for the Control treatment was not allowed to vary among sites due to limitations in the number of parameters permitted by our sample size. The *basic* and *site-*

*specific allelopathy models* were compared to a *null model* in which seedling performance was predicted just as a function of the site and the seedling initial size (i.e., setting the multiplier  $X$  to 1 in equation 1). By doing this, we assessed whether including the neighboring effects of *Ailanthus* into a model significantly improved its explanatory power.

## PARAMETER ESTIMATION AND COMPARISON OF ALTERNATE MODELS

We used simulated annealing, a global optimization procedure, to determine the most likely parameters (i.e., the parameters that maximize the log likelihood) given our observed data (Goffe *et al.* 1994). We used three different error structures depending on the nature of the response variables. We analyzed survival of individual transplanted seedlings using a logistic regression in which the probabilistic scientific model provided the likelihood function. For emergence and survival in the sowing experiment we assumed a binomial error structure. For growth variables we used a normal error structure with the variance as a power function of the mean. This required estimating an additional parameter to determine the scaling of the variance to the mean. Details on the likelihood functions and the software code used for the simulated annealing algorithm are provided in Appendix S3. Alternate models were compared using the Akaike Information Criterion corrected for small sample sizes ( $AIC_c$ ) (Burnham & Anderson 2002). Models with a difference in  $AIC_c < 2$  units are considered to have equivalent empirical support. When the difference in  $AIC_c$  between two models is  $> 2$ , the model with the lowest  $AIC_c$  is considered to have larger empirical support. We used asymptotic 2-unit support intervals to assess the strength of evidence for individual maximum likelihood parameter estimates (Edwards 1992). These are simply the range of parameter estimates for which “support” (log-likelihood) is within 2 units of the maximum log likelihood, and were determined by incrementally varying parameter estimates above and below the maximum likelihood estimate until log-likelihood had dropped by 2 units. The  $R^2$  of the regression ( $1 - SSE/SST$ ) of observed vs predicted was used as a measure of goodness of fit (SSE, sum of squares error; SST, sum of squares total). All analyses were done using

software written specifically for this study using Delphi for Windows (Version 7, Borland Software Corp.).

## Results

### SEEDLING TRANSPLANT EXPERIMENT

The *null model* (ignoring the neighborhood effects of *Ailanthus*) was the best fit for survival of the three study species (Table 1), indicating that *Ailanthus* did not influence seedling survival during the course of the experiment. However, the *basic allelopathy model* (including the influence of *Ailanthus*) was the best fit for 11 out of 14 species-specific models for growth variables (Table 1). Thus, *Ailanthus* had an effect on extension growth, extension biomass, leaf biomass, and leaf area of *A. rubrum*; on extension growth, extension biomass, root biomass, leaf biomass, and leaf area of *A. saccharum*; and of extension growth and extension biomass of *Q. rubra* (Table 1). The *site-specific allelopathy model* (assuming different allelopathic effects of *Ailanthus* among sites) was never the best model. Model  $R^2$  for the best models ranged between 0.10-0.33 for *A. rubrum*, 0.28-0.35 for *A. saccharum*, and 0.17-0.49 for *Q. rubra* (Table 1).

Initial seedling size had a minor influence on performance of *A. rubrum* seedlings as indicated by small values of the  $\lambda$  parameter ( $\lambda = 0-0.25$ ), and a larger influence on performance of *Q. rubra* seedlings ( $\lambda = 0.47-0.91$ ; Table 2). The  $\lambda$  values for *A. saccharum* varied considerably depending on the response variable ( $\lambda = 0-0.94$ ; Table 2). The exponent  $\alpha$  (equation 3) controls the scaling of the influence of *Ailanthus* size on ANI, and hence on seedling performance. In 9 of the 11 cases where the *basic allelopathy model* was the best model,  $\alpha = 0$  offered a better fit to the data than  $\alpha = 2$  (Table 2), indicating that the influence of *Ailanthus* was simply proportional to the density of *Ailanthus* ( $\text{DBH} \geq 2\text{cm}$ ) in the neighborhood, regardless of their size. In contrast, *Ailanthus* influence was strongly influenced by distance, as shown by large values of the parameter  $\beta$  (i.e.,  $\beta \geq 1$ ; Table 2). In most cases the influence of *Ailanthus* dropped to effectively zero within the first 5 m from the

trunk of a neighboring tree (Fig. 1). Among species, distance decay in the effect of *Ailanthus* was somewhat steeper for the two maples than for *Q. rubra* (Fig. 1).

For *A. rubrum*, the values of the  $\gamma$  parameter in the Control treatment varied between almost neutral for leaf biomass ( $\gamma = 0.05$ ) and area ( $\gamma = -0.02$ ) to positive for extension growth ( $\gamma = 0.41$ ) and biomass ( $\gamma = 0.43$ ). When AC was added to the soil, the  $\gamma$  values increased significantly for the four variables ( $\gamma = 0.99$ - $1.11$ ; Table 2), indicating much larger positive effects of *Ailanthus* on *A. rubrum* seedling performance when potential allelochemical effects were reduced by the activated carbon. Thus, the extension growth, extension biomass, leaf biomass, and leaf area of *A. rubrum* seedlings in the AC treatment were as much as 2.5-3 times larger at high values of the *Ailanthus* neighborhood index (ANI) than at low values (Fig. 2a-d). For *A. saccharum*, the  $\gamma$  values were always highly negative in the Control treatment ( $\gamma = -1.02$  to  $-0.21$ ; Table 2), indicating a decrease in seedling performance as ANI increases. However, the addition of AC shifted the sign of the  $\gamma$  parameter to almost neutral or positive ( $\gamma = -0.09$  to  $0.55$ ), indicating a shift in the net interaction among *A. saccharum* seedlings and *Ailanthus* from negative to positive when allelochemical effects were ameliorated. The largest positive effect of AC on *A. saccharum* seedlings was on root biomass, which increased almost twofold under the maximum influence of *Ailanthus* (Fig. 2g). For *Q. rubra*,  $\gamma$  values were negative in all cases, with both extension growth and biomass diminishing under the influence of *Ailanthus* (Fig. 2j-k). However, the magnitude of the negative net interaction with *Ailanthus* was much larger in the Control ( $\gamma = -1.57$  and  $\gamma = -0.96$ ) than in the AC treatment ( $\gamma = -0.48$  and  $\gamma = -0.45$ ; Table 2 and Fig. 2).

#### SEED SOWING EXPERIMENT

The goodness of fit of the models for the sowing experiment were in general lower than for the transplant experiment ( $R^2 = 0.04$ - $0.28$ ; Table 3). The *null model* was the best fit for both emergence and survival of *A. rubrum* seedlings (Table 3), indicating that there was no



detectable neighborhood effect of *Ailanthus* on these variables. However, we have to qualify this result by noting that there were very low percentages of seed emergence (i.e., 2-13%) and survival (i.e., 0-28%) of *A. rubrum* seedlings in all the three sites. Due to the low rates of *A. rubrum* emergence and survival, there were not enough live seedlings at the end of the experiment for the analyses of growth variables. In the case of *Q. rubra*, the *basic allelopathy model* (including the effect of *Ailanthus*) was the best fit for most response variables (Table 3). However, since the difference in AIC between the *basic allelopathy model* and the *null model* (assuming no effect of *Ailanthus*) was never larger than 2 units, there is not strong support for the effect of *Ailanthus* on *Q. rubra* emergence and 1-year stem biomass, leaf biomass and leaf area. As for the transplant experiment, the *site-specific allelopathy model* was never the best fit (Table 3).

## Discussion

Our results suggest that the production of allelochemical compounds by the invasive tree *Ailanthus altissima* has important negative effects on seedling growth of dominant native tree species in these forests. To our knowledge, this is the first study showing allelopathic effects of an invasive species on coexisting native species exposed to real spatio-temporal variation of allelochemical production and activity. We have shown in a separate study that *Ailanthus* increases the availability of key soil resources, including N and Ca, within its neighborhood (Gómez-Aparicio & Canham, *in press*). Depending on how sensitive a native species is to the allelochemical effects of *Ailanthus*, the net effect (i.e. the combined effects of allelopathy and changes in soil resources) of the presence of this invasive tree in the vicinity of a seedling varied from strongly positive to strongly negative, relative to the average effect of native species.

SPECIES-SPECIFIC RESPONSE OF NATIVE TREE SEEDLINGS TO ALLELOCHEMICALS

Results from this study show a strong species-specific response of native seedlings to both the presence of *Ailanthus* in the neighborhood and the reduction of allelochemical interference by activated carbon (AC). In the absence of AC, the net interaction between *Ailanthus* and *A. rubrum* was generally positive (relative to the average effects of the native neighbors), with seedlings growing taller and having more biomass with increasing exotic tree influence (Fig. 2a-d). Moreover, the addition of AC to the soil multiplied this positive effect three-fold. These two results together suggest that, even though an important chemical interference exists between the two species, *Ailanthus* have other, positive effects on *A. rubrum* seedlings that allow the seedlings to benefit from proximity to the exotic even in the presence of allelochemicals. A potential mechanism of facilitation would be the increase in soil fertility reported for *Ailanthus* trees in the same study sites (Gómez-Aparicio & Canham, *in press*). In fact, previous studies have suggested that *A. rubrum* is N-limited in northeastern forests (Finzi & Canham 2000; Catovsky *et al.* 2002), and that it responds to increases in soil nutrients even at low light levels (Canham *et al.* 1996).

In contrast to the response of *A. rubrum*, the net influence of *Ailanthus* on *A. saccharum* seedlings in the absence of AC was negative, with seedling extension growth, biomass and leaf area decreasing due to the influence of the exotic tree (Fig. 2e-i). However, the addition of AC to the soil shifted the net interaction from negative to neutral or positive. The largest positive effect of activated carbon was on the root system of *A. saccharum* seedlings, with root biomass increasing almost two-fold under the maximum influence of *Ailanthus*. This result suggests that when allelochemicals are reduced, *A. saccharum* also benefits from the presence of *Ailanthus*, presumably due to its positive effect on soil fertility. In fact, there are several studies showing *A. saccharum* to be Ca-limited in these forests (Kobe *et al.* 2002; Juice *et al.* 2006). However, in contrast to *A. rubrum*, *A. saccharum* invested in root biomass instead of in aboveground biomass. These differences among species agree with the observation that shade-tolerant species such as *A. saccharum* usually have short periods of aboveground growth and high levels of stored carbon in the

1 roots, whereas more shade-intolerant species such as *A. rubrum* usually exhibit shoot  
2 growth throughout the growing season and maximize aboveground biomass at the expenses  
3 of root allocation (Marks 1975; Canham *et al.* 1996; Kobe 1997).

4 *Quercus rubra* was the only one of the three native seedlings that never benefited  
5 from the presence of *Ailanthus* in its neighborhood under either treatment. However, the  
6 magnitude of the net negative interaction decreased significantly when allelochemicals were  
7 reduced in the soil using AC, once again showing the importance of allelochemical  
8 interference as a depressor of growth in this native tree species. For example, while  
9 extension growth and biomass were reduced by 60-80% in the Control treatment due to the  
10 presence of *Ailanthus* in the neighborhood, they only decreased by 35-40% in the AC  
11 treatment. The fact that the influence of *Ailanthus* was negative even when allelochemicals  
12 were reduced with AC could indicate a higher sensibility of *Q. rubra* than the two maples to  
13 the secondary compounds produce by the exotic. On the other hand, the lack of a positive  
14 effect of the proximity to *Ailanthus* in the AC treatment is consistent with the fact that *Q.*  
15 *rubra* is more conservative in the use of resources than the two maples, usually being  
16 insensitive to increases in soil fertility (Canham *et al.* 1996; Tripler *et al.* 2002; Zaccherio &  
17 Finzi 2007).

18 Our experimental design does not allow us to discern whether the allelopathic effects  
19 were due to direct toxic effects on the seedlings, indirect effects on nutrient uptake (i.e.,  
20 reduced root or mycorrhizal activity, see Nilsson *et al.* 1993), or both. Accordingly, we can  
21 not determine to what extent the differential species response to the presence of *Ailanthus*  
22 and to the AC were due to differences in sensitivity to allelochemicals, in resource use, or  
23 both. Regardless of the specific mode of action, our results clearly showed that the  
24 allelopathic effects of an invasive species can generate strongly species-specific responses  
25 within the native tree community.

# WHAT A NEIGHBORHOOD APPROACH TELLS US ABOUT ALLELOPATHY: THE IMPORTANCE OF SIZE AND DISTANCE TO *AILANTHUS*

The use of neighborhood models for the study of allelopathy allowed us to gain useful insights on how the allelopathic effects of an invasive species vary as a function of the size and spatial distribution of the invading trees. These aspects of allelopathic interactions between plants have been very rarely explored, presumably because most studies have been conducted under controlled conditions in the lab or the greenhouse. To explore the importance of *Ailanthus* size in its interaction with native seedlings, we fit models assuming different scaling factors (i.e., parameter  $\alpha$  in equation 3) for the effect of DBH on the *Ailanthus* neighborhood index (ANI), and therefore on seedling performance. We found that models in which the effect of *Ailanthus* did not increase with DBH (i.e.,  $\alpha = 0$ ) were in most cases a better fit than models where the effect was assumed to scale with tree biomass (i.e.,  $\alpha = 2$ ). This result is in accordance with the results of Lawrence *et al.* (1991), who found young *Ailanthus* saplings to produce higher concentrations of inhibitory compounds than mature trees. These authors suggested that once an individual is established, the advantages of producing secondary metabolites for competitive or anti-herbivore purposes could be lower, and their biosynthesis may be interrupted. In the field of secondary chemistry and plant defense, this line of reasoning is known as the “plant age hypothesis” (Bryant *et al.* 1992), and predicts a decrease in plant secondary chemistry with ontogeny. If this hypothesis applies to *Ailanthus* and other invasive plant species, then there is a reason to expect allelopathy to be a more important interaction during the early stages of invasion (i.e., colonization or expansion phase; Shigesada *et al.* 1995; Radosevich *et al.* 2003), when the invader population is characterized by a young age structure and exponential growth, than in advance stages (i.e., saturation phase) once growth rates stabilize and the age structure of the population consolidates (but see Dietz & Edwards 2006).

Our approach also allowed us to explore the variation in the influence of *Ailanthus* on seedling performance as a function of the distance to the invader (i.e., parameter  $\beta$  in

equation 3). The influence of *Ailanthus* showed a sharp decrease with distance, tending to zero within 5 m from the invader (Fig. 1). For some of the response variables (i.e., leaf area) the effect of *Ailanthus* was restricted to the first 2 m from the trunk of a neighboring tree. Since toxins have been identified in all tissues of *Ailanthus* (i.e. leaves, trunk, stems, roots), this localized spatial pattern could be supported by several non-exclusive processes. First, it could be the result of *Ailanthus* toxins moving in stemflow and throughfall (Lawrence *et al.* 1991). Also, we have analyzed litterfall dispersal functions for *Ailanthus* and found that most of the litter was concentrated within 5 m from the trunk of adult trees (Gómez-Aparicio & Canham, *in press*). Finally, the influence of plants belowground is often presumed to decrease exponentially with distance to the stem (Casper *et al.* 2003), suggesting that root exudation of allelochemicals should also suffer a sharp decrease with distance. In fact, in one of the few available studies of spatial patterns of allelochemicals in the soil, Jose and Gillespie (1998) found that levels of the phenolic compound juglone (release by roots into the soil) diminished exponentially within a distance of 5 m from *Juglans nigra* L. (black walnut) trees. We suggest that since ailanthone (the main allelochemical compound identified in *Ailanthus*) quickly loses its toxicity in the soil, biological activity is probably restricted to areas of relatively high and continuous inputs (e.g., close to the trunk). However, our results indicate that the shape of the “chemical footprint” of an invader could vary depending on the sensitivity of different native species. Thus, the effect of *Ailanthus* on *Q. rubra* decreased more slowly with distance than for the two maples, a result in agreement with the higher sensitivity to allelochemicals suggested for this species in our study.

## IMPLICATIONS FOR FOREST COMPOSITION

It has long been recognized that patterns of growth and survival in the understorey influence successional dynamics and community composition in forests (Spurr & Barnes 1980; Pacala *et al.* 1996). By inducing changes in these key demographic traits, invasive tree species can have more pervasive effects on the composition of the native forest community than simply

1 by co-opting space. Our results showed that, through the release of allelochemical  
2 compounds, *Ailanthus* had a strongly differential potential to suppress seedling growth of  
3 different native dominant tree species in our study sites. Although we did not detect any  
4 effect of allelopathy in terms of survival after 2 years, it is not unlikely that the observed  
5 reductions in growth could affect seedling survival in the long term (Kobe *et al.* 1995). Within  
6 species, the probability of survival of tree seedlings and saplings under the low-light  
7 conditions typical of forest understories has been generally reported to be a positive function  
8 of their growth rate (Kobe *et al.* 1995; Kobe 1996; Walters & Reich 1996, 2000). Enhanced  
9 growth rates would allow seedlings to out-compete slower growing neighbors and, as a result  
10 of an improved overall carbohydrate status, to better cope with pathogens, drought episodes,  
11 and other mortality causes. Therefore, the negative effects of *Ailanthus* on seedling growth  
12 during the last year of the experiment might have depressed survival in the following year  
13 (e.g., Walters & Reich 1996), as well as in the long-term due to a continuous exposure to  
14 allelochemicals (e.g., Jose *et al.* 2006). Long-term studies would be necessary to fully  
15 understand the consequences of allelopathic interactions with exotics for the survival and  
16 growth of native species, and the resulting impacts on community composition.

17       Because both the overall interaction with *Ailanthus* and the effects of allelopathy  
18 were highly species-specific, there are reasons to believe that *Ailanthus* invasion will alter  
19 competitive interactions and relative abundances of native species in these forests.  
20 Interestingly, of the three native species considered in this study, *A. rubrum* was the only  
21 species that consistently showed a net positive response to the presence of *Ailanthus*, even  
22 in the presence of allelochemicals. One of the most widespread changes in the forest  
23 composition of the eastern US in the last century has been the increase in the abundance of  
24 *A. rubrum* (Larsen 1953; Abrams 1998). This increase has been explained on the basis of  
25 the ability of this “super generalist” to act as both an early and late successional species, and  
26 to thrive on sites with contrasting soil conditions. Our results suggest that *Ailanthus* invasion  
27 might constitute another factor promoting the dominance of *A. rubrum* at the expense of

coexisting species such as *A. saccharum* or *Q. rubra*. Identifying the underlying mechanisms for the positive response of *A. rubrum* to the presence of *Ailanthus* (i.e., higher tolerance to allelochemicals, greater ability to capitalize on high fertility patches created by *Ailanthus*) deserves further study.

Unfortunately, the death of all *Ailanthus* seedlings at the beginning of the experiment precluded us from obtaining conclusions about autotoxicity and the potential role of allelopathy as a mechanism providing competitive advantage to conspecific seedlings and saplings during the process of invasion. However, if results from laboratory experiments are applicable in the field, then we could expect *Ailanthus* seedlings to be highly resistant to their own allelochemicals (Heisey 1996). *Ailanthus* growth rates are reported to be much higher than in any native species the invader has been compared to (Knapp & Canham 2000; P. H. Martin & C. D. Canham, *unpublished data*). The production of allelochemicals that suppress growth in coexisting species but not in their own seedlings and saplings might farther magnify the differences between the invader and natives in their ability to overtop competitors and rapidly reach canopy, contributing to the success of *Ailanthus* invasion in northeastern temperate forests. Taken together, our results indicate that allelopathy is an important mechanism to take into account when trying to understand the causes and consequences of plant invasions. However, this study also strongly suggests that the real significance of the allelopathic effects of an invasive species can not be assessed independently of its target community, or in isolation of other resource interactions involving the invader and the native community.

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5

## 6 **Supplementary Material**

7 The following supplementary material is available for this article:

8 Appendix S1. Results of the *modified basic allelopathy models*.

9 Appendix S2. Summary of among-treatment differences (AC vs. Control) in performance for  
10 seedlings with and without *Ailanthus* trees in the neighborhood.

11 Appendix S3. Pascal source code for the likelihood functions and the simulated annealing  
12 algorithm used in this study.

**Table 1.** Comparison of alternate models (using AIC<sub>c</sub>) for performance variables of transplanted seedlings of the three native species. The *null model* predicts seedling performance only as a function of the site and the seedling size. The other two models include a third term to account for the neighborhood effects of *Ailanthus* on seedlings. This term is either maintained constant for the three study sites (*basic allelopathy model*) or is allowed to vary among sites (*site-specific allelopathy model*). The best model (lowest AIC<sub>c</sub>) is indicated in boldface type. Also reported are the number of parameters (NP), the sample size (*n*), and the R<sup>2</sup> of the model.

Species	AIC <sub>c</sub>			NP	<i>n</i>	R <sup>2</sup>
	Null model	Basic allelopathy model	Site-specific allelopathy model			
<i>Acer rubrum</i>						
Survival	<b>162.63</b>	162.76	175.24	4	116	
Extension growth	630.22	<b>626.42</b>	638.06	8	70	0.33
Extension biomass	687.48	<b>681.25</b>	695.48	8	70	0.26
Root biomass	<b>846.38</b>	850.53	860.27	4	71	0.10
Leaf biomass	934.54	<b>874.64</b>	880.12	8	69	0.26
Leaf area	601.15	<b>592.98</b>	608.58	8	69	0.28
<i>Acer saccharum</i>						
Survival	<b>159.31</b>	160.15	173.56	4	118	
Extension growth	554.46	<b>551.84</b>	554.69	8	73	0.31
Extension biomass	470.82	<b>467.62</b>	473.25	8	72	0.35
Root biomass	790.26	<b>785.85</b>	791.16	8	71	0.30
Leaf biomass	756.45	<b>748.05</b>	755.39	8	60	0.28
Leaf area	521.69	<b>510.89</b>	525.66	8	59	0.33
<i>Quercus rubra</i>						
Survival	<b>167.85</b>	167.95	181.56	4	117	
Extension growth	443.29	<b>441.16</b>	450.78	8	53	0.49
Extension biomass	459.28	<b>457.27</b>	469.25	8	53	0.36
Leaf biomass	<b>659.44</b>	666.92	674.39	4	51	0.20
Leaf area	<b>499.86</b>	504.77	512.20	4	51	0.17

**Table 2.** Parameter estimates and two-unit support intervals (in brackets) for the most parsimonious models for performance variables of transplanted seedlings of the three native species.

Species	Site <sub>AM</sub>	Site <sub>DEF</sub>	Site <sub>NM</sub>	$\lambda$	$\alpha$	$\beta$	$\gamma$ AC	$\gamma$ Control
<i>Acer rubrum</i>								
Survival	0.59 [0.51-0.64]	0.69 [0.61-0.75]	0.54 [0.49-0.64]	0.25 [0.21-0.40]				
Extension growth (mm)	36.01 [33.08-40.22]	19.31 [18.13-22.51]	23.12 [20.36-24.98]	0 [0-0.09]	0	0.90 [0.84-0.96]	1.11 [1.02-1.45]	0.41 [0.34-0.52]
Extension biomass (mg)	18.29 [16.45-20.22]	7.03 [5.39-8.51]	9.14 [7.67-11.02]	0.09 [0-0.19]	0	1.11 [1.05-1.18]	0.99 [0.79-1.11]	0.43 [0.33-0.51]
Root biomass (mg)	186.40 [146.23-217.45]	112.44 [89.14-126.73]	149.73 [131.56-157.68]	0.15 [0.06-0.26]				
Leaf biomass (mg)	70.78 [61.18-80.38]	53.80 [40.98-65.79]	68.54 [56.29-81.49]	0.12 [0.03-0.23]	0	2.54 [2.46-2.64]	1.08 [0.99-1.14]	0.05 [-0.14 to 0.16]
Leaf area (cm <sup>2</sup> )	29.47 [22.16-37.29]	21.38 [13.34-29.84]	28.79 [19.31-37.78]	0.21 [0.13-0.31]	0	1.45 [1.44-1.46]	1.05 [0.86-1.18]	-0.02 [-0.17 to 0.11]
<i>Acer saccharum</i>								
Survival	0.46 [0.34-0.53]	0.68 [0.54-0.76]	0.65 [0.59-0.71]	0.42 [0.24-0.51]				
Extension growth (mm)	31.52 [29.78-33.45]	13.32 [12.26-14.56]	13.88 [12.78-15.76]	0 [0-0.14]	2	1.14 [1.01-1.21]	0.10 [0.05-0.18]	-1.02 [-1.27 to -0.79]
Extension biomass (mg)	22.81 [17.72-30.35]	4.65 [3.58-5.47]	8.33 [7.65-9.24]	0.12 [0.01-0.23]	0	1.21 [1.14-1.36]	0.03 [0.01-0.15]	-0.47 [-0.61 to -0.34]

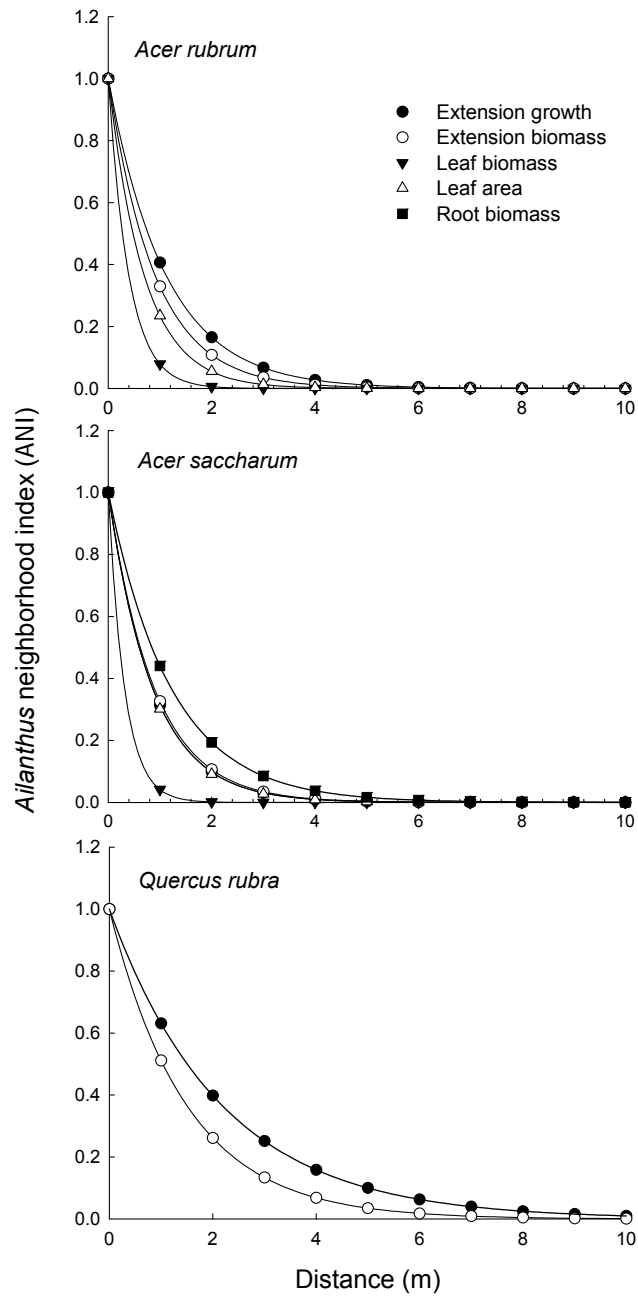


**Table 2** (Continued)

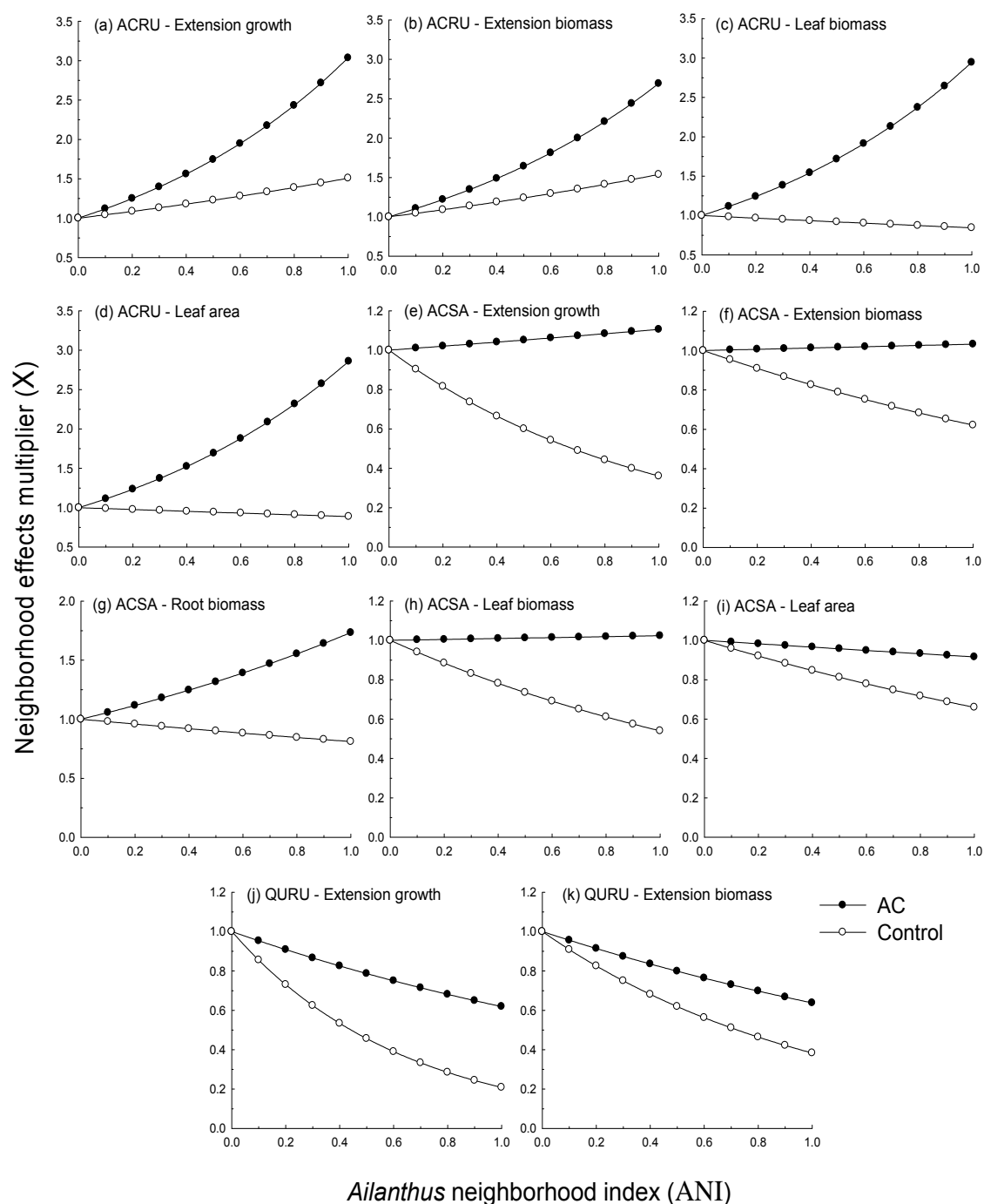
Species	Site <sub>AM</sub>	Site <sub>DEF</sub>	Site <sub>NM</sub>	$\lambda$	$\alpha$	$\beta$	$\gamma$ AC	$\gamma$ Control
<i>Acer saccharum</i>								
Root biomass (mg)	263.02 [243.89-309.64]	189.04 [167.87-228.42]	212.23 [198.45-248.03]	0.54 [0.42-0.65]	0	0.82 [0.70-1.19]	0.55 [0.38-0.72]	-0.21 [-0.28 to -0.17]
Leaf biomass (mg)	155.80 [132.96-172.89]	82.42 [68.43-97.16]	134.04 [114.47-152.56]	0.94 [0.71-1.20]	0	2.82 [2.65-3.01]	0.02 [0.01-0.04]	-0.62 [-0.73 to -0.53]
Leaf area (cm <sup>2</sup> )	77.65 [47.24-109.32]	59.89 [36.59-84.14]	96.27 [68.45-119.83]	0.80 [0.69-0.93]	0	1.19 [1.01-1.32]	-0.09 [-0.12 to -0.04]	-0.42 [-0.51 to -0.34]
<i>Quercus rubra</i>								
Survival	0.50 [0.33-0.67]	0.45 [0.29-0.56]	0.34 [0.20-0.45]	0.52 [0.34-0.67]				
Extension growth (mm)	54.01 [48.10-59.9]	6.81 [6.23-7.39]	26.89 [22.23-29.49]	0.91 [0.39-1.42]	2	0.46 [0.34-0.79]	-0.48 [-0.54 to -0.36]	-1.57 [-1.66 to -1.49]
Extension biomass (mg)	21.53 [20.42-22.41]	4.21 [3.22-4.79]	11.21 [10.15-11.95]	0.81 [0.65-0.99]	0	0.67 [0.44-0.89]	-0.45 [-0.61 to -0.29]	-0.96 [-1.31 to -0.64]
Leaf biomass (mg)	158.10 [151.23-165.23]	100.53 [94.27-107.29]	131.19 [119.25-143.12]	0.47 [0.36-0.60]				
Leaf area (cm <sup>2</sup> )	66.21 [60.50-71.66]	46.76 [41.82-51.20]	65.74 [61.34-71.15]	0.64 [0.59-0.69]				

**Table 3.** Comparison of alternate models (using AIC<sub>c</sub>) for performance variables of *Acer rubrum* and *Quercus rubra* seedlings in the sowing experiment. The best model (lower AIC<sub>c</sub>) is indicated in boldface type. Also reported are the number of parameters (NP), the sample size (*n*), and the R<sup>2</sup> of the model.

Species	AIC <sub>c</sub>			NP	<i>n</i>	R <sup>2</sup>
	Null model	Basic allelopathy model	Site-specific allelopathy model			
<i>Acer rubrum</i>						
Emergence	<b>257.53</b>	262.98	270.21	3	120	0.20
Survival	<b>79.85</b>	81.98	86.65	3	48	0.04
<i>Quercus rubra</i>						
Emergence	632.14	<b>631.59</b>	637.74	7	103	0.11
Survival	<b>401.33</b>	401.76	406.76	3	101	0.03
Stem biomass	1034.24	<b>1033.52</b>	1040.25	7	84	0.23
Leaf biomass	1119.86	<b>1118.16</b>	1123.27	7	77	0.28
Leaf area	658.28	<b>656.98</b>	665.98	7	76	0.25



**Fig. 1** Predicted decrease of the influence of *Ailanthus* (estimated as ANI, equation 3) on seedling performance as a function of the distance to *Ailanthus* trees. For simplicity of the presentation of results, the parameter  $\alpha$  was set to 0 in equation 3.



**Fig. 2** Predicted variation in the neighborhood effects ( $X$ ), and therefore in seedling performance, as a function of the *Ailanthus* influence index (ANI) using equation 2 and  $\gamma$  values reported in Table 2. Values of  $X > 1$  indicate positive neighborhood effects, whereas values of  $0 \leq X < 1$  indicate negative neighborhood effects. Only response variables for which the *basic allelopathy model* was the best fit (Table 1) are shown. ACRU, *Acer rubrum*; ACSA, *Acer saccharum*; QURU, *Quercus rubra*.