Article

Interaction between *Ailanthus altissima* and Native *Robinia pseudoacacia* in Early Succession: Implications for Forest Management

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Abstract: The goal of this study was to discover the nature and intensity of the interaction between an exotic invader *Ailanthus altissima* (Mill.) Swingle and its coexisting native *Robinia pseudoacacia* L. and consider management implications. The study occurred in the Mid-Appalachian region of the eastern United States. *Ailanthus altissima* can have a strong negative influence on community diversity and succession due to its allelopathic nature while *R. pseudoacacia* can have a positive effect on community diversity and succession because of its ability to fix nitrogen. How these trees interact and the influence of the interaction on succession will have important implications for forests in many regions of the world. An additive-replacement series common garden experiment was established to identify the type and extent of interactions between these trees over a three-year period. Both *A. altissima* and *R. pseudoacacia* grown in monoculture were inhibited by intraspecific competition. In the first year, *A. altissima* grown with *R. pseudoacacia* tended to be larger than *A. altissima* in monoculture, suggesting that *R. pseudoacacia* may facilitate the growth of *A. altissima* at the seedling stage. After the second year, *R. pseudoacacia* growth decreased as the proportion of coexisting *A. altissima* increased, indicating inhibition of *R. pseudoacacia* by *A. altissima* even though the *R. pseudoacacia* plants were much larger aboveground than the *A. altissima* plants. In early successional sites *A. altissima* should be removed, particularly in the presence of *R. pseudoacacia* in order to promote long-term community succession.

Keywords: competition; early succession; forest invasions; invasive species; forest management

1. Introduction

The negative impacts of invasive plant species on native plant populations, plant community structure, and ecosystem nutrient cycling are well documented. Invasive plants have displaced native plant species [1], deteriorated the quality of native forests [2,3], changed soil chemical properties [4] and altered soil microflora [5]. The success of invasive species depends on the nature of the habitat at the time of invasion, the functional traits of introduced plants, and the interactions with other species after the first establishment of the invasive species. Some invasive plants such as *Microstegium vimineum* (Trin.) A. Camus and *Alliaria petiolate* (M.Bieb.) Cavara & Grande become dominant in forest systems by outcompeting other native species [6,7]. However, other invasive plants are less-dominant (distributed sparsely in the forest), but can still have measurable effects on forest regeneration during succession and understory diversity following succession, such as *Lythrum salicaria* L. and *Ailanthus*

altissima [8,9]. In general, many introduced invasive plants will encounter and interact with native plants that have similar habitat requirements and similar functional traits early in succession. The effect of the invader on forest development will, in part, be dependent upon the ability of the exotic plant species to successfully compete with native plants for resources during succession [10].

The interactions between introduced exotic plants and native plants are important filters to biological invasion. Invasive species are often thought to be better competitors compared with native species. However, many tests of competition between invasive and native species do not consider the similarities of the functional attributes of the exotic invader and the native species [11,12]. Indirect competition can be defined as a negative interaction between individuals that occurs when both species utilize at least one common limited resource [13]. Therefore, indirect competition is most likely to occur between functionally similar species because they are most likely sharing a similar niche space [14]. There are often members of the native species pool that have similar functional traits to the invading species even though they are not closely related. Consequently, it is most likely that invasive species will encounter and compete with a member of the native species pool that has invasive properties particularly in early succession. However, it is also possible that the success of the exotic invasive species is due to facilitation by native species [15]. The possibility of facilitation is more likely to occur when the invading species is at relatively low density. Furthermore, the interaction between particular invasive species and native species could switch between facilitation and competition depending on environmental conditions, succession sere, plant developmental stage, and the neighborhood of other species in the community [16,17]. We are interested in understanding how exotic invasive plants of low relative abundance interact with native plants (competition, facilitation, both, or coexistence), especially the implications that these interactions have for long-term succession and forest management.

We selected two tree species that are both fast-growing, early-successional species, which reproduce by both seeds and root sprouts: *Ailanthus altissima* (Mill.) Swingle (tree of heaven) and *Robinia pseudoacacia* L. (black locust); the taxa names are based on the Integrated Taxonomic Information System (https://www.itis.gov). Both species prefer disturbed sites with high light intensity, and occur together in the eastern deciduous forests of the US. [18]. *Ailanthus altissima* has been an invasive tree in US forests for more than 200 years, yet is found at relatively low density compared to some other invasive species [19,20]; *Robinia pseudoacacia* is native to the Mid-Appalachian mountain region, but also is viewed as an invasive species worldwide [11,21]. Both species are among the most abundant trees on the planet because of their ability to grow fast, their high reproduction rate, their tolerance to extreme environments, and their use by several cultures for horticulture, forestry, agriculture and medicine. As such they are frequently found as coexisting invaders following forest disturbance world-wide [22,23].

We propose that that these two species will encounter each other frequently in the early successional stands of many temperate forests world-wide including the Mid-Appalachian mountain region. In fact, a previous study has indicated that these species are clumped together in selected post-logging sites in the Mid-Appalachian region [18]. Their interaction could result in competition for early succession resources. However, *R. pseudoacacia*, a tree with nitrogen-fixing rhizobial bacteria, increases the availability of nitrogen in post-disturbance sites [24,25] and increases the richness and abundance of non-native species [25,26]. Thus, it is also possible that *R. pseudoacacia* will facilitate the growth and success of *A. altissima* by providing nitrogen to the higher-nitrogen-demanding *A. altissima*. It is also possible that *R. pseudoacacia* will be a superior competitor and minimize the growth of *A. altissima* during early succession.

Our overall goal was to address the following questions concerning the type, intensity and mechanisms of the interactions between these two target species: (1) What are the overall effects of treatment and year on the annual biomass increment for each species? (2) Is there evidence of intraspecific competition for both species based on the annual biomass increment? (3) Does the intensity or type of the interspecific interaction change during different stages from seedling to sapling? We hypothesized that the intensity of the competitive interaction, based on competition indices, would

increase as the plants aged from seedlings to saplings. Moreover, we hypothesized that the native species would facilitate the growth of the invasive species at the seedling stage, but compete with the invasive species at the sapling stage.

In this study, we evaluate the type and intensity of the interaction between the two selected tree species from seedling to sapling. Both species are known to be "ecosystem engineers" with potentially opposite effects on community development. As mentioned above, *R. pseudoacacia* has a documented positive effect on succession [25,26], while *A. altissima* has a documented negative effect on succession [8]. Our approach was to establish a common garden study, within the native range of *R. pseudoacacia*, in which seedlings of both species were planted in an additive-replacement series design and their growth patterns were followed for three years, during which time the two species became saplings. We discuss the ecological and forest management implications of the results.

2. Materials and Methods

2.1. Study Species and Site Description

Seeds of *A. altissima* were collected in early November 2010 from existing trees at Blandy Experimental Farm (Boyce, VA, USA, N 39° 3.82′ W 78° 3.87′), where this experiment was conducted; seeds of *R. pseudoacacia* were collected in October, 2010 from roadside trees near Jefferson National Forest in Montgomery County, VA, USA. (N 37° 2.81′ W 80° 4.44′). All seeds were germinated in a Virginia Tech greenhouse in April 2011 after stratification, and then transplanted into 25.4 cm deep tree seedling sleeves with potting soil (Sungro Metro-Mix 300 series; Sun Gro Horticulture Canada Ltd., Abbotsford, BC, Canada) laced with 5% field soil from the Blandy Experimental Farm to induce nodulation. Plants were grown in a greenhouse until transported to the experiment site for transplanting in June 2011.

This field site was originally a post-agricultural field that had been fallow for at least 10 years. The site was sprayed with herbicide (Round-up, Monsanto, St. Louis, MO, USA; active ingredient = Glyphosate (*N*-(phosphonomethyl) glycine) twice over a three-week period to control the previous plants before the site was prepared for planting. The site was fenced during the three years of the experiment to reduce herbivory by deer and rabbits.

A weather station was installed in the experimental site for continuous monitoring of ground and leaf-height air temperature, and precipitation. The average growing season (May–October) monthly high/low temperature and total precipitation in the three years of the study were: 24.5 °C/12.9 °C, 65.6 cm in 2011; 25 °C/11.9 °C, 81.7 cm in 2012; 24.4 °C/11.4 °C, 73.4 cm in 2013.

2.2. Experimental Design

The experimental design was an additive-replacement series (Figure 1A). This competition approach is also known as a response surface design, which enables us to evaluate the effects of different proportions of each species on each other (without the confounding effect of total density) across a set of different total densities [27]. Each experimental unit was a 2 m by 2 m square plot, separated by at least 1 m on all sides of each plot. The plots were laid out into six rows with each row separated by 2 m from the rows on either side. The experimental plots were randomly located within and across rows, resulting in 14 treatments that included four different tree densities (one to four plants plot), all possible species combinations under each density, and five replicates for each treatment. Within the plots that had more than one tree, a constant distance of 1 m was kept between neighboring trees in order to allow growth over three years and to reflect common distances between trees in local early successional stands. Although the distance between each plant was constant, the number of plants per 1 m^2 in the center of the plot reflects a change in plant density. Our data on mapping both *A. altissima* and *R. pseudoacacia* seedlings (currently unpublished) in a southern Appalachian forest indicate some clumping, but distances of 1 m between seedlings are common. The trees were arranged in the 1 m^2 center of the plot as far away from the plot border as possible (Figure 1B). The spatial

arrangement of neighboring plants in each plot was set up randomly to avoid the effect of different layouts. The seedlings of *A. altissima* and *R. pseudoacacia* (about two months old and 20–30 cm in height) were transplanted and established successfully in June 2011.
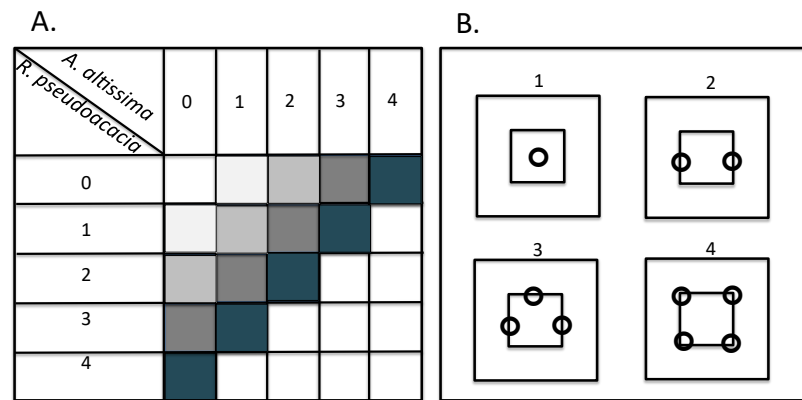

Figure 1. Common garden competition experiment layout: (**A**) design of the additive-replacement treatments. The design consists of three replacement series (South West-North East diagonal directions in the left panel) at three densities 2, 3, 4 plants per plot. Boxes with an X label are not included as treatments in the experiment. (**B**) The design for tree planting in the plots at the field site. Each plot was 2 m × 2 m and all seedlings were planted within the center 1 m × 1 m space. The open circles in the 1 m × 1 m space represent how the plants were positioned in the 1, 2, 3 and 4 plants per plot treatments. Diagram is not drawn to scale.

In addition to the experimental plots, 12 extra plots were established to grow trees that were destined to be harvested, to formulate a dimensional analysis after each growing season. We included these extra plots because the experimental trees could not be harvested for biomass estimates during the three-year study. The extra plots were monocultures of three or four plants per plot, resulting in 21 extra trees from each species. In the early fall of each year, seven plants of each species were randomly selected for harvest in order to formulate annual dimension analyses.

The experiment ran from June 2011 to November 2013. No additional watering or nutrients were applied to the plots except weekly watering during the first month after planting. Weeds were mowed around the experimental plots and removed from within the plots on a weekly basis during the growing season. After three seasons of growth the trees were large enough for the canopies of the adjacent plots to touch. Therefore, the experiment was terminated after three years because the plots would not be independent aboveground in future years.

2.3. Dimension Analysis, Competition Indices and Data Analysis

The annual, estimated, aboveground, biomass increment, defined as the end biomass minus the beginning biomass in each growing season, was chosen as the primary measurement of plant fitness for the competition analysis. At the beginning and end of each growing season, the height and basal diameter were measured for every tree in all plots. The height of each plant was determined by comparing the plant height to a pole graduated in cm or a meter stick the first year, and the basal diameter was determined with a caliper. Also, at the end of each growth season, before leaf fall, the seven randomly selected extra trees of each species were harvested at ground level, separated into leaf and stem, and put into a 60 °C oven until completely dry (typically four to seven days for leaves, 15–35 days for stems) to get dry biomass measurements. Subsamples of the leaves were taken from randomly selected plants of the seven extra trees to calculate the specific leaf area before the first year harvest. After obtaining the best regression equation for each species, the estimated, aboveground biomass (referred to as "biomass" from this point on) for each individual of *A. altissima* and *R. pseudoacacia* in the experimental plots was calculated based on its height and basal diameter

measurements. The annual biomass increment for each tree was determined by subtracting the spring biomass value from the fall biomass value.

A repeated measurement ANOVA was used to detect the impacts of: (1) tree density (total for both species); (2) proportion of the other species in the plot; and (3) year (one, two, three) on biomass increment. Students' *t*-tests were applied to pairwise comparisons of the different tree densities and proportions of other species for each year separately. We used the Students' *t*-test instead of the Tukey post-hoc test because the Tukey post-hoc test assumes independency of the data across the groups, which is not appropriate for repeated measure ANOVA.

The final biomass after the three growing seasons was analyzed by two-way ANOVA with the density and proportion of the other species in the plot as two factors. Students' *t*-tests were applied to pairwise comparisons of the final total biomass values.

The interpretation of the outcome of competition depends critically on how the competition was measured and which indices were used [28]. We evaluated two ways of quantifying the neighboring plant effect on target species biomass increment. The first and most common method used in the literature, was an evaluation of biomass increment in relation to the number of neighboring plants of the other species. The second way was to evaluate the target species biomass increment in relation to the total biomass of the neighboring species. The second method has been considered more appropriate when two species with a large size difference are compared [29,30].

To evaluate the competition effect and its intensity, we reviewed the existing indices in the literature and chose two competition indices that were appropriate for our experimental design—(1) substitution rate/competition coefficient (S), and (2) relative interaction intensity (RII) to evaluate the type and intensity of the interaction between the two species [31–33].

The substitution rate is computed based on multivariate regression coefficients to evaluate the relative intensity of intraspecific and interspecific competition, which are obtained by the following equations:

$$\text{Mean biomass increment per plot } A.\ altissima = B_o + B_{aa}\ (D_{aa}) + B_{aarp}\ (D_{rp}) \tag{1}$$

$$\text{Mean biomass increment per plot } R.\ pseudoacacia = B_o + B_{rp}\ (D_{rp}) + B_{rpaa}\ (D_{aa}) \tag{2}$$

where

D_{aa}: density of *A. altissima* in the plot

D_{rp}: density of *R. pseudoacacia* in the plot

B_o: estimated intercept in the model

B_{aa}: estimated coefficient for intraspecific competition of *A. altissima*

B_{rp}: estimated coefficient for intraspecific competition of *R. pseudoacacia*

B_{aarp}: estimated coefficient for interspecific competition of *R. pseudoacacia* on *A. altissima*

B_{rpaa}: estimated coefficient for interspecific competition of *A. altissima* on *R. pseudoacacia*

The substitution rate (also called the competition coefficient) for *A. altissima*: $S_{aa} = |B_{aarp}/B_{aa}|$ and for *R. pseudoacacia* $S_{rp} = |B_{rpaa}/B_{rp}|$ was calculated [31,32]. To measure the interaction type and intensity for these two plant mixtures, the relative interaction intensity (RII) was calculated.

$$\text{RII} = \frac{B_w - B_o}{B_w + B_o} \tag{3}$$

where

B_w: Biomass observed for target plant when growing with other plants

B_o: Biomass of target plant growing alone in the absence of inter/intraspecific interactions

RII was chosen over other frequently used competition indices because it has robust mathematical and statistical properties, and allows for clear interpretation. RII has a continuous range from −1 (competitive exclusion) to 1 (symbiosis), and a positive number indicates facilitation while a negative number suggests competition. The more negative the RII, the greater the interspecific competition. RII offers the most consistent results among the interaction indices that are commonly used [33].

Since there were only five replicates for plots with only one plant per plot for each species in our experimental design, the usual calculation of a mean B_o could result in a bias when calculating the RII for the other 45 plots. In order to reduce the possibility of this bias, we used a non-parametric bootstrap to make sure that the B_o we used was randomly selected [34]. For each mixture plot, we first computed the average of calculated B_w, then computed RII 2000 times by bootstrapping the B_o value from the five different biomass increment values from the monoculture plots, and obtained the average RII value for this plot. After computing the RII for each mixed species plot, a repeated measurement two-way ANOVA was applied to analyze the competition indices. We also used a rank order technique to analyze the competitive effect of various treatments. For each year, we ranked the treatments by RII values from the lowest (more competition) to the highest (possibly facilitation) to perform a rank order analysis. The three ranked numbers (from 2011 to 2013) were added together for each treatment to obtain the overall rank, which was used to indicate competition intensity.

3. Results

3.1. Growth Patterns and Dimension Equations

At the end of the first growing season the plants were relatively small, with an average (mean ± standard deviation) height of 1.24 ± 0.71 m and 0.52 ± 0.43 m for *R. pseudoacacia* and *A. altissima*, respectively. The plants had not formed a multi-branched architecture at this stage. After the second growing season the trees attained 3.85 ± 1.49 m and 1.48 ± 1.63 m height on average for *R. pseudoacacia* and *A. altissima*, respectively. The final average heights of the saplings after three years of growth were 4.58 ± 2.04 m for *R. pseudoacacia* and 2.03 ± 2.12 m for *A. altissima*. Following a late freeze in the spring of the second year, *A. altissima* became partially coppiced. Therefore, we measured the height and diameter for all the main stems of each plant (coppice) to increase the accuracy of the biomass estimates. Consequently, the height and diameter of *A. altissima* had increased variance in later years.

The dimensional data from 2011 to 2012 were combined to formulate our regressions between biomass, height and diameter for both species (Table 1). The fitting power of the combined regressions was improved compared with the regressions formed using the dimensional data from each year alone. The combined regression was used to predict the biomass for the first and second year. In order to fit the regression equations for biomass, a square root transformation was needed for *A. altissima* in all three years, while log transformation was needed to fit linear regressions for *R. pseudoacacia* in the first two years to meet the normality assumption (Table 1). The adjusted R^2 for these four equations were all ≥0.95, which indicated that our biomass estimate was robust. The basal diameter was more important for predicting biomass than the height, which is reasonable because the canopies of both species spread widely.

Table 1. Dimension analysis of total above-ground dry weight (biomass) for *Ailanthus altissima* and *Robinia pseudoacacia* based on the basal diameter and height for three growing seasons 2011–2013.

	Biomass Estimation Equation and Adjusted R^2	
	[a] *Ailanthus altissima*	*Robinia pseudoacacia*
2011	[b] Biomass (g) = (−4.94247 + 1.974 × Height (m) + 7.266 × Diameter (cm) + 0.74 × (Height − 1.4963) × (Diameter − 2.5354))^2 R^2 = 0.951	Biomass (g) = Exp (2.5812 + 1.6176 × Diameter (cm) − 0.1 × Diameter^2) R^2 = 0.947
2012		
2013	Biomass (g) = (−10.43578 + 1.952572 × Height (m) + 9.263966 × Diameter (cm) + 0.795541 × (Height−2.37) × (Diameter − 3.7924)) ^{2} R^2 = 0.976	Biomass (g) = −5847.114 − 361.3571 × Height (m) − 2052.2315 × Diameter (cm) + 287.6451 × (Height − 3.358) × (Diameter − 5.871) R^2 = 0.966

[a] All plants were grown in a common garden setting in Boyce, VA, USA; [b] Regression equations and adjusted R^2 of those equations are presented for the combined data set (2011 and 2012) and the data set for 2013 alone.

There was a significant difference in the biomass increment between the two species ($p < 0.0001$) and across the three years ($p < 0.0001$, Table 2). The biomass increment for *R. pseudoacacia* in the first growing season was approximately double that of *A. altissima* (Figure 2). In the second growing season, the biomass increment for both species increased significantly ($p < 0.0001$) by six to eight times that of the first growing season. However, the biomass increment during the third growing season was slightly smaller than that of the second growing season when data of both species were combined ($p = 0.0017$). The significant down-turn in annual biomass increment in the third year was primarily due to *R. pseudoacacia*. However, the effect of density, species proportion and their interaction were not significant (Table 2).

Table 2. Repeated measurement ANOVA result of total above-ground, dry biomass increment for *Ailanthus altissima* and *Robinia pseudoacacia* from a three-year competition experiment, 2011–2013.

Fixed Effect	[a] Num DF	Den DF	*F* Value	*p* Value
[b] *A. altissima*				
[c] Density	2	85	0.43	0.6546
[d] % of *R. pseudoacacia*	5	85	0.28	0.9235
Density by % of *R. pseudoacacia*	10	85	0.40	0.5300
Year	2	186	118.48	<0.0001
R. pseudoacacia				
Density	2	86	0.94	0.3942
% of *A. altissima*	5	86	0.93	0.4665
Density by % of *A. altissima*	10	86	0.67	0.4170
Year	2	187	152.39	<0.0001

[a] Num DF = degrees of freedom of numerator; Den DF = degree of freedom of denominator; Density = effect of number of trees per plot on mean biomass increment; [b] All plants were grown in a common garden setting in Boyce, VA, USA; [c] Density = the density of all trees in the plot (2, 3, 4 trees per 4 m^2 plot); [d] Percentage = effect of subject tree percentage in the plots (75%, 67%, 50%, 33%, 25%, 0%); Year = effect of different years on mean biomass increment.
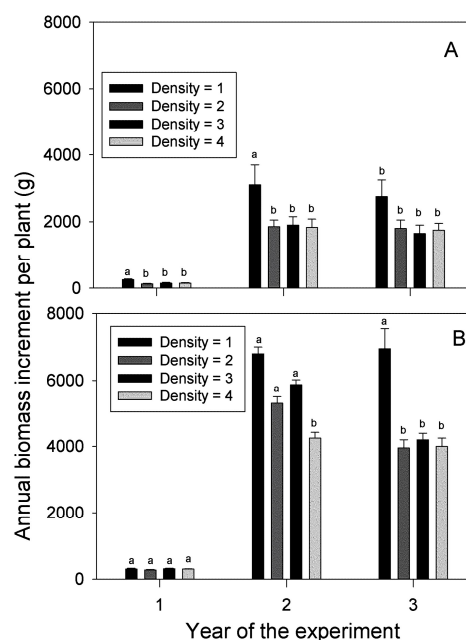

Figure 2. Mean annual total above-ground dry-weight (biomass) increment per tree for monoculture plots (area = 4 m^2) of *Ailanthus altissima* (**A**) and *Robinia pseudoacacia* (**B**) growing in a common garden in Boyce, VA, USA, during three consecutive growing seasons. Density 1 = 0.25 tree m^{-2}; Density 2 = 0.5 tree m^{-2}; Density 3 = 0.75 tree m^{-2}; Density 4 = 1 tree m^{-2}. Error bars represent 1 standard error on each side of the mean. *N* = 5 plots per treatment. Lower case letters above each bar represent comparisons by Students' *t*-test at $p < 0.05$.

3.2. Intraspecific Competition

In monocultures, the largest individual biomass increment (Figure 2A,B) was found in the lowest density plots (density = 1) in all three years (data for both species combined), but the effect of density was not significant at the $\alpha = 0.05$ level. Pairwise comparison for *A. altissima* indicated that the biomass increment was significantly larger in the lowest density monoculture than that of all other monoculture densities (density = 2, 3, or 4 trees per plot) in year 1 ($p = 0.032$, 0.047, and 0.037 respectively) and year 2 ($p = 0.030$, 0.023, and 0.013 respectively). For year 3, the difference in biomass increment was not significant between any pair of monoculture density for *A. altissima* (Figure 2A).

Surprisingly, in monoculture, *R. pseudoacacia* showed a trend of increasing biomass increment as the density increased in year 1, but the trend was not significant. This trend was reversed in the next two growing seasons (Figure 2B). The difference in individual biomass increment between the monoculture densities was only significant between the highest density and the lowest density group in year 2 ($p = 0.032$). There was a significant or barely significant difference in biomass increment in the pairwise comparison between the lowest density monoculture and other density monocultures for *R. pseudoacacia* in year 3 ($p = 0.026$, 0.053, 0.035, respectively) (Figure 2B). In general, increasing density from two trees per plot to three and four trees per plot in monoculture did not affect the biomass increment significantly in all three years for either species (Figure 2).

3.3. Interspecific Facilitation or Competition

The individual biomass increment of *A. altissima* tended to be higher in the presence of *R. pseudoacacia* than in the presence of itself at density 2 in all three years, suggesting the facilitation of *A. altissima* by the presence of *R. pseudoacacia* (Figure 3A–C). However, this trend was not statistically significant ($p = 0.65$, 0.42, 0.57 in year 1, 2 and 3). There was no significant difference in the biomass increment of *A. altissima* among the different proportions of *R. pseudoacacia* treatments at higher densities. The effect of the density and proportion of *R. pseudoacacia* on *A. altissima* were not significant at the $\alpha = 0.05$ level when all treatments and years were combined (Table 2).

The individual biomass increment of *R. pseudoacacia* tended to increase in the presence of *A. altissima* at density 2 in all three years (Figure 3D–F), which suggests facilitation at this density, but this increase was not statistically significant ($p = 0.27$, 0.31, 0.42, in the respective three years). However, average biomass increment of *R. pseudoacacia* individuals decreased slightly as the proportion of *A. altissima* increased at density 3 (Figure 3D–F). There was one tree with a negative biomass increment for both species in the density 4 monoculture group, which caused the monoculture group to have a lower observed average value than the actual value. The effect of the number of neighboring *A. altissima* on the biomass increment of *R. pseudoacacia* individuals was not significant at the $\alpha = 0.05$ level when all treatments and years were combined (Table 2). It is important to note that the biomass increments of individuals in the mixture treatments were the result of the combined effects of both intra- and inter-specific interactions.
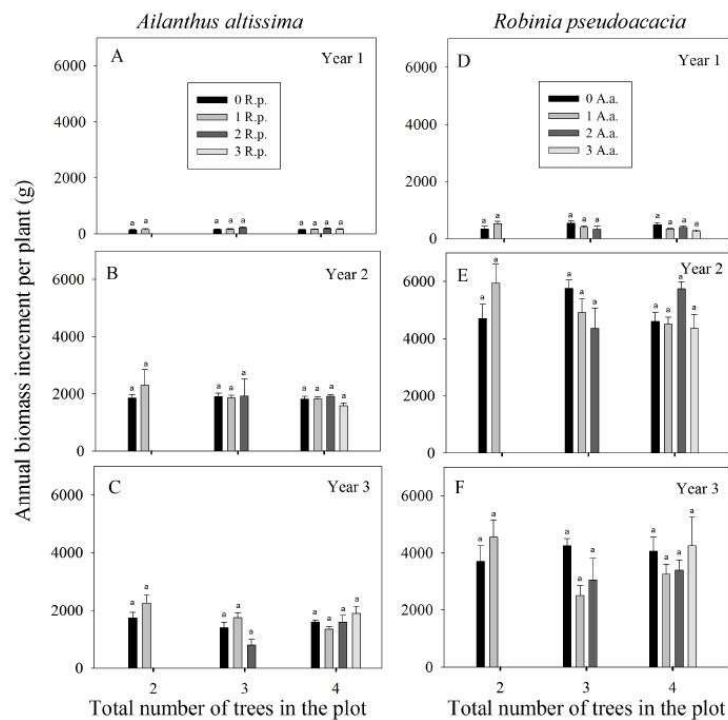
Figure 3. Mean annual total above-ground dry-weight (biomass) increment per tree for *Ailanthus altissima* (**A**–**C**) and *Robinia pseudoacacia* (**D**–**F**) growing in substitutive combinations at three densities in a common garden in Boyce, VA, USA, during three consecutive growing seasons (Year 1–3). Left side, from top to the bottom are total biomass increments of *A. altissima* in the presence of different proportions of *R. pseudoacacia* for years 1, 2 and 3, respectively. Experimental plots were 4 m^2 in area. The density of trees in the plot were 2 (0.5 trees m^{-2}), 3 (0.75 trees m^{-2}), and 4 (1 tree m^{-2}). 0 R.p. = a monoculture of *A. altissima*; 1 R.p. = 1 *R. pseudoacacia* plot^{-1}; 2 R.p. = 2 *R. pseudoacacia* plot^{-1}; 3 R.p. = 3 *R. pseudoacacia* plot^{-1}. Right side, from top to the bottom are biomass growth of *R. pseudoacacia* in year 1 2 and 3, respectively. 0 A.a. = a monoculture of *R. pseudoacacia*; 1 A.a. = 1 *A. altissima* plot^{-1}; 2 A.a. = 2 *A. altissima* plot^{-1}; 3 A.a. = 3 *A. altissima* plot^{-1}. Error bars represent 1 standard error on each side of the mean. *N* = 5 plots per treatment. Lower case letters above each bar represent post-hoc comparisons by Students' *t*-test at *p* < 0.05.

The final, total biomass per individual of both species after three years of the experiment (Figure 4) was analyzed to evaluate the cumulative effect of three years of plant interaction. *Ailanthus altissima* plants in density 1 had a significantly greater biomass per individual compared with plants in density 2, 3 and 4 (*p* = 0.043, 0.022 and 0.008 respectively). The final biomass of *A. altissima* individuals in monocultures of density 1 was significantly greater than monocultures with the other three densities (*p* < 0.0001), but there were no significant differences among the other three monocultures (Figure 4). For *R. pseudoacacia*, density was a significant factor. Plants in density 1(Figure 4) had significantly greater biomass per individual when compared with plants in density 2, 3 and 4 (*p* = 0.003, 0.018 and 0.001). *Robinia pseudoacacia* grown in 50% *A. altissima* (combining densities 2 and 4) had significantly greater final biomass per individual (*p* = 0.024, 0.035) than those grown with 33% or 67% *A. altissima* (combining data from densities 3 and 4).
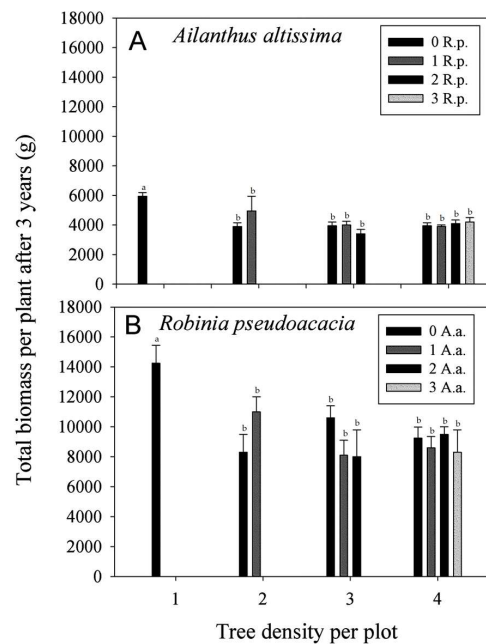
Figure 4. The total above-ground dry biomass per tree for *Ailanthus altissima* (**A**) and *Robinia pseudoacacia* (**B**) growing in substitutive combinations at four densities in a common garden in Boyce, VA, USA, at the end of three consecutive growing seasons. The left panel is total biomass of *A. altissima* in the presence of different proportions of *R. pseudoacacia*, and the right panel is the total biomass of *R. pseudoacacia* in the presence of different proportions of *A. altissima*. Experimental plots were 4 m^2 in area. The density of trees in the plot was 1 (0.25 trees m^{-2}), 2 (0.5 trees m^{-2}), 3 (0.75 trees m^{-2}), and 4 (1 tree m^{-2}). 0 R.p. = a monoculture of *A. altissima*; 1 R.p. = 1 *R. pseudoacacia* plot^{-1}; 2 R.p. = 2 *R. pseudoacacia* plot^{-1}; 3 R.p. = 3 *R. pseudoacacia* plot^{-1}. 0 A.a. = a monoculture of *R. pseudoacacia*; 1 A.a. = 1 *A. altissima* plot^{-1}; 2 A.a. = 2 *A. altissima* plot^{-1}; 3 A.a. = 3 *A. altissima* plot^{-1}. Error bars represent one standard error on each side of the mean. *N* = 5 plots per treatment. Lower case letters above each bar represent post-hoc comparisons by Tukey's Honest Significant Difference (HSD) test at *p* < 0.05.

3.4. Competition Indices

In all three years, all the coefficients of regression had a negative sign (Table 3), indicating that competitive interactions occurred either between or within both species. The intraspecific competition intensity for both *A. altissima* and *R. pseudoacacia* tended to increase over time (Table 3). The intraspecific competition intensity for *R. pseudoacacia*, increased from years 1 to 2, but then decreased in year 3 (Table 3). The interspecific competitive effect of *R. pseudoacacia* on *A. altissima*, indicated by B$_{aarp}$, tended to increase over the three years (Table 3). The interspecific competitive effect of *A. altissima* on *R. pseudoacacia*, indicated by B$_{rpaa}$ also increased over the three years, suggesting strong interspecific competition between *A. altissima* on *R. pseudoacacia*, and that competitive effect increased through time.

The substitution rate (S) values suggested that intraspecific competition was dominant in *A. altissima*, but interspecific competition became more important for *A. altissima* as time passed (S$_{aa}$ was smaller than 1 and increased over the three years, Table 3). For *R. pseudoacacia*, interspecific competition was significant and the dominant factor over all three years, especially years 1 and 3 (S$_{rp}$ was bigger than 1, Table 3). *Robinia pseudoacacia* experienced an equally significant and stronger intraspecific and interspecific competitive effect in year 2, but the intraspecific competitive effect was slightly stronger (Table 3).

Despite the general high p-values (greater than 0.05), multiple comparisons of RII did reveal consistent patterns for both species across treatments (Tables 4 and 5). Most RII values were negative for *A. altissima*, suggesting that a competitive effect, either intraspecific or interspecific, had occurred.

Two-way ANOVA results suggested that density had a significant effect on the RII of *A. altissima* in year 1. Specifically, RII at density 2 was significantly lower than at density 3 (p = 0.0376). On the other hand, the proportion of the neighboring *R. pseudoacacia* trees was not a significant factor in year 1 (p = 0.091). Neither the effect of density nor proportion of the *R. pseudoacacia* was significant in years 2 and 3. There was, however, a trend towards higher density groups having lower RIIs (Table 4), suggesting more intense competition as the tree density increased in both years. The ranking of the average RII value of *A. altissima* on a yearly basis across all treatments (Table 5) from highest to lowest was year 3 (RII = −0.061), year 1 (RII = −0.130) and year 2 (average RII = −0.175).

Table 3. Coefficients of interspecific and intraspecific competition intensity between *Ailanthus altissima* and *Robinia pseudoacacia* growing in a common garden experiment in Boyce, VA, USA, over a three-year period (2011–2013).

	Competition Indices					
	A. altissima			*R. pseudoacacia*		
Year	[a] B_{aa}	B_{aarp}	S_{aa}	B_{rp}	B_{rpaa}	S_{rp}
1	[b] −17.23	−3.54	0.20	−10.38	−63.99	6.61
2	−176.31	−70.24	0.39	−634.31	−582.31	0.92
3	−193.28	−174.14	0.90	−256.95	−598.27	2.33

[a] B_{aa} = coefficient of intraspecific competition for *A. altissima*; B_{rp} = coefficient of intraspecific competition for *R. pseudoacacia*; B_{aarp} = interspecific competitive effect of *R. pseudoacacia* on *A. altissima*; B_{rpaa} = the interspecific competitive effect of *A. altissima* on *R. pseudoacacia*; S_{aa} = substitution index for *A. altissima*; S_{rp} Substitution index for *R. pseudoacacia*; [b] Negative values for coefficient of competition indicate competition occurred. Substitution indices greater than one indicate that the interspecific competition effect is larger than the intraspecific competition effect.

Table 4. Mean relative interaction intensity (RII) for three densities of *Ailanthus altissima* and *Robinia pseudoacacia* growing in a common garden additive-replacement series experiment in Boyce, VA, USA, over a three-year period (2011–2013).

	Density (No. Tree Per Plot)					
	A. altissima			*R. pseudoacacia*		
	[a] 2	3	4	2	3	4
Year 1	[b] −0.175 A [c]	−0.070 B	−0.107 AB	−0.077 A	−0.065 A	−0.095 A
Year 2	−0.096 A	−0.179 A	−0.171 A	−0.149 A	−0.177 A	−0.131 A
Year 3	0.013 AB	−0.069 B	−0.089 B	−0.223 A	−0.255 A	−0.221 A

[a] Data are grouped by tree density (2, 3, or 4 m^{-2}) irrespective of species composition. [b] More negative RII values indicate greater competitive effect; [c] Capital letters (A, B, C) indicate results of the Tukey's HSD test. The mixture treatments with no shared letter are the ones that had significant differences based on Tukey's Honest Significant Difference (HSD) test.

Table 5. Mean relative interaction intensity (RII) for the 12 mixtures of *Ailanthus altissima* and *Robinia pseudoacacia*.

	Results for *A. altissima*								
	2A [a,b]	1A1R	3A	2A1R	1A2R	4A	3A1R	2A2R	1A3R
Year 1	−0.296 C [c]	−0.095 AB	0.004 A	−0.213 BC	0.018 A	−0.106 ABC	−0.084 AB	−0.084 AB	−0.153 ABC
Year 2	−0.195 AB	−0.029 A	−0.140 AB	−0.193 AB	−0.209 AB	−0.120 AB	−0.165 AB	−0.144 AB	−0.254 B
Year 3	−0.047 AB	−0.021 A	−0.002 A	−0.069 AB	−0.151 AB	0.010 A	−0.265 B	−0.052 AB	−0.050 AB
	Results for *R. pseudoacacia*								
	2R	1R1A	3R	1R2A	2R1A	4R	1R3A	2R2A	3R1A
Year 1	−0.233 AB	0.034 A	0.002 AB	−0.216 AB	0.039 AB	0.007 AB	−0.253 B	−0.154 AB	0.021 AB
Year 2	−0.233 A	−0.090 A	−0.121 A	−0.285 A	−0.110 A	−0.094 A	−0.236 A	−0.168 A	−0.045 A
Year 3	−0.321 A	−0.153 A	−0.262 A	−0.361 A	−0.114 A	−0.135 A	−0.251 A	−0.304 A	−0.194 A

[a] 2A, 2R, 1A1R, 3A, 3R, 1A2R, 2A1R, 4A, 4R, 1A3R, 2A2R, 3A1R of *Ailanthus altissima* ("A") and *Robinia pseudoacacia* ("R") growing in a common garden additive-replacement series experiment in Boyce, VA, USA, over a three year period (2011–2013); [b] More negative RII values indicate greater competitive effect; [c] Capital letters (A, B, C) indicate results of the Tukey's HSD test. The mixture treatments with no shared letter are the ones that had significant difference based on Tukey's HSD test.

4. Discussion

4.1. Is the Interaction between Species Competition, Facilitation or Coexistence?

The type of interaction between these two species was mainly competition rather than facilitation. The negative effect of competition on plant growth affected *R. pseudoacacia* more than it did *A. altissima*. In this three-year period, the influence of *R. pseudoacacia* on the vegetative growth of *A. altissima* was either neutral or slightly facilitated, while, in most treatments, the growth of *R. pseudoacacia* trees was inhibited by neighboring *A. altissima.* For *R. pseudoacacia,* the competitive impact of *A. altissima* was stronger than competition with itself, but only when *A. altissima* made up greater than 50% of the plants in the plot. For *A. altissima*, there was less intraspecific competition than that for *R. pseudoacacia*, which would promote higher density natural stands of *A. altissima* relative to *R. pseudoacacia*.

The interspecific competition outcomes for the biomass increment from this experiment were not as clear as the intraspecific competition results because of greater variation within each treatment group, and because the outcomes reflected the combined effects of both intraspecific and interspecific competition. The competition coefficient result supports an interspecific competitive interaction between these two species. Overall, our results were consistent with previous theories of density-dependent regulation in plants. Based on our findings, we predict that *R. pseudoacacia* will be negatively impacted by neighboring *A. altissima,* wherever these two species co-occur. Our experimental design used a consistent 1 m spacing between trees. Although we changed the density on an area basis (1–4 m^{-2}), the distance between the trees was the same in all density treatments. It is possible that the constant distance between trees caused our biomass increment per tree to be similar for the treatments in year 2 and 3.

The growth of *R. pseudoacacia* was most inhibited by *A. altissima* when the latter was dominant in the neighborhood. When *R. pseudoacaia* was dominant there was not a similar competitive effect on *A. altissima*. Otherwise, intraspecific competition was more important than interspecific competition for *R. pseudoacacia*. This exemplifies the importance of early-stage removal of the invasive species *A. altissima* in forests, (i.e., before *A. altissima* increases in abundance via sprouting or seeds). Such removal is especially important near *R. pseudoacacia,* in order to eliminate the negative impact of this invasive species on the native nitrogen-fixing symbioses associated with the native *R. pseudoacacia,* their influence on ecosystem nitrogen cycling and their effect on succession. This finding supports the early detection and rapid response approach for invasive species control [35]. Overall, competition was the main interaction between these species. Moreover, we found that the competitive effect stronger from *A. altissima* on *R. pseudoacacia* than in reverse. Although some suggestion of facilitation was observed at the seedling and sapling levels, there is not likely to be any facilitation of *A. altissima* by *R. pseudoacacia* in Appalachian forests.

4.2. Does the Interaction between Species Change from Seedling to Sapling?

Our results suggest that studying different developmental stages of the interactions between species is important. Most previous studies of the competition between native and invasive plants have focused on grasses and forbs, because of their short life cycle and because they are much easier to manipulate compared with trees [36]. However, interactions with invasive trees could be very different from the results of studies with invasive herbaceous species [37,38]. Tree interactions may also shape the community structure and function and impact other species more significantly than understory species [39–41]. The impact of invasive trees on native trees can occur for a long time period after a disturbance [42–44]. Studies like ours should occur over a longer time period to better understand the interactions between invasive and native trees. Although we only conducted this experiment for three years, we discovered a shift of interaction type and variation in competition intensity for trees from the seedling stage to the sapling stage. In relation to our second question, we found that the negative effect of the invasive tree *A. altissima* on native *R. pseudoacacia* became stronger as the plants transitioned from seedlings to saplings. One possible reason would be that *A. altissima* grew

larger and as a result had a stronger interaction with neighbors in year 2 and year 3. Also, intraspecific competition became stronger for both species as time passed, especially during the second growing season when growth was most rapid. However, we recognize that our results may be because the spacing per plant size was large at the seedling stage (resulting in low competition), but the same distance per plant size was small at the sapling stage (resulting in higher competition).

Our findings indicate that any negative impact of *A. altissima* on *R. pseudoacacia* is dependent on the size of *A. altissima*. These results further support an early control strategy for the invasive *A. altissima*. Alternatively, these data suggest that some native species could be found that out-compete *A. altissima* in the early years of succession, but by the third year of succession it may be too late to use any native species to reduce the growth of *A. altissima*.

Previous studies have shown that the type of interaction between a pair of plant species can switch quickly in response to environmental conditions, even on a daily basis [45]. At any particular time, the overall result of competition or facilitation is a cumulative effect. Therefore, the results from this study complement previous research [46], which showed that seedlings of *R. pseudoacacia* have a facilitative effect (due to the effect of nitrogen fixation on soil nitrogen availability) on the growth of *A. altissima* seedlings when the soil nutrient level may be low. In locations with equal numbers of both species, *R. pseudoacacia* will also facilitate the growth of *A. altissima*. Moreover, at times or places where the population of locust leaf miners are low, the competitive effects of *A. altissima* may also be low. Although the intensity of competition or the possibility for facilitation may change within a season, our analyses were limited to the overall effect of a whole growing season each year. Thus, over the three-year period that the plants transition from seedling to sapling, competition is the dominant interaction between *R. pseudoacacia* and *A. altissima* and *A. altissima* is the better competitor.

4.3. What Are the Forest Management Implications of This Research?

Our results suggest that very early in succession, at the seedling stage, *R. pseudoacacia* may facilitate the growth of *A. altissima*, as it has been shown to do with other native and exotic species [26]. The facilitation may be enhanced at sites with low nitrogen availability [46], but not at high nutrient concentrations [47]. The intensity of the intraspecific competition for both species was highly correlated with plant size, which suggests that indirect competition for the same resources, such as light and nutrients, is the cause of intraspecific competition. When the two species co-exist, our findings suggest that the growth of invasive *A. altissima* would not be negatively affected by *R. pseudoacacia*; even when *R. pseudoacacia*'s density is greater than that of *A. altissima*; conversely, the native *R. pseudoacacia* would be suppressed by *A. altissima*, particularly at high densities of *A. altissima.* Given *A. altissima*'s prolific seed production and ability to sprout, we would expect this negative competitive effect to increase with time. However, *R. pseudoacacia* saplings accumulate much greater amounts of above-ground biomass and leaf area than *A. altisisma* saplings, suggesting that in early successional sites when trees attain sapling size *R. pseudoacacia* is a better competitor for above-ground resources than *A. altissima*. Consequently, *A. altissima*'s ability to negatively affect *R. pseudoacacia*'s growth rate in our study may be due to *A. altissima*'s ability to better compete for below-ground resources, which was also found in greenhouse studies of seedlings [47]. Thus, the cause of inhibition by *A. altissima* on the much larger, above-ground *R. pseudoacacia* ought to be the result of either more effective below-ground competition or a negative effect of allelopathy on root growth and the nitrogen-fixing bacteria associated with *R. pseudoacacia* [46,48].

Thus, it is important to consider the management of both species simultaneously. These two species are likely to co-occur in post-harvest or early secondary succession forest sites world-wide. They have opposite effect on forest soil development (particularly nitrogen availability and litter depth) and opposing effects on forest development. *Ailanthus altissima* can reduce both canopy tree regeneration and understory diversity while *R. pseudoacacia,* in its native habitat, typically gives way to forest succession [24,49]. The effects of both species on the forest become accentuated with time. Therefore, early post-harvest management plans need to minimize the negative effects of *A. altissima* on

R. pseudoacacia in order to optimize long-term forest regeneration. Indeed, despite a shared nonnative status and lack of enemies, *A. altissima* has spread faster than *R. pseudoacacia* in Northern Italy over the last thirty years [22], though planted *R. pseudoacacia* has increased the dominance of nitrophilous species in some European forests in part due to stalled succession caused by the short-rotation cycles typical of energy tree plantations [50].

Ailanthus altissima predominantly colonizes rapidly after forest harvests or at other sites with high light, such as road cuts [18,51–53]. In fact, across South Africa, most *A. altissima* trees colonized within the first five years of a disturbance [53]. In *R. pseudoacacia's* native range, it is important to remove *A. altissima* early in forest development, particularly when the *A. altissima* trees are proximal to *R. pseudoacacia* trees, because the presence of *A. altissima* in early succession forests will inhibit the positive effect of *R. pseudoacacia* on forest regeneration. The removal of *A. altissima* must be carried out at an early developmental age because following root system establishment, cutting and injecting herbicide may not fully eradicate the plants due to extensive root growth and subsequent root suckering [54]. Once *A. altissima* plants attain reproductive age (post-sapling age), there will be little opportunity to reduce the negative effect of these trees on forest health due to their high seed production [55], strong legacy effects on soil development [23] and propensity to form monoculture stands.

The coexistence of *R. pseudoacacia* and *A. altissima* seedlings following harvest is likely to enhance the successful recruitment of *A. altissima* because the *R. pseudoacacia* may facilitate the growth of *A. altissima* at the seedling stage. Digging or carefully directed herbicide application of the *A. altissima* seedlings out of post-management sites, particularly around *R. pseudoacacia* trees, may be one of the most effective management plans for reducing the negative effect of *A. altissima* on forest regeneration in *R. pseudoacacia's* native range. Waiting until later to manage *A. altissima* will have a negative effect on *R. pseudoacacia* and will not be successful in managing *A. altissima* or promoting forest health. Moreover, the management of *A. altissima* becomes a higher priority if *R. pseudoacacia* is also in the early post-disturbance site.

5. Conclusions

The results of a replacement-series competition study clarified the interaction between two important invasive trees that have opposite effects on forest regeneration. *Ailantus altissima* and *R. pseudoacacia* are likely to coexist in high light and early disturbance sites world-wide. When coexisting, *R. pseudoacacia* may facilitate the growth of *A. altissima* at the seedling stage. However, at the sapling stage and thereafter, *A. altissima* will inhibit the growth of *R. pseudoacacia*, particularly where *A. altissima* has a higher density than *R. pseudoacacia*. Therefore, *A. altissima* will likely override the positive effects that *R. pseudoacacia* has on forest development and forest health. It is crucial to remove *A. altissima* at the seedling stage, by digging or carefully directed herbicide application, before it can have negative effects on forest health, particularly in the presence of *R. pseudoacacia*.

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