

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

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Summary

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

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

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

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

5. *Synthesis.* 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 cannot be assessed independently of its target community, or in isolation of other resource interactions involving the invader and the native community.

Key-words: *Acer rubrum*, *Acer saccharum*, activated carbon, *Ailanthus altissima*, allelopathy, field experiment, invasive species, neighbourhood models, plant interactions, *Quercus rubra*, seedling performance

Introduction

Biological invasions are recognized as one of the most important causes of ecosystem degradation and biodiversity loss worldwide (Vitousek *et al.* 1996; Mack *et al.* 2000). As a result, there has been extensive research to unravel the causes and consequences of the introduction of new species into natural

systems. Ironically, by serving as research tools, invasive species have contributed enormously to advances in our understanding of the mechanisms by which individual species can alter community structure and ecosystem processes (Vitousek 1986; Lodge 1993; Bruno *et al.* 2005). A notable example of how invasions have stimulated ecological research is in the revitalization of the interest in biochemical interactions among plants (Callaway & Maron 2006). The ecological consequences of allelopathy, or the negative effects of one

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plant on another by the release of chemical compounds into the environment (*sensu* Muller 1966), has been greeted with scepticism for decades (Harper 1977; Keeley 1988). As a result, resource-based interactions such as competition have been usually invoked as the explanation for the effects of invasive plant species on community structure (Levine *et al.* 2003). However, recent studies present compelling evidence that allelopathic interactions between invasive and native species can be one of the mechanisms underlying the remarkable success of some of the most aggressive plant invaders (Bais *et al.* 2003; Callaway & Ridenour 2004; Prati & Bossdorf 2004; Stinson *et al.* 2006).

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

In this paper, we test for allelopathic effects under natural conditions of one of the most important invasive tree species of temperate forests in the northeastern United States, *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae). Members of the family Simaroubaceae are known to produce quassinoid compounds with a wide range of effects on insects, fungi, protozoa, viruses and cancer cells (Polonsky 1973, 1985). Several studies have shown that extracts of all parts of *Ailanthus* (i.e. roots, leaves, trunk) inhibit germination and growth of several plant species in bioassays or glasshouse experiments (Mergen 1959; Voigt & Mergen 1962; Heisey 1990a,b; De Feo *et al.* 2003). At least 10 quassinoids, together with alkaloids and other secondary products, have been isolated from different parts of the plant (see references in Heisey & Heisey 2003). One quassinoid, ailanthone, has been identified as the major compound responsible for phytotoxic effects (Lin *et al.* 1995; Heisey 1996). However, ailanthone is rapidly inactivated in non-sterile soils (Heisey 1990b, 1996), so its actual allelopathic effect under field conditions may be less (if any) than what laboratory experiments indicate. *Ailanthus* thus represents an example of a successful invader for which presumed

allelopathic effects are invoked when explaining its invasive success (e.g. Kowarik 1995; Vilá *et al.* 2006; Webster *et al.* 2006), but for which no evidence of allelopathic effects under natural conditions is currently available.

We investigated the importance of allelochemical interference by *Ailanthus* on the emergence, survival and growth of native tree seedlings by using activated carbon (AC) to reduce potential allelopathic effects in a 2-year field experiment. We used a spatially-explicit, neighbourhood analysis to develop models that explain the observed spatial variation in the effects of the AC on seedling performance as a function of the size, abundance and distribution of *Ailanthus* trees in the immediate neighbourhood. A similar neighbourhood approach was successfully used in a parallel study to analyze the impacts of *Ailanthus* on nutrient cycling in the same study sites (Gómez-Aparicio & Canham 2008). Results from that study showed that *Ailanthus* increases nutrient availability (i.e. pH, exchangeable Ca, exchangeable K, total N) and cycling rates (i.e. net nitrification) in surface soil, presumably due to the extraordinarily high nutrient concentration in its leaf litter (as much as four times higher than in native tree species). For example, soil Ca and N pools were twofold higher in neighbourhoods dominated by *Ailanthus* than in neighbourhoods dominated by native species such as *Acer saccharum*, *Fraxinus americana* or *Quercus rubra*. These results imply that *Ailanthus* could have positive effects on the native seedling community, due to increases in soil fertility. This highlights the need for an analysis of the relative importance of allelopathy in a natural setting where other interactions (i.e. facilitation) may also take place. Specifically, we asked the following questions: (i) Does *Ailanthus* interfere with native tree seedlings via allelopathic exudates? (ii) Are allelopathic effects species-specific? (iii) How does the magnitude of the allelopathic effects vary with the size and spatial distribution of *Ailanthus* in the neighbourhood? (iv) What role does allelopathy play in the net effect of *Ailanthus* on native seedlings?

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 an invader, the arsenal of biochemical defences found in all *Ailanthus* tissues suggests allelopathy as another potential mechanism of invasion.

The experiment was conducted in three forest stands in north-western 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 Amesville (41°58'N, 73°27'W), the second located in the Dark Entry Forest (DEF) 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 Amesville (AM) and New Milford (NM) are Dystric Eutrochrepts derived from calcareous glacial outwash over limestone bedrocks, whereas soils at DEF are Typic Dystrichrepts derived from glacial till over mica-schist bedrocks (Hill *et al.* 1980). All sites are in second-growth stands (80–130 years) 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 *A. saccharum* Marsh. (sugar maple), *F. americana* L. (white ash), *Q. 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 approximately 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 *A. rubrum* L., *A. saccharum* and *Q. 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. Twenty planting locations were selected per site, stratified along a gradient of distance from and abundance of *Ailanthus* in the immediate neighbourhood (defined as a 25-m radius circle around each planting location). We identified and mapped every *Ailanthus* tree with a DBH ≥ 2 cm within each of the 60 neighbourhoods ($n = 337$ trees), using a laser rangefinder with a digital compass (Laser Technology Inc., Centennial, CO). Relative basal area of *Ailanthus* in the neighbourhoods varied between 0% and 70%.

At each planting location, two 20 × 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 AC (GC Powdered Activated Carbon, General Carbon Corp., Paterson, NJ) 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. AC is frequently used in allelopathy experiments because it acts as an adsorbant for many large organic compounds, therefore minimizing allelopathic effects while having minor impacts on nutrient dynamics (Cheremisinoff & Ellerbusch 1978). AC has been successfully used to test for allelopathic interactions in a large number of studies (see review in Hierro & Callaway 2003), and has been recommended as an effective approach for allelopathy studies in the field (Inderjit & Callaway 2003).

Three seedlings (one of each of the three native tree species) were planted in each plot ($n = 360$ seedlings). We measured the initial stem height, extension growth of the stem, basal diameter, number of leaves and diameter of each expanded leaf at the time of planting. In order to facilitate accurate remeasurement of stem height, a small mark was made on the stem of each seedling at the ground level. Within the initial pool of seedlings collected for transplanting, a random subsample ($n = 30$ per species) was taken to the laboratory at the beginning of the experiment for measurement of initial stem height,

stem dry biomass and dry biomass, area and diameter of all leaves. The objective was to generate, for each species, regressions of (i) stem dry biomass as a function of stem height, (ii) leaf area as a function of leaf diameter (measured from the base to the tip of the leaves), and (iii) leaf dry biomass as a function of leaf area. These regressions ($R^2 > 0.9$ in all cases, data not shown) allowed non-destructive estimations of initial stem biomass, initial leaf area and initial leaf biomass for each experimental seedling using field measurements (see below).

For each experimental seedling, survival, stem height, stem extension growth, number of leaves and diameter of each individual leaf were sampled twice, once at the end of the first growing season (September 2005) and once at the end of the second growing season (September 2006). Seedlings alive in September 2006 were harvested and taken to the laboratory where leaves were removed and measured for total area using a leaf area meter (LI-COR Inc., Superior St. Lincoln, NE). Roots were rinsed by hand, and the root and shoot systems were separated at ground level (using the marks on the stems). Roots, stems and leaves were dried for 48 h at 60 °C and weighed. The extension growth of the stem for the second growing season was separated from the rest of the stem and weighed separately. We considered the biomass of the extension growth as a more accurate estimation of the effects of AC on biomass allocation to stems than the total stem biomass. As some seedlings had finished their annual growth by the time the experiment started (June 2005), we decided to conduct statistical analyses using growth data only for the second growing season. Specifically, we considered six response variables: (i) survival after the two years of the experiment; (ii) extension growth in 2006; (iii) dry biomass of the 2006 extension growth; (iv) root dry biomass; (v) leaf dry biomass in 2006; and (6) leaf area in 2006. Due to the difficulties of excavating *Q. rubra* roots without losing a significant part of the root system, we decided not to consider root biomass as a response variable in the analyses for this species.

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

The transplant experiment was initially designed including *Ailanthus* as a fourth seedling species. Given the difficulty of finding natural seedlings of *Ailanthus* in our study sites, seeds were germinated in the glasshouse in May 2005 and *Ailanthus* seedlings transplanted to the field at the same time as the native species. *Ailanthus* seedlings were transplanted to individual 20 × 20 cm plots 30 cm away from the native plots (in order to avoid potential allelochemical interference among seedlings), using the same soil treatments used for the plots containing native tree seedlings. However, even though dead *Ailanthus* seedlings were replaced during the first 3 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 × 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 five seeds, each line were 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 above-ground. Seeds were sown in November 2005, and emergence was monitored every 2 weeks during April–June 2006.

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

NEIGHBOURHOOD ANALYSES OF SEEDLING EMERGENCE, SURVIVAL AND GROWTH

We used a neighbourhood approach to the study of allelopathy in which seed emergence, seedling survival and seedling growth were analyzed as a function of: (i) the study site; (ii) the initial size of the seedling (only in the case of transplanted seedlings); and (iii) the size, abundance and spatial distribution of *Ailanthus* in the neighbourhood. 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:

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

The first term in the model, 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 neighbouring *Ailanthus* for $j = 1 \dots 3$ study sites. The second term, Size^λ , controls for the effects of initial plant size on seedling performance in the transplant experiment, as a function of the parameter λ , 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: (i) initial stem height was used as the size estimator for survival and extension growth; (ii) initial stem biomass (calculated indirectly using regressions, see above) as the size estimator for extension biomass and root biomass; (iii) initial leaf biomass (calculated using regressions) as the size estimator for (final) leaf biomass; and (iv) 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 neighbourhood

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

$$X = \exp \gamma \left(\frac{\text{ANI}_i}{\text{ANI}_{\max}} \right) \quad \text{eqn 2}$$

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

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

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

We estimated a separate γ parameter in eqn 2 for each of the two treatments (i.e. for AC vs. the control). The parameter γ is an exponential decay coefficient, and defines the sign and steepness of the variation in the neighbourhood effects (X), and therefore in seedling performance (Y), due to an increment in ANI. Positive values of γ would indicate a positive effect of the presence of *Ailanthus* neighbours relative to the mean effects of the native neighbours, whereas negative γ values would indicate a negative effect of the presence of *Ailanthus* relative to the presence of native neighbours. The difference in the γ 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 neighbouring *Ailanthus* at each site (i.e. term Site_j in eqn 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* neighbours were considered in the analyses (see Appendix S2).

We also explored the effect of light on seedling performance by adding a fourth term (GLI^b) to the *basic allelopathy model* (eqn 1). However, as 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 γ (eqn 2) for the AC treatment was allowed to vary as a function of the site (*Site-specific allelopathy model*). The value of γ 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 eqn 1). By doing this, we assessed whether including the neighbouring 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 (AIC_c) corrected for small sample sizes (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 two-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 two 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 two units. The R^2 of the regression ($1 - \text{SSE}/\text{SST}$, sum of squares error (SSE); sum of squares total (SST)) of observed vs. predicted was used as a measure of goodness-of-fit. All analyses were done using software written specifically for this study using Delphi for Windows (Version 7, Borland Software Corp., Cupertino, CA).

Results

SEEDLING TRANSPLANT EXPERIMENT

The *null model* (ignoring the neighbourhood 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

Table 1. Comparison of alternate models (using AIC_c) for performance variables of transplanted seedlings of the three native species

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

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 neighbourhood 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_c) is indicated in boldface type. Also reported are the number of parameters (NP), the sample size (n), and the R² of the model.

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 _{AM}	Site _{DEF}	Site _{NM}	λ	α	β	γ AC	γ 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 ²)	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]
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 ²)	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 ²)	66.21 [60.50–71.66]	46.76 [41.82–51.20]	65.74 [61.34–71.15]	0.64 [0.59–0.69]				

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 and 0.33 for *A. rubrum*, 0.28 and 0.35 for *A. saccharum*, and 0.17 and 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 λ parameter ($\lambda = 0–0.25$), and a larger influence on performance of *Q. rubra* seedlings ($\lambda = 0.47–0.91$; Table 2). The λ -values for *A. saccharum* varied considerably depending on the response variable ($\lambda = 0–0.94$; Table 2). The exponent α (eqn 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* (DBH ≥ 2 cm) in the neighbourhood, regardless of their size. In contrast, *Ailanthus* influence was strongly influenced by distance, as shown by large values of the parameter β (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 neighbouring 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 γ 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 γ 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

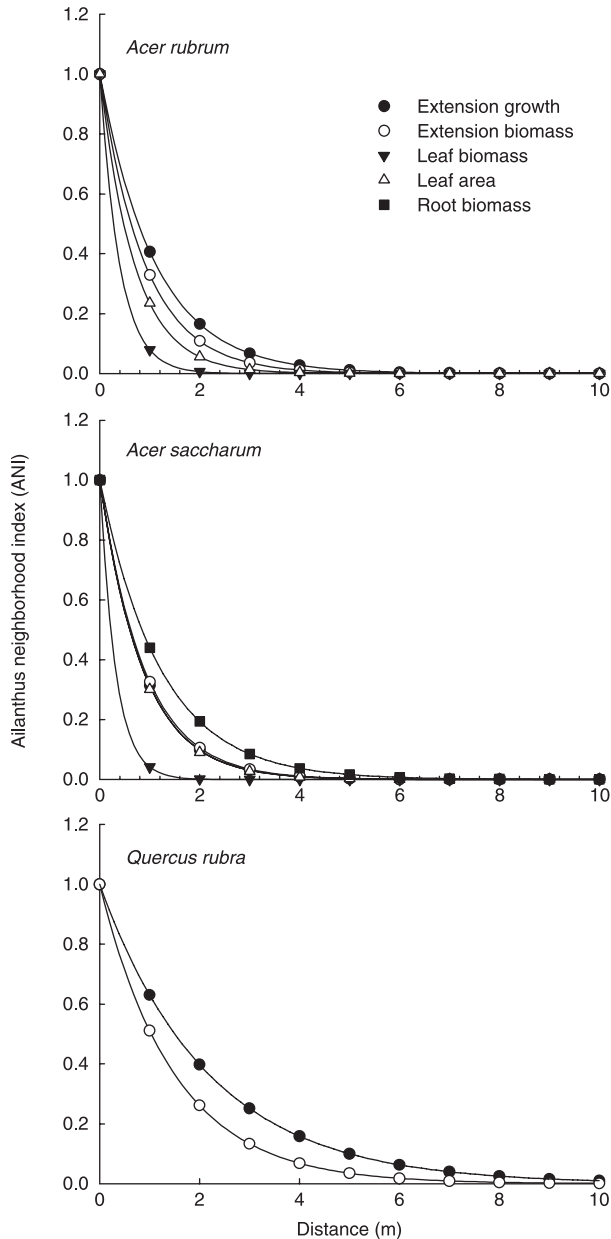


Fig. 1. Predicted decrease of the influence of *Ailanthus* (estimated as ANI, eqn 3) on seedling performance as a function of the distance to *Ailanthus* trees. For simplicity of the presentation of results, the parameter α was set to 0 in eqn 3.

potential allelochemical effects were reduced by the AC. 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 to 3-times larger at high values of the ANI than at low values (Fig. 2a–d). For *A. saccharum*, the γ 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 γ 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*, γ 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 neighbourhood 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, as the difference in AIC between the *basic allelopathy model* and the *null model* (assuming no effect of *Ailanthus*) was never larger than two 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 *A. 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 neighbourhood (Gómez-Aparicio & Canham 2008). 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 neighbourhood and the reduction of allelochemical

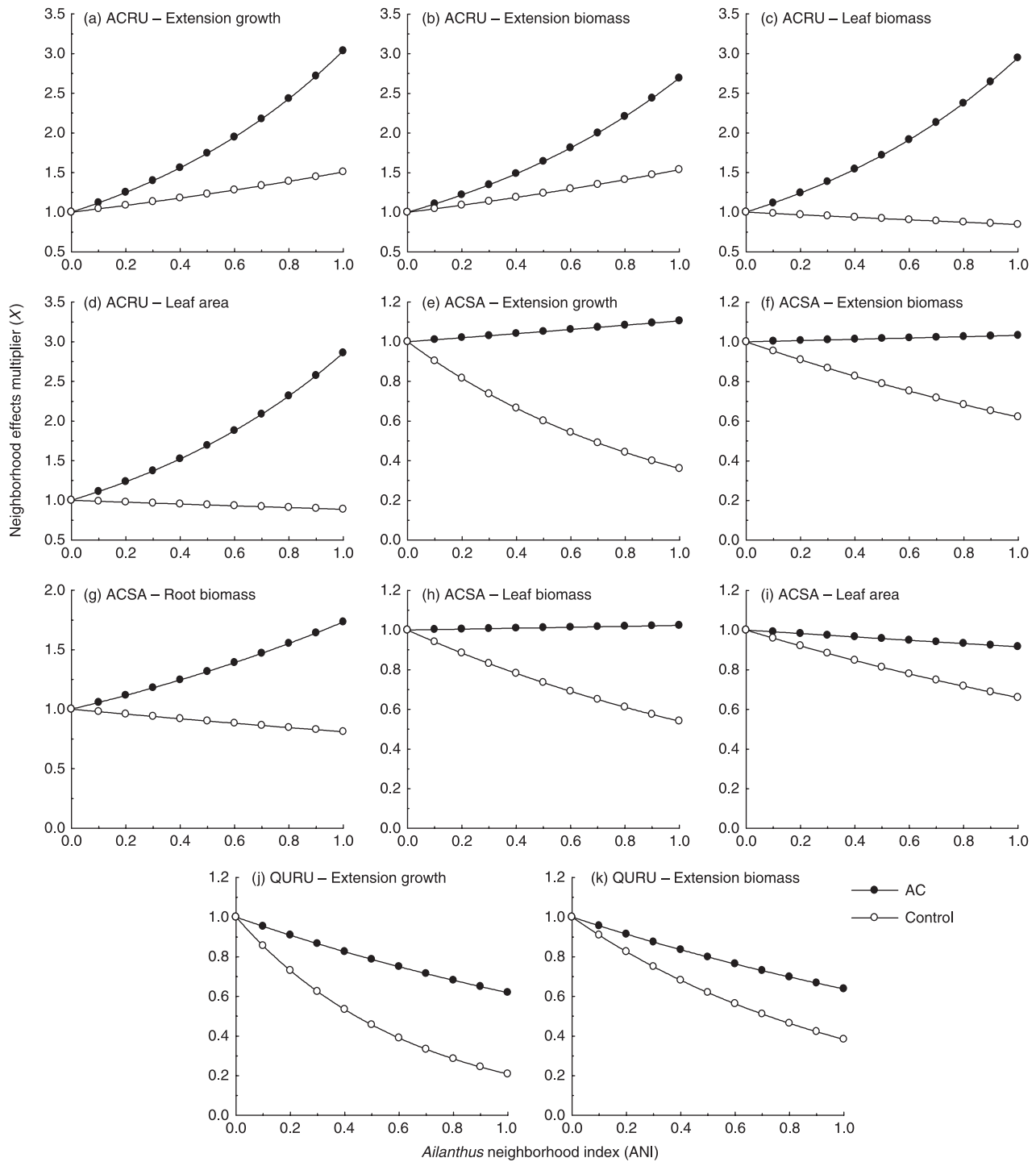


Fig. 2. Predicted variation in the neighbourhood effects (X), and therefore in seedling performance, as a function of the *Ailanthus* influence index (ANI) using eqn 2 and γ values reported in Table 2. Values of $X > 1$ indicate positive neighbourhood effects, whereas values of $0 \leq X < 1$ indicate negative neighbourhood 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*.

interference by 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 neighbours), 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

Table 3. Comparison of alternate models (using AIC_c) for performance variables of *Acer rubrum* and *Quercus rubra* seedlings in the sowing experiment

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

The best model (lower AIC_c) is indicated in boldface type. Also reported are the number of parameters (NP), the sample size (n), and the R² of the model.

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 2008). 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 AC was on the root system of *A. saccharum* seedlings, with root biomass increasing almost twofold 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 above-ground biomass. These differences between species agree with the observation that shade-tolerant species such as *A. saccharum* usually have short periods of above-ground growth and high levels of stored carbon in the roots, whereas more shade-intolerant species such as *A. rubrum* usually exhibit shoot growth throughout the growing season and maximize above-ground biomass at the expenses of root allocation (Marks 1975; Canham *et al.* 1996; Kobe 1997).

Quercus rubra was the only one of the three native seedlings that never benefited from the presence of *Ailanthus* in its neighbourhood under either treatment. However, the magnitude of the net negative interaction decreased significantly when allelochemicals were reduced in the soil using AC, once again showing the importance of allelochemical interference

as a depressor of growth in this native tree species. For example, while extension growth and biomass were reduced by 60–80% in the Control treatment due to the presence of *Ailanthus* in the neighbourhood, they only decreased by 35–40% in the AC treatment. The fact that the influence of *Ailanthus* was negative even when allelochemicals were reduced with AC could indicate a higher sensibility of *Q. rubra* than the two maples to the secondary compounds produce by the exotic. On the other hand, the lack of a positive effect of the proximity to *Ailanthus* in the AC treatment is consistent with the fact that *Q. rubra* is more conservative in the use of resources than the two maples, usually being insensitive to increases in soil fertility (Canham *et al.* 1996; Tripler *et al.* 2002; Zaccherio & Finzi 2007).

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

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

The use of neighbourhood 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 very rarely been explored, presumably because most studies have been conducted under controlled conditions in the laboratory or the

glasshouse. To explore the importance of *Ailanthus* size in its interaction with native seedlings, we fit models assuming different scaling factors (i.e. parameter α in eqn 3) for the effect of DBH on the 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 defence, 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 β in eqn 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 neighbouring tree. As 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 2008). Finally, the influence of plants below-ground 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 & 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 as 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 by co-opting space. Our results showed that, by the release of allelochemical compounds, *Ailanthus* had a strongly differential potential to suppress seedling growth of different native dominant tree species in our study sites. Although we did not detect any effect of allelopathy in terms of survival after 2 years, it is not unlikely that the observed reductions in growth could affect seedling survival in the long term (Kobe *et al.* 1995). Within species, the probability of survival of tree seedlings and saplings under the low-light conditions typical of forest understoreys has been generally reported to be a positive function of their growth rate (Kobe *et al.* 1995; Kobe 1996; Walters & Reich 1996, 2000). Enhanced growth rates would allow seedlings to out-compete slower growing neighbours and, as a result of an improved overall carbohydrate status, to better cope with pathogens, drought episodes, and other mortality causes. Therefore, the negative effects of *Ailanthus* on seedling growth during the last year of the experiment might have depressed survival in the following year (e.g. Walters & Reich 1996), as well as in the long-term due to a continuous exposure to allelochemicals (e.g. Jose *et al.* 2006). Long-term studies would be necessary to fully understand the consequences of allelopathic interactions with exotics for the survival and growth of native species, and the resulting impacts on community composition.

Because both the overall interaction with *Ailanthus* and the effects of allelopathy were highly species-specific, there are reasons to believe that *Ailanthus* invasion will alter competitive interactions and relative abundances of native species in these forests. Interestingly, of the three native species considered in this study, *A. rubrum* was the only species that consistently showed a net positive response to the presence of *Ailanthus*, even in the presence of allelochemicals. One of the most widespread changes in the forest composition of the eastern United States in the last century has been the increase in the abundance of *A. rubrum* (Larsen 1953; Abrams 1998). This increase has been explained on the basis of the ability of this 'super generalist' to act as both an early and late successional species, and to thrive on sites with contrasting soil conditions. Our results suggest that *Ailanthus* invasion 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, unpubl. data). The production of allelochemicals that suppress growth in coexisting species but not in their own seedlings and saplings might further 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 cannot 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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References

- Abrams, M.D. (1998) The red maple paradox. *Bioscience*, **48**, 355–364.
- Bais, H.P., Vepachedu, R., Gilroy, S., Callaway, R.M. & Vivanco, J.M. (2003) Allelopathy and exotic plant invasion: from molecules and genes to species interactions. *Science*, **301**, 1377–1380.
- Bazzaz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351–371.
- Bruno, J.F., Fridley, J.D., Bromberg, K.D. & Bertness, M.D. (2005) Insights into biotic interactions from studies of species invasions. *Species Invasions: Insights into Ecology, Evolution and Biogeography* (eds D.F. Sax, J.J. Stachowicz & S.D. Gaines), pp. 13–40. Sinauer Associates Inc., Sunderland, Massachusetts.
- Bryant, J.P., Reichardt, P.B., Clausen, T.P., Provenza, F.D. & Kuropat, P.J. (1992) Woody plant-mammal interactions. *Herbivores: their Interactions with Plant Secondary Metabolites*, Vol. 2, 2nd edn (eds G.A. Rosenthal & M.R. Berenbaum), pp. 344–371. Academic Press, San Diego, California.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer-Verlag, New York.
- Callaway, R.M. & Maron, J.L. (2006) What have exotic plant invasions taught us over the past 20 years? *Trends in Ecology and Evolution*, **21**, 369–374.
- Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment*, **2**, 436–443.
- Canham, C.D. (1988) An index for understory light levels in and around canopy gaps. *Ecology*, **69**, 1634–1638.
- Canham, C.D. (1989) Different responses to gaps among shade-tolerant tree species. *Ecology*, **70**, 548–550.
- Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V. & Schnurr, J. (1996) Biomass allocation and multiple resource limitation in tree seedlings. *Canadian Journal of Forest Research*, **26**, 1521–1530.
- Casper, B.B., Schenk, H.J. & Jackson, R.B. (2003) Defining a plant's below-ground zone of influence. *Ecology*, **84**, 2313–2321.
- Catovsky, S., Kobe, R.K. & Bazzaz, F.A. (2002) Nitrogen-induced changes in seedling regeneration and dynamics of mixed conifer-broad-leaved forests. *Ecological Applications*, **12**, 1611–1625.
- Cheremisinoff, P.N. & Ellerbusch, F. (1978) *Carbon Adsorption Handbook*. Ann Arbor Science Publishers, Ann Arbor, Michigan.
- De Feo, V., De Martino, L., Quaranta, E. & Pizza, C. (2003) Isolation of phytotoxic compounds from tree of heaven (*Ailanthus altissima* Swingle). *Journal of Agricultural and Food Chemistry*, **51**, 1177–1180.
- Dietz, H. & Edwards, P.J. (2006) Recognition that causal processes change during plant invasion helps explain conflicts in evidence. *Ecology*, **87**, 1359–1367.
- Edwards, A.W.F. (1992) *Likelihood-Expanded Edition*. Johns Hopkins University Press, Baltimore, Maryland.
- Feret, P.P. (1985) *Ailanthus*: variation, cultivation, and frustration. *Journal of Arboriculture*, **11**, 361–368.
- Finzi, A.C. & Canham, C.D. (2000) Sapling growth in response to light and nitrogen availability in a southern New England forest. *Forest Ecology and Management*, **131**, 153–165.
- Goffe, W.L., Ferrier, G.D. & Rogers, J. (1994) Global optimization of statistical functions with simulated annealing. *Journal of Econometrics*, **60**, 65–99.
- Gómez-Aparicio, L. & Canham, C.D. (2008) Neighborhood models of the effects of invasive tree species on ecosystem processes. *Ecological Monographs*, **78**, in press.
- Harper, J.L. (1977) *Population Biology of Plants*. Academic Press, London.
- Heisey, R.M. (1990a) Allelopathic and herbicidal effects of extracts from tree of heaven (*Ailanthus altissima*). *American Journal of Botany*, **77**, 662–670.
- Heisey, R.M. (1990b) Evidence for allelopathy by tree of heaven. *Journal of Chemical Ecology*, **16**, 2039–2055.
- Heisey, R.M. (1996) Identification of an allelopathic compound from *Ailanthus altissima* (Simaroubaceae) and characterization of its herbicidal activity. *American Journal of Botany*, **83**, 192–200.
- Heisey, R.M. & Heisey, T.K. (2003) Herbicidal effects under field conditions of *Ailanthus altissima* bark extract, which contains ailanthone. *Plant and Soil*, **256**, 85–99.
- Hierro, J.L. & Callaway, R.M. (2003) Allelopathy and exotic plant invasion. *Plant and Soil*, **256**, 29–39.
- Hill, D.E., Sautter, E.H. & Gunick, W.N. (1980) Soils of Connecticut. *Bulletin Number 787*. Connecticut Agricultural Experiment Station, New Haven, Connecticut.
- Hu, S.Y. (1979) *Ailanthus*. *Arnoldia*, **39**, 29–50.
- Inderjit & Callaway, R.M. (2003) Experimental designs for the study of allelopathy. *Plant and Soil*, **256**, 1–11.
- Jose, S. & Gillespie, A.R. (1998) Allelopathy in black walnut (*Juglans nigra* L.) alley cropping. I. Spatio-temporal variation in soil juglone in a black walnut-corn (*Zea mays* L.) alley cropping system in the Midwestern USA. *Plant and Soil*, **203**, 191–197.
- Jose, S., Williams, R. & Zamora, D. (2006) Belowground ecological interactions in mixed-species forest plantations. *Forest Ecology and Management*, **233**, 231–239.
- Juice, S.M., Fahey, T.J., Siccama, T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R. & Richardson, A.D. (2006) Response of sugar maple to calcium addition to northern hardwood forest. *Ecology*, **87**, 1267–1280.
- Keeley, J.E. (1988) Allelopathy. *Ecology*, **69**, 292–293.
- Knapp, L.B. & Canham, C.D. (2000) Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. *Journal of the Torrey Botanical Society*, **127**, 307–315.
- Kobe, R.K. (1996) Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecological Monographs*, **66**, 181–201.
- Kobe, R.K. (1997) Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. *Oikos*, **80**, 226–233.
- Kobe, R.K., Likens, G.E. & Eagar, C. (2002) Tree seedling growth and mortality responses to manipulations of calcium and aluminium in a northern hardwood forest. *Canadian Journal of Forest Research*, **32**, 954–966.
- Kobe, R.K., Pacala, S.W., Silander, J.A. & Canham, C.D. (1995) Juvenile tree survivorship as a component of shade tolerance. *Ecological Applications*, **5**, 517–532.
- Kowarik, I. (1995) Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. *Journal of Vegetation Ecology*, **6**, 853–856.
- Larsen, J.A. (1953) A study of an invasion by red maple of an oak woods in southern Wisconsin. *American Midland Naturalist*, **49**, 908–914.

- Lawrence, J.G., Colwell, A. & Sexton, O.J. (1991) The ecological impact of allelopathy in *Ailanthus altissima* (Simaroubaceae). *American Journal of Botany*, **78**, 948–958.
- Levine, J.M., Vilá, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London B*, **270**, 775–781.
- Lin, L.J., Peiser, G., Ying, B.P., Mathias, K., Karasina, F., Wang, Z., Itatani, J., Green, L. & Hwang, S. (1995) Identification of plant growth inhibitory principles in *Ailanthus altissima* and *Castela tortuosa*. *Journal of Agricultural and Food Chemistry*, **43**, 1708–1711.
- Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends in Ecology and Evolution*, **8**, 133–137.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences and control. *Ecology*, **10**, 689–710.
- Marks, P.L. (1975) On the relation between extension growth and successional status of deciduous trees of the northeastern United States. *Bulletin of the Torrey Botanical Club*, **102**, 172–177.
- Mergen, F. (1959) A toxic principle in the leaves of *Ailanthus*. *Botanical Gazette*, **121**, 32–36.
- Muller, C.H. (1966) The role of chemical inhibition (allelopathy) in vegetational composition. *Bulletin of the Torrey Botanical Club*, **93**, 332–351.
- Nilsson, M.C. (1994) Separation of allelopathy and resource competition by the boreal dwarf shrub *Empetrum hermaphroditum* Hagerup. *Oecologia*, **98**, 1–7.
- Nilsson, M.C., Högberg, P., Zackrisson, O. & Fengyou, W. (1993) Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus sylvestris*. *Canadian Journal of Botany*, **71**, 620–628.
- Nilsson, M.C., Zackrisson, O., Sterner, O. & Wallstedt, A. (2000) Characterization of the differential interference effects of two boreal dwarf shrub species. *Oecologia*, **123**, 122–128.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K. & Ribbens, E. (1996) Forest models defined by field measurements: estimation, error analyses and dynamics. *Ecological Monographs*, **66**, 1–43.
- Polonsky, J. (1973) Quassinoid bitter principles. *Fortschritte der Chemie Organischer Naturstoffe*, **30**, 101–150.
- Polonsky, J. (1985) Quassinoid bitter principles II. *Fortschritte der Chemie Organischer Naturstoffe*, **47**, 221–264.
- Prati, D. & Bossdorf, O. (2004) Allelopathic inhibition of germination by *Alliaria petiolata* (Brassicaceae). *American Journal of Botany*, **91**, 285–288.
- Radosevich, S.R., Stubbs, M.M. & Ghersa, C.M. (2003) Plant invasions: process and patterns. *Weed Science*, **51**, 254–259.
- Shigesada, N., Kawasaki, K. & Takeda, Y. (1995) Modeling stratified diffusion in biological invasions. *American Naturalist*, **146**, 229–251.
- Spurr, S.H. & Barnes, B.V. (1980) *Forest Ecology*, 3rd edn. John Wiley and Sons, New York.
- Stinson, K.A., Campbell, S.A., Powell, J.R., Wolfe, B.E., Callaway, R.M., Thelen, G.C., Hallett, S.G., Prati, D. & Klironomos, J.N. (2006) Invasive plant suppresses the growth of native tree seedlings by disrupting below-ground mutualisms. *Public Library of Science Biology*, **4**, 727–731.
- Tripler, C.E., Canham, C.D., Inouye, R.S. & Schnurr, J.L. (2002) Soil nitrogen availability, plant luxury consumption, and herbivory by white-tail deer. *Oecologia*, **133**, 517–524.
- Vilá, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galanidis, A., et al. (2006) Local and regional assessment of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. *Journal of Biogeography*, **33**, 853–861.
- Vitousek, P.M. (1986) Biological invasions and ecosystem properties: can species make a difference? *Ecology of Biological Invasions of North America and Hawaii* (eds H.A. Mooney & J.A. Drake), pp. 163–176. Springer-Verlag, New York.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468–478.
- Voigt, G.K. & Mergen, F. (1962) Seasonal variation in toxicity of *Ailanthus* leaves to pine seedlings. *Botanical Gazette*, **123**, 262–265.
- Walters, M.B. & Reich, P.B. (1996) Are shade tolerance, survival, and growth linked? Low light and, nitrogen effects on hardwood seedlings. *Ecology*, **77**, 841–853.
- Walters, M.B. & Reich, P.B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology*, **81**, 1887–1901.
- Webster, C.R., Jenkins, M.A. & Jose, S. (2006) Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. *Journal of Forestry*, **104**, 366–374.
- Zaccherio, M.T. & Finzi, A.C. (2007) Atmospheric deposition may affect northern hardwood forest composition by altering soil nutrient supply. *Ecological Applications*, **17**, 1929–1941.
- Zackrisson, O. & Nilsson, M.C. (1992) Allelopathic effects by *Empetrum hermaphroditum* on seed germination of two boreal tree species. *Canadian Journal of Forest Research*, **22**, 1310–1319.

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Supplementary material

The following supplementary is available from this article:

Appendix S1. Results of the modified basic allelopathy models.

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

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

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