# Analysis of interactions between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*)

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# Abstract

Invasive exotic plants can persist and successfully spread within ecosystems and negatively affect the recruitment of native species. The exotic invasive *Ailanthus altissima* and the native *Robinia pseudoacacia* are frequently found in disturbed sites and exhibit similar growth and reproductive characteristics, yet each has distinct functional roles such as allelopathy and nitrogen fixation, respectively. A four-month full additive series in the greenhouse was used to analyze the intraspecific and interspecific interference between these two species. In the greenhouse experiment, the inverse of the mean total biomass (g) response per plant for each species was regressed on the density of each species and revealed that the performance of the plants was significantly reduced by interspecific interference and not by intraspecific interference (p < 0.05). Other biomass traits such as root dry weight, shoot dry weight, stem dry weight, and leaf dry weight were also negatively affected by interspecific interference. Competition indices such as Relative Yield Total and Relative Crowding Coefficient suggested that *A. altissima* was the better competitor in mixed plantings. *Ailanthus altissima* consistently produced a larger above ground and below ground relative yield while *R. pseudoacacia* generated a larger aboveground relative yield in high density mixed species pots.

# Introduction

Invasion of exotic plant and animal species into regions that were previously separated by biogeographic barriers is a key problem resulting from current land disturbances and change (D'Antonio and Vitousek 1992; Vitousek 1992). Not only do invasive species persist and spread into ecosystems, they can also alter basic ecosystem processes such as hydrology, nutrient cycling, soil erosion rates, (Vitousek and Walker 1989), fire frequency and intensity (D'Antonio and Vitousek 1992), and recruitment of native species (Mooney and Drake 1989). Biotic invasions can cause an ecosystem to become homogenized and can decrease regional diversity by accelerating the extinction of native species (D'Antonio and Vitousek 1992). Therefore, competition between invasive and native species is a globally important issue that merits attention.

The research we report here concerns seedlings of the invasive exotic *Ailanthus altissima* (Miller) Swingle (Simaroubaceae) and their interaction with seedlings of the native *Robinia pseudoacacia* L. (Fabaceae). Numerous ecological traits are comparable between *A. altissima* and *R. psuedoacacia*. Both species establish in disturbed sites in most temperate regions of the United States, have aggressive reproductive qualities, and exhibit similar growth habits. It is no surprise that these qualities place these two species on the list of the 40 most invasive woody angiosperm species from 40 different genera (Rejmanek and Richardson 1996). However, each of these tree species has a different functional attribute that is critical to succession and ecosystem processes. *Ailanthus altissima* inhibits post-disturbance succession by creating a relatively toxic soil environment (Lawrence et al. 1991) and *R. pseudoacacia* promotes post-disturbance succession by enriching soil by nitrogen fixation (Boring and Swank 1984). Therefore, the functional characteristics of these two species can have divergent impacts on ecosystem processes (Hooper and Vitousek 1997; Schwartz et al. 2000). Thus, understanding how *A. altissima* and *R. pseudoacacia* interact will lead to important questions regarding ecosystem functioning within post disturbance succession. For example, will post disturbance sites with a high frequency of *A. altissima* have arrested succession compared to disturbed sites with a high frequency of *R. pseudoacacia*?

Within the limitations of a short-term greenhouse study, our goal is to look at the interference between seedlings of the two species and determine whether this interference favors *A. altissima* over *R. pseudoacacia.* This study provides preliminary evidence needed to develop hypotheses about potential initial interactions between the species as seedlings in the post-disturbance environment. Vegetation analysis has shown that these two species co-occur following disturbances and have the potential to interact (Call and Nilsen 2003). The term interference will be used in this study to cover both competition and allelopathy (Harper 1977).

Two unifying hypotheses were formulated with the expectation that the allelopathic qualities of the roots, large leaves, and rapid growth of *A. altissima* would negatively affect the growth of *R. pseudoacacia*. 1) Interspecific interference of *A. altissima* seedlings and *R. pseudoacacia* seedlings are greater than intraspecific interference within either species and, 2) *A. altissima* has a greater performance than *R. pseudoacacia* and replacement design where the relative proportions of each tree species were varied independently of one another over a range of densities.

In order to assess the interspecific and intraspecific interference of the two species, the specific questions we addressed (generated from (Connolly et al. 2001)) were: 1) was there an effect of one species on the other species' performance based on comparisons of total biomass and biomass allocation in mixtures to that in the monocultures? and 2) which species dominated (total biomass and biomass allocation) at the time of harvest? Biomass at the time of harvest was used as a measure of resource capture and, thus, interference between the species. Root and shoot responses were also considered because allocation among plant growth compartments in species mixtures compared to that in monocultures may indicate the location of most intense interference (Brouwer 1962; Chapin 1980).

## Materials and methods

# Species descriptions

Ailanthus altissima (tree-of-heaven) was introduced to the United States in 1784 (Hu 1979) and is considered a 'weed' tree because of its ability to grow quickly in disturbed habitats and to reproduce rapidly by thin papery samaras, stump sprouts, and root suckers (Brizicky 1962). Ailanthus altissima can create clumped stands of trees when a full seed cluster germinates in one location (Pan and Bassuk 1986). This pattern is further enhanced when stump sprouts grow from the original stem of the tree and suckers originate from the roots (Illick and Brouse 1926). Efficient dispersal and reproductive qualities and the ability to create dense monocultures, are characteristics of an invading plant species (Bazzaz 1986). Root plasticity allows A. altissima to adapt to a wide range of soils (Pan and Bassuk 1985). There is also evidence that the roots and stems of A. altissima exude chemicals that can negatively affect nearby plants (Heisey 1990; Heisey 1996). These compounds possibly enable A. altissima to create dense stands that dominate an area and curb growth of other plant species (Mergen 1959).

One problem with invasive plants is their role in altering native plant recruitment. In this study, the native tree of concern was R. pseudoacacia. The native range of R. pseudoacacia is the Appalachian region of Eastern North America yet its range today is more extensive. It has been widely planted for its resistant wood, distinct flowers, nitrogen-fixing root nodules, and rapid growth (Young and Young 1992). Robinia pseudoacacia is frequently found in disturbed areas and can tolerate a range of pH levels in the soil (Bossard et al. 2000). Robinia pseudoacacia replaces nitrogen lost following forest disturbances (Boring and Swank 1984). Young four-year old stands of R. pseudoacacia in the southern Appalachians fix approximately 30 kg N ha<sup>-1</sup> year  $^{-1}$  (Boring and Swank 1984) and are eventually replaced by trees typical of later successional stages (White et al. 1988; Dzwonko and Loster 1997), and enhance the growth of the adjacent trees (Chapman 1935).

#### **Experimental design**

Ailanthus altissima seeds collected from a tree in Giles County, VA were spread out and dried but were not stratified (Graves 1990). The seeds were placed on saturated blotting paper in closed petri dishes in a dark incubator with temperatures alternating diurnally from 30 °C ( $\pm$  0.5 °C, 16 hr) to 20 °C ( $\pm$  0.5 °C, 8 hr). Separately, *Robinia pseudoacacia* seeds from several roadside trees in Montgomery County, VA were stratified for 60 days, soaked in a 10% bleach solution for several minutes, and mechanically scarified (Sadhu and Kaul 1989).

After germination, each seedling was transplanted to a seedling cell with Metro Mix®. Greenhouse day and night temperatures and hours of light were between 21-32 °C and 10h: 14h throughout the experiment. After germination and early establishment, seedlings were randomly planted in masonry sand in 5-gallon pots (approximately 15 cm in diameter) according to a numbered grid on the pot surface. Similar sized individuals were selected from each species. Mixtures consisted of selected proportions of 1, 2, 3, 5, 6, 7, 10, and 14 total plants (Figure 1). Monoculture pots consisted of one species without the presence of the other. Sixty-four grams of Osmocote® (15-9-12) (the lowest nutrient level for plants according to the manufacturer) 8-9 month release at 21 °C was added to each pot. Pots were watered regularly to field capacity and were completely randomized on two greenhouse benches. The pots were rotated along the benches every other week to minimize the effect of the spatial variation in greenhouse microclimate.

After 4 <sup>1</sup>/<sub>2</sub> months, the plants were harvested during 14 consecutive days. In order to have the maximum number of plants at harvest and due to the experimental impracticality of growing the trees beyond this point within the restraints of the pots and greenhouse, we selected these harvest dates. Above ground parts were separated into stems and leaves. Leaves were counted and leaf area and petiole area were determined with a LICOR-3100 Area Meter (LiCor Inc., Nebraska, USA). The sand was washed from the roots. Stem length, number of branches, and root biomass were recorded. All tissues were dried in a forced air oven at 80 °C for approximately 48 hours to constant weight.

#### Data analysis

Multiple linear regression (Spitters 1983), Relative Yield Total (De Wit 1960), and Relative Crowding Coefficient (De Wit 1960) were used to assess the interspecific and intraspecific interference between *A. altissima* and *R. pseudoacacia*. A regression of the inverse mean biomass per plant on density was performed for each species in mixture and monoculture. This is a method used to describe plant yield/density relationship (Shinozaki and Kira 1956; Willey and Heath 1969; Spitters 1983). The equations were:

1/(mean biomass per plant (g) A. altissima) = B<sub>0</sub> + B<sub>AA</sub>(D<sub>AA</sub>) + B<sub>AA</sub>(D<sub>RP</sub>)

1/(mean biomass per plant (g) *R. pseudoacacia*) =  $B_0 + B_{RP}(D_{RP}) + B_{RPAA}(D_{AA})$ 

 $B_{AA}$  represents the intraspecific effect of *A. altissima* on itself,  $B_{AARP}$  indicates the interspecific effect of *R. pseudoacacia* on *A. altissima*,  $B_{RP}$  represents the intraspecific effect of *R. pseudoacacia* on itself, and  $B_{RPAA}$  indicates the interspecific effect of *A. altissima* on the biomass of *R. pseudoacacia*. D represents the density (number) of plants per pot.  $B_0$  is the intercept and the reciprocal of the biomass of an isolated plant (Spitters 1983). Three mixture pots contained outlier responses of *R. pseudoacacia* with standard deviations greater than 1.0 and were removed from the analysis.

From the slopes of the regression analysis, substitution rates, also known as 'competition coefficients' (Firbank and Watkinson 1985), were calculated to measure the influence of each species on itself and on the other component species (Spitters 1983; Connolly 1987). This absolute value expressed how each species 'perceived' the other component species in comparison to individuals of its own species and was a measure of interspecific interference. The substitution rates for *A. altissima* ( $S_{AA}$ ) and *R. pseudoacacia* ( $S_{RP}$ ) were, respectively:

$$S_{AA} = |B_{AARP}/B_{AA}|$$
$$S_{RP} = |B_{RPAA}/B_{RP}|$$

The responses of plant parts to the density of the two

species were considered in the analysis. The log of the mean weight of plant parts (roots, shoots, etc.) was regressed on the log of the weight of the entire plant to show this linear relationship (Kira et al. 1956). This analysis refers to allocation changes in response to plant density and may be related to a mechanism of interference.

$$\log wp = \log k + h \log w$$

wp represents the weight of the part of interest per plant, w is the total biomass of the plant,  $\log k$  is the intercept, and h is the slope of the line. This allometric relationship was used in the reciprocal multiple linear regression of the mean weight plant part on total density of the two species with the following equation (Shinozaki and Kira 1956; Willey and Heath 1969):

$$\frac{1}{(\text{plant part (g) } A. altissima)^{1/h}} = B_0 + B_{AA}(D_{AA}) + B_{AARP}(D_{RP})$$

1/(plant part (g) *R. pseudoacacia*)<sup>1/h</sup> = B<sub>0</sub> + B<sub>RP</sub>(D<sub>RP</sub>) + B<sub>RPAA</sub>(D<sub>AA</sub>)

The Relative Yield Total (RYT) was calculated to determine if the species were sharing or interfering with each other for resources by comparing their interspecific yield per pot to their intraspecific yield per pot in monoculture (De Wit 1960; De Wit and Van der Bergh 1965; Harper 1977; Snaydon 1991).

Relative yield total (RYT) = 
$$\frac{WAARP}{WAA} + \frac{WRPAA}{WRP}$$

WAA and WRP were the mean dry weights per pot (g) of *A. altissima* and *R. pseudoacacia*, respectively, in monocultures, and WAARP and WRPAA were the mean dry weights per pot (g) of *A. altissima* and *R. pseudoacacia*, respectively, when grown in mixture at a total pot density corresponding to the total pot density of the monocultures. RYT for total biomass and below ground responses at densities of 2, 6, 10, and 14 total plants were calculated.

The Relative Crowding Coefficient (RCC) for the relative mean total biomass per pot (g) was calculated for each replacement density to indicate the relative aggressiveness of the two species. RCC indicates which species performed better in mixture and had the stronger interspecific competitive ability compared to its intraspecific performance in monoculture according to the following equation (Harper 1977).

Relative crowding coefficient (RCC) = 
$$\frac{WAARP}{WRPAA} - \frac{WAA}{WRP}$$

RCC values greater than one indicated that *A. altissima* had the competitive advantage in the mixture over *R. pseudoacacia* and values less than one indicated an interspecific competitive advantage in the mixture for *R. pseudoacacia*. The RCC was only calculated for the equally balanced mixtures (e.g., 1:1, 3:3) using total biomass per pot, above ground biomass per pot, and below ground biomass per pot. The RYT and RCC, used as supplements to the earlier analyses, were interpreted according to their definitions (Harper 1977) and did not include statistical analyses.

#### Results

### Intraspecific and interspecific interference

The results revealed that interspecific interference was more intense than intraspecific interference. For both species, an increase in density of the other species caused a significant decrease (p < 0.05) in total biomass per plant as seen by positive slopes for the interspecific term in the regression (Table 1). Plots of predicted values in three dimensions showed negative influences of interspecific interference (gray strap lines) and a less negative relationship of intraspecific interference (monoculture and black strap lines) in both species (Figures. 2A and 2B). The substitution rates for total biomass responses were greater than one (Table 1).

Multiple regressions of shoot and stem biomass indicated significant interspecific responses for both species (Table 1). However, root and leaf biomass showed significant interspecific responses only for *A. altissima*. The intraspecific responses were significant for *A. altissima* for all biomass components. However, intraspecific response of *R. pseudoacacia* was significant only for total biomass.

#### Exploitation of resources

Analysis of the exploitation of resources indicated that A. altissima was the better interspecific competi-



*Figure 1.* Greenhouse Experimental Design. Full additive design for the greenhouse experiment. Each square represents a pot treatment (n=32). The density (number) of *R. pseudoacacia* and A. *altissima* seedlings in each pot are indicated (n = 336 per species).

tor at the majority of pot densities, yet R. pseudoacacia had a larger competitive advantage at the highest pot density. Relative Yield Total (RYT) values for total biomass and root biomass per pot were the largest at total pot density of two plants (Figure 3A, Figure 4A). Ailanthus altissima had a greater relative yield in mixture compared to its monocultures at this low density in the replacement diagram, whereas this greater yield in mixture was not evident for R. pseudoacacia. In mixtures with total densities of six and ten plants (Figure 3B,C, 4B,C), A. altissima had a greater relative yield than R. pseudoacacia in the 50:50 mixtures and the RYT decreased. At a total density of 14 plants (Figure 3D, Figure 4D), the RYT of A. altissima and R. pseudoacacia was close to one. The RYT for total biomass and below ground biomass decreased towards one at high densities (Figure 3, Figure 4). The Relative Crowding Coefficient (RCC) for total, above ground, and belowground biomass per pot was dominated by A. altissima at lower density levels and by R. pseudoacacia at the highest density level (Table 2).

# Discussion

#### Intraspecific and interspecific interference

In accordance with the first hypothesis, interspecific interference between species had a greater negative effect than intraspecific interference upon multiple biomass responses for both species. The interspecific slopes were similar for both species, indicating comparable biomass responses to the presence of the other component species. The substitution rates indicated that interspecific interference played a larger role on total biomass production than intraspecific interference.

There was greater interspecific interference in the high-density mixtures than the low-density mixtures since the RYT was close to one as the total pot density increased. The species may have been sharing or competing for the same resources more at this density than at the lower densities (Harper 1977; Snaydon 1991). This is likely since the growth of a plant is negatively affected by decreasing available space and resources with increasing total density (Firbank and Watkinson 1990). At low pot densities, RYT values greater than one indicated that the two species were not fully sharing or competing for the same re-



*Figure 2.* Reciprocal simple linear regression 'lines' for the interspecific (gray strap lines) and intraspecific (black strap lines) additive series in the experiment for the inverse mean total biomass responses (g) per plant for (A) *A. altissima* and (B) *R. pseudoacacia.* Strap lines are used solely increase ease of seeing relationships in the Figure. The statistical results are found in Table 1.

Table 1. Regression for the inverse mean biomass (g) responses per plant of A. altissima and R. pseudoacacia. Standard errors are in parentheses. Total biomass substitution rates are included for each species. Means with SD greater than 1.0 were excluded. Equations for the regressions are included in the text.

Response	Species	Intraspecfic slope	р	Interspecific slope	р	$\mathbb{R}^2$	Sub Rates
TOTAL BIOMASS (g)	A. altissima	- 0.013 (0.01)	0.22	0.026 (0.01)	< 0.01	0.14	1.92
	R. pseudoacacia	- 0.014 (0.02)	0.37	0.029 (0.01)	< 0.05	0.09	2.03
SHOOT BIOMASS (g)	A. altissima	-0.020(0.01)	0.21	0.035 (0.01)	< 0.05	0.13	
	R. pseudoacacia	-0.105(0.12)	0.38	0.217 (0.10)	< 0.05	0.08	
STEM BIOMASS (g)	A. altissima	-0.057(0.05)	0.25	0.137 (0.04)	< 0.01	0.17	
	R. pseudoacacia	- 0.174 (0.16)	0.27	0.313 (0.14)	< 0.05	0.10	
LEAF BIOMASS (g)	A. altissima	-0.028(0.02)	0.20	0.046 (0.02)	< 0.05	0.12	
	R. pseudoacacia	-0.126(0.14)	0.36	0.159 (0.12)	0.19	0.04	
ROOT BIOMASS (g)	A. altissima	-0.046(0.04)	0.27	0.108 (0.03)	< 0.01	0.15	
-	R. pseudoacacia	-0.199 (0.24)	0.41	0.222 (0.21)	0.29	0.03	



*Figure 3.* Replacement diagrams indicating the mean relative yield total biomass (g) per pot for *A. altissima* (closed circles), *R. pseudoacacia* (open circles), and Relative Yield Total (triangles) at different constant densities and proportions of species. A) Total density of 2 plants, B) Total density of 6 plants, C) Total density of 10 plants, and D) Total density of 14 plants. The numerator of the ratios indicates the density of *A. altissima* and the denominator indicates the density of *R. pseudoacacia*.

sources (Harper 1977; Snaydon 1991). There were weaker interspecific interactions at this density as

both species produced a greater relative total biomass in mixture than when they were in monoculture.



*Figure 4.* Replacement diagrams indicating the mean relative yield below ground biomass (g) per pot for *A. altissima* (closed circles), *R. pseudoacacia* (open circles), and Relative Yield Total (triangles) of different constant densities and proportions of species. A) Total density of 2 plants, B) Total density of 6 plants, C) Total density of 10 plants, and D) Total density of 14 plants. The numerator of the ratios indicates the density of *A. altissima* and the denominator indicates the density of *R. pseudoacacia*.

Table 2. Mean Relative Crowding Coefficient (RCC) of the mean total biomass of *A. altissima* against *R. pseudoacacia*. RCC values for mean above ground, below ground, and total biomass (g) per pot. The proportions of the species in the mixture are indicated in parentheses, with the density of *A. altissima* listed first.

Total den- sity	RCC <sub>AARP</sub> for mean total biomass (g) per pot	$RCC_{AARP}$ for mean above ground biomass (g) per pot	$RCC_{\rm AARP}$ for mean below ground biomass (g) per pot
2 (1:1)	1.45	1.30	2.16
6 (3:3)	1.40	1.28	2.15
10 (5:5)	1.88	1.91	1.80
14 (7:7)	0.65	0.58	0.87

# Above ground interference

Analysis of the RYT and RCC of plant parts revealed different competitive attributes for *A. altissima* and *R. pseudoacacia* that could lead to further studies regarding resource use by these species. Analysis of

above ground biomass indicated that *A. altissima* performed better in mixture than did *R. pseudoacacia*. Having greater above ground biomass can be an indicator of competitive ability (Gaudet and Keddy 1988). However, the vertical stem growth of several *R. pseudoacacia* individuals was faster than *A*. altissima individuals early in the experiment (Call, personal observation). Also, in 40% of the pot mixtures, R. pseudoacacia produced one dominant individual plant that exceeded 50% of the total pot biomass, whereas A. altissima produced plants of the same disproportionate size in only 10% of the pot mixtures. The tall, dominant R. pseudoacacia individuals with large leaf area, numerous leaves, large stem volume, and multiple branching reduced multiple biomass traits of A. altissima by increasing competition for light. Competition for light has been shown to create biomass inequalities between competing plant individuals (Weiner 1985). Similarly, plant architecture, which can determine how plants obtain resources, has been shown to be a factor in the degree of asymmetry observed between plants (Thomas and Weiner 1989). These above ground traits of R. pseudoacacia enabled it to have an above ground advantage over A. altissima at high-density levels where asymmetric competition can be intense (Weiner 1985).

#### Below ground interference

The below ground biomass responses for these species in this study can suggest future hypotheses for below ground interference. The below ground biomass of *A. altissima* was reduced by interspecific interference. There is evidence that shading or defoliation can reduce root growth and resource uptake within as few as 24 hours (Massimino et al. 1981; Caldwell et al. 1987). It is likely that the presence of *R. pseudoacacia*, particularly the large dominant individuals discussed earlier, with large height, branching, and leaf area could have inhibited root performance of *A. altissima*.

However, compared to its monoculture, the below ground performance of *A. altissima* in mixture was greater than that of *R. pseudoacacia*. The RCC index for mean root biomass per pot revealed that *A. altissima* had the greater competitive below ground advantage in the mixtures. Competition for below ground resources can negatively affect plant growth and establishment (Donald 1958; Casper and Jackson 1997), which can have a greater negative effect on mean plant biomass compared to solely above ground interactions (Wilson 1988; Weiner 1986). Below ground competition for resources has been observed to be size symmetric as plants deplete resources proportional to their size (Weiner et al. 1997; Cahill and Casper 2000). Below ground interactions can be strong when roots overlap and increase in abundance. Since *A. altissima* consistently generated a relatively large below ground biomass, it was likely a strong competitor against *R. pseudoacacia* since root biomass is related to competitive intensity (Cahill and Casper 2000).

The apparent below ground advantage of *A. altissima* in this experiment may be due to a number of factors. An early study on *A. altissima* indicated that this species is capable of rapidly developing a root mass for extensive surface lateral roots to aid in establishment at a site (Davies 1943-44). This was evident during the harvest when roots of *A. altissima* were extensively spread throughout the pot, sometimes penetrating into the root mass of *R. pseudoacacia*. This suggests that *A. altissima* has aggressive roots that can rapidly obtain resources, an attribute for a strong competitor for resources (Grime 1977).

# Summary

Despite faults inherent in plant competition studies, this analysis showed that the presence of both A. altissima and R. pseudoacacia negatively affected the performance of the other. Each species exhibited competitive attributes enabling it to dominate. The below ground dominance of A. altissima could be a strong benefit in situations when soil resources are limited and root competition is intense (Wilson and Tilman 1993). Ailanthus altissima could have an advantage over R. pseudoacacia by becoming established in an early-disturbed area, when light is not limiting. On the other hand, the occasional dominant above ground biomass and the specific architecture of R. pseudoacacia could be a competitive advantage when competition for light is important (Weiner 1990). It is evident that each species could be a good competitor in different situations and at different times (Grime 1977).

Studies of how these two species are naturally dispersed and associated in the field under different degrees of disturbances (Call and Nilsen 2003) could be helpful in drawing more conclusions regarding their interactions, as would longer-term (several years) interference experiments. Understanding the effects that an invasive species can have on the recruitment of native species is crucial to managing native biodiversity and natural ecosystems. This study showed that *A. altissima* and *R. pseudoacacia* do negatively interfere with each other, suggesting possible competitive interactions, although the mechanisms are unresolved. Further studies should examine the specific interactions between root nodulation of *R. pseudoa-cacia* and interactions with the allelopathic qualities of *A. altissima*.

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