

Analysis of intraspecific and interspecific interactions between the invasive exotic tree-of-heaven (*Ailanthus altissima* (Miller) Swingle) and the native black locust (*Robinia pseudoacacia* L.)

Lara J. Call

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Committee:
E.T. Nilsen, Chair
R.H. Jones
D.M. Porter

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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. 1) A four-month full additive series in the greenhouse and 2) spatial point pattern analysis of trees in a silvicultural experiment were used to analyze the intraspecific and interspecific interference between these two species. In the greenhouse experiment, total biomass responses per plant for both species were significantly affected by interspecific but not by intraspecific interference ($p < 0.05$). 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. However, *R. pseudoacacia* exhibited more variation for multiple biomass traits, occasionally giving it an above ground advantage in some mixed species pots. Analysis of spatial point patterns in the field with Ripley's K indicated that the two species were positively associated with each other along highly disturbed skid trails in the majority of the field sites. Locally, increased disturbances could lead to more opportunities for *A. altissima* to invade, negatively interact with *R. pseudoacacia* (as was evident in the greenhouse study), and become established in place of native species.

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1.0 INTRODUCTION

Ecological issues associated with global climate change are increasingly important as human impacts extend across all ecosystems. Three crucial ecological issues are: 1) altered composition of carbon dioxide in the atmosphere, 2) changes in the nitrogen cycle, and 3) land-use and cover change (Vitousek 1994). Primary among these issues is land-use and cover change and the ecosystem changes that result. Land-use and cover change is concerned with alterations made upon the land by humans (land-use) and its biotic cover (land cover) and the resulting effects upon the physical environment (Meyer & Turner 1992). The magnitude of land disturbance caused by humans plays a major role in overall global change (Vitousek 1994).

1.1 Invasive Plants

1.11 *History*

The invasion of exotic plant and animal species into regions that were previously separated by biogeographic barriers is one key problem of land use and cover change (D'Antonio & Vitousek 1992). Frequently, plant species are introduced into new areas because of their economic value as crop species, timber trees, forage plants, or for ornamental use (Heywood 1989). Many invasive plants introduced into North America have been transported from Europe, Asia, and the Mediterranean Basin (Heywood 1989). Biotic invasions are both intentional and accidental events that place formerly isolated species into contact with each other, faster than the normal rate of evolution (D'Antonio & Vitousek 1992).

1.12 *Definition*

The definition of an invader is a species that has colonized, successfully persisted, and spread into an ecosystem in which it did not exist before (Mooney & Drake 1989; Reichard & Hamilton 1997). The probability of a successful invasion corresponds to the type and degree of disturbance, the number of non-native propagules, the time period in which the community is exposed to the imported propagules (Rejmánek 1989), and the properties of the exotic species or the native species of concern (Lonsdale 1999). If a species has been observed to invade other regions in the world, there is a high probability that it will be an invasive

plant somewhere else (Reichard & Hamilton 1997). According to a comparative plant study, invasive plants exhibit characteristics of r-selected plants with short juvenile periods, short intervals between large seed crops, and small seed masses. These qualities allow an invasive plant to reproduce quickly and consistently (Rejmánek & Richardson 1996). Invasive plants have also been suggested to exhibit “general purpose genotypes” (gpg), which are heterozygous genotypes that are advantageous when moving into new areas where tolerance of new conditions will be necessary for establishment (Baker & Stebbins 1965).

1.13 *Mechanisms and Impact*

Land disturbances (typically generated by humans) cause the environment to become more susceptible to invasion due to the immediate fluctuation of resources following a disturbance. This sharp increase or decrease in available resources can facilitate an exotic invasion (Davis *et al.* 2000). The invader is either able to gain access to these resources when the native species cannot, or the invader is able to use the resources more efficiently than the native species (Vitousek 1986). One study suggests that invasive species are able to successfully compete with the native species because natural competitors of the invasive species are not present, which enables the invader to maximize its competitive potential (Callaway & Aschehoug 2000).

Not only can invasive species persist and spread into an ecosystem, they can also alter basic ecosystem processes such as hydrology, nutrient cycling, soil erosion rates, (Vitousek & Walker 1989), and fire frequency and intensity (D’Antonio & Vitousek 1992). Changes made in key ecosystem processes can have a feedback effect on global changes such as climate and atmospheric composition (D’Antonio & Vitousek 1992). Invasive species can also prevent recruitment of native species (Mooney & Drake 1989) by negatively affecting the fecundity, survival, and fitness of native plants (Gould & Gorchov 2000). These alterations of the ecosystem can place the invasive species at an advantageous and dominant role over native species in the ecosystem (Vitousek 1990; Walker & Vitousek 1991).

For example, an invasive plant species that alters the biogeochemical processes of an ecosystem is exemplified in the invasion in Hawaii by *Myrica faya* Aiton. This is a nitrogen-fixing evergreen tree native to

the Canary Islands, which has led to suppression of the native *Metrosideros polymorpha* Gaudich (Walker & Vitousek 1991). Through the process of actively fixing nitrogen, *M. faya* has been a successful invader and its growth rate and dominance in the ecosystem have surpassed that of *M. polymorpha* (Walker & Vitousek 1991).

Invasive species also impact ecosystem processes by preventing native species recruitment. An example of this is the displacement of native plants such as *Taxodium ascendens* Brongn. (pond cypress) by *Melaluca quinquenervia* (Cav.) (melaluca) in Florida (Meyers 1983). *Melaluca quinquenervia* successfully invades the transition zone from pinelands to swamps that cypress typically inhabits and forms a dense canopy that prevents establishment of native plants (Meyers 1983). In California, the invasive plant *Cytisus scoparius* L. (Link) (Scotch broom) displaces native plants and does not significantly respond to introduced vertebrate and invertebrate herbivores (Bossard & Rejmánek 1994). Similarly, the invasive vine *Lonicera japonica* Thunb. ex Murray (Japanese honeysuckle) suppresses growth of the successional native *Liquidambar styraciflua* L. (sweetgum) (Dillenburg *et al.* 1993), thus having a negative effect upon the recruitment of successional trees by reducing their vigor.

Invasive species compete with native species and may render them extinct (Mooney & Drake 1989). Therefore, biotic invasions can cause an ecosystem to become homogenized and can decrease regional diversity by accelerating the extinction of native species (D'Antonio & Vitousek 1992). The competition between invasive and native species is an important issue that merits attention. Estimated species extinctions due to biotic invasion are greater than that resulting from climate or atmospheric changes (D'Antonio & Vitousek 1992). This research will look at the invasive plant *Ailanthus altissima* (Miller) Swingle (Simaroubaceae) and its interaction with the native *Robinia pseudoacacia* L. (Fabaceae).

1.2 *Ailanthus altissima* (Miller) Swingle

1.21 Morphological traits

Ailanthus altissima (Miller) Swingle is a species in the Simaroubaceae (Quassia Family). It can grow 9-18 meters tall, has alternately arranged compound leaves, heart-shaped leaf scars, and a disagreeable smell when leaves are crushed and is sometimes called the “stink tree” (Hu 1979). The fruits are 2-5 cm brown

samaras with one seed in the center of each wing (Fig 1.1). Female trees produce pistillate flowers and fruits and male trees produce staminate flowers that are infamous for their odor (Hu 1979). Flower morphology is very variable and some plants have been observed to have perfect flowers (Feret 1973). A small tree that is 12 inches in diameter can produce a million seeds in one year (Illick & Brouse 1926).

1.22 History

Ailanthus altissima was introduced from Peking to Europe in the 1740s from the collection of a Jesuit priest who had mistaken *A. altissima* for a lacquer tree (Hu 1979). In 1751, the seeds were sent to Philip Miller in England (Hu 1979). The tree was spread throughout Europe and England when it was discovered that a silkworm, *Samia cythia*, produced a high quality silk when grown on *A. altissima* leaves (Feret 1985; Frank 1986) and that the tree exhibited rapid growth and beautiful foliage (Hu 1979). In 1784, seeds were sent to William Hamilton in Philadelphia and were planted where the University of Pennsylvania is found today; a sucker from the original tree can be found in the Bartram Botanical Garden in Philadelphia (Davies 1942). A second importation resulted from the demand for small pollution tolerant city trees in New York City in the 1820's (Davies 1942; Hu 1979). It is possible that the seeds were also imported into California during the Chinese immigration (Feret 1985), since this tree had medicinal and cultural importance to the Chinese (Hoshovsky 1999). As early as 1888, the invasive qualities of *A. altissima* were recorded in a report stating that the tree had spread through Virginia and neighboring states (Curtiss 1888). It has become completely naturalized in 48 counties in North Carolina (Patterson 1976).

Early attempts to name *A. altissima* were widespread and led to confusion. In 1751, Philip Miller, Superintendent of the Physic Garden at Chelsea, planted the seeds in his garden and attempted to place the name *Toxicodendron altissima* Miller on the genus for the tree (Hu 1979). In 1785, The French naturalist Desfontaines gave the name *Ailanthus glandulosa* Desfontaines (after the glands found beneath the leaves) to the type species of the genus, a name that was commonly recognized in Europe until 1919 (Davies 1942; Brizicky 1962). The final nomenclature of *A. altissima* was refined in 1916 when Walter T. Swingle, of the United States Department of Plant Industry, named the tree *Ailanthus altissima* (Miller) Swingle (Hu 1979).

The Manual of Cultivated Trees and Shrubs Hardy in North America lists two species of *Ailanthus* and three horticultural varieties; *A. altissima*, (smooth twigs and small fruits) and *A. vilmoriniana* Dode (prickly twigs and larger fruits) are the recognized species in North America (Rehder 1940). There are 15 species of *Ailanthus*, of which *A. altissima* is the northernmost species (Brizicky 1962). Compared to the original Chinese *A. altissima*, the American *A. altissima* is genetically different and has possibly experienced much mutation and recombination (Feret & Bryant 1974).

Ailanthus altissima has been examined for its uses as an ornamental plant, a reforestation tree for disturbed sites, fuel wood production, potential use as fodder for domestic animals, afforestation, and a cure for dysentery (Hu 1979; Feret 1985). Though not widely advocated today, *A. altissima* was also used as a source of honey (Melville 1944) and was considered to be a good candidate for pulpwood (Illick & Brouse 1926). It has also been cultivated and utilized for erosion control around the Black Sea and in the mountains of Morocco (Pieglar 1993).

1.23 Reproductive and Life strategies

Today, *A. altissima* is considered a “weed” tree because of its capabilities to grow rapidly and to reproduce by thin papery samaras, stump sprouts, and suckers (Brizicky 1962). Its surprisingly rapid reproductive growth was observed in a greenhouse study in which 40% of *A. altissima* seedlings flowered within six weeks after germination (Feret 1973). *Ailanthus altissima* can create clumped stands of trees when the full seed clusters from the female tree fall to the ground to germinate (Pan & Bassuk 1986). Stump sprouts grow from the original stem of the tree and root sprouts originate from the roots (Illick & Brouse 1926). The sprouts are a result of damage to the “mother” tree (Davies 1943-1944). In one year, the average growth of a tree sprout from a stump is 6.0 feet, 2.7 feet for root sprouts, and 1.3 feet for seedlings (Illick & Brouse 1926). The root sprouts that grow from the roots can also extend far from the original tree, and once a sprout was found 87 feet from the tree (Illick & Brouse 1926). The height of *A. altissima* and its ability to reproduce vegetatively enables this tree to dominate the ground layer, the first and second shrub layers, and the upper canopy in a forest (Kowarik 1995). Davies (1935) observed a dense group of *A. altissima* that was

approximately half an acre consisting of 32 stumps. Having efficient dispersal and reproductive qualities is characteristic of an invading plant species such as this one (Bazzaz 1986).

In an urban setting, *A. altissima* is adaptable for a wide range of soils due in part to the plasticity of its roots (Pan & Bassuk 1985). The roots of *A. altissima* are comparably longer, more extensive, less branched and wider spreading than other trees in similar urban environments (Pan & Bassuk 1986). The roots are also shallow and have been observed to have an enlarged storage body at the root base (Davies 1943-1944).

Because of its tolerance for different soil conditions, *A. altissima* has been used in revegetation of acid mines where soils have a low pH, very low soluble-salt concentrations, and low phosphorous levels (Plass 1975). *Ailanthus altissima* has even been found sprouting on the side of a vertical calcareous castle wall in Portugal (Almeida *et al.* 1994). It can also be found on rich alluvial soils, limestone outcroppings, sterile soils, bottomland coves, and occasionally on clay soils (Feret 1985).

Ailanthus altissima frequently occurs in disturbed sites that have open gaps for sunlight and has been categorized as being shade-intolerant (Grime 1965), but recently it has been observed in an old-growth forest in New York (Knapp & Canham 2000). This study suggests that the growth of *A. altissima* is gap-obligate (rapid growth to canopy height at a single period), whereas a study in West Virginia indicated that the tree exhibited gap-facultative characteristics (Kowarik 1995). The slow ramet growth of *A. altissima* under the canopy in the resource poor habitat suggested that *A. altissima* has a plastic clonal growth response. Despite the differences in the results of under canopy growth observed, both of these studies show that the success of *A. altissima* is not limited to highly disturbed sites.

Allelopathy

There is evidence that the roots and stems of *A. altissima* exude chemicals that can affect nearby plants. The quassinoid ailanthone has been extracted from *A. altissima* and has been identified as having antifeedant and insect growth inhibiting activity (Kraus *et al.* 1994; Heisey 1996). There are likely other compounds found in *A. altissima*; yet ailanthone was the only one easily removed with polar solvents such as water and methanol (Heisey 1996).

The toxicity of *A. altissima* is likely a defense mechanism against pathogens and insects. For example, unpublished data from Heisey found that a methanol extract from *A. altissima* was toxic to gypsy moths. Also, the toxins show herbicidal effects. One or more compounds in a root bark extract sprayed on premergence and postmergence plants significantly suppressed growth (Heisey 1990b). Lawrence *et al.* (1991) studied similar herbicide effects where extracts from tissues of *A. altissima* suppressed germination of *Lactuca* seeds. Mergen (1959) was able to show negative responses from 35 gymnosperm and 10 angiosperm species when solutions from *A. altissima* leaf extracts were applied to cut surfaces of the trees. Also, toxic chemicals from the inner pericarp and the naked seed inhibited cress radicle growth (Heisey 1990b). Heisey's (1990a) laboratory experiments have shown that extracts from the roots and inner bark contained the highest degree of toxicity. Leachate of small, detached root bark of *A. altissima* significantly suppressed the growth of *Lepidium sativum* L. (rock cress) suggesting the release of toxins into the soil.

Chemical compounds from *A. altissima* are transmitted to nearby plants by the following ways: 1) leaching from leaves and stems to the ground, 2) leaching of fallen, decaying stems, leaves, and roots, or 3) seepage of toxins from the roots and shoots directly into the soil (Lawrence *et al.* 1991). However, the compound ailanthone quickly loses its toxicity from decomposition in nonsterile soil, possibly because of microbial degradation (Heisey 1996).

Chemicals produced by *A. altissima* are at high amounts in the young invading trees that possibly aid in the young tree's initial establishment into the ecosystem. Older well-established stands of *A. altissima* do not produce as many chemical compounds as do the younger ramets (Lawrence *et al.* 1991). The allelopathic qualities and clonal reproduction of *A. altissima* enable this species to create dense stands that dominate an area and curb growth of other plant species (Mergen 1959). However, it is not clear if the allelopathic qualities of *A. altissima* significantly affect the distribution of plants in an ecosystem, because there are many other factors that can influence plant distributions (Lawrence *et al.* 1991). For example, in an old-field study, mice showed a preference for consuming white pine, sugar maple, and white ash while avoiding *A. altissima* (Ostfeld *et al.* 1997). This can give *A. altissima* an advantage over other species during early establishment.

However, it is possible that the presence of *A. altissima* can affect plant responses to its toxic compounds. The toxic properties of *A. altissima* are able to affect phenotypic differences in plant populations when they are exposed to these toxic stresses. For example, a population of *Teucrium canadense* L. (germander) exposed to *A. altissima* contaminated soil tolerated toxic conditions with *A. altissima* better than a population of plants not formerly exposed to the toxins (Lawrence *et al.* 1991).

Only a few cases have indicated the effects of chemicals or products from *A. altissima* upon humans. The substance aianthone inside the bark is a potential irritant to the skin. One patient experienced a rash-like allergy after being in contact with the sap of *A. altissima* (Derrick & Darley 1994). It has also been noted that its pollen can induce allergic symptoms in some patients (Munemasa *et al.* 1993).

Despite its invasive qualities, *A. altissima* is not always able to dominate an ecosystem. It is susceptible to a number of fungal pathogens. Several types of fungi attack the foliage, stem, roots, and trunk of the tree (Hepting 1971; Feret 1985). Feret (1985) also observed much difficulty in planting and establishing *A. altissima* seedlings in the field. He found that the tree required well-aerated soils, plenty of water, and was sensitive to the cold winter temperatures in Virginia. *Ailanthus altissima* is not associated with excessively dry conditions and is thus never found in association with dry soil trees such as pines and junipers, even though it can attain drought hardiness after becoming established (Feret 1985). Also, in an old-field study (Ostfeld *et al.* 1997), high densities of voles were observed to prefer consuming seedlings of *A. altissima* rather than white pine seedlings. Older trees that approach trunk diameters of 3 feet or age greater than 40 years usually decay from heart rot (Illick & Brouse 1926).

1.3 *Robinia pseudoacacia* L.

1.31 Morphological traits

Robinia pseudoacacia is a deciduous tree that grows 9–30 meters tall and has alternate compound leaves typical of plants in the pea family (Fig 1.2). In the late spring, white, fragrant, pea-like flowers can be found, and the fruit is in the form of 4-8 cm flat pods that contain 4-10 small dark brown seeds.

1.32 History

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 valued resistant wood, distinct flowers, nitrogen-fixing root nodules, and rapid growth (Young & Young 1992). It has become naturalized and is considered an invasive plant in California and other western states (Bossard *et al.* 2000). *Robinia pseudoacacia* was brought to Europe in the 17th century and has spread throughout Central Europe and is now considered a pest (Holzener 1982). *Robinia pseudoacacia* is typically found in open disturbed areas such as roadsides, can tolerate a range of pH levels in the soil (Bossard *et al.* 2000), and has been planted on reclaimed surface mines (Zeleznik & Skousen 1996).

1.33 Reproductive and Life strategies

Like *A. altissima*, *R. pseudoacacia* reproduces and spreads by seed dispersal and root sprouts. It is considered an opportunistic species that aggressively enters into disturbed areas and quickly grows comparatively faster than other trees for 10-20 years (Boring & Swank 1984b; Elliot *et al.* 1997). In optimal conditions, it can average 4 feet of growth per year (USDA 1965).

Despite the early rapid growth rate of *R. pseudoacacia*, dense stands of black locust can eventually decline due to a decrease in vitality and increased susceptibility to the painted locust stem borer, *Megacyllene robiniae* Forst. (Chittenden 1904; Boring & Swank 1984b; USDA 1999) or leaf damage from the larvae and beetles of the leaf miner, *Odontata dorsalis* Thunb. (Chittenden 1904; USDA 1999). In many situations, whether the stem borer is present or not, *R. pseudoacacia* gradually decreases in vigor and is succeeded by more shade tolerant and long-lived plant species (Boring & Swank 1984b; Elliot *et al.* 1998). In addition to these pests, *R. pseudoacacia* is also negatively affected by heart rot (*Fomes rimosus*) following damage by the stem borer (USDA 1965).

Although *R. pseudoacacia* is not allelopathic like *A. altissima*, the inner bark, root sprouts, and wilted leaves have been found to contain a phytotoxin called “robin” and a glucoside robinin. These compounds have been observed to be poisonous to livestock and humans if ingested (Hardin 1966).

Nitrogen fixation

Succession is the process of sequential changes in relative abundances of dominant species in ecosystems as the once-dominant species are replaced by others (Huston & Smith 1987). *Robinia pseudoacacia* influences secondary forest succession by fixing nitrogen that prepares the soil for incoming late successional species (Boring & Swank 1984b). Cumulative fixation of nitrogen by *R. pseudoacacia* replaces nitrogen lost following forest disturbances (Boring & Swank 1984a). Nitrogen fixation by *R. pseudoacacia* increases rapidly and then gradually declines following a disturbance (Gorham *et al.* 1979). The fixed nitrogen from *R. pseudoacacia* primarily ends up in biomass accumulation in the stems, leaves, and twigs that eventually cycle into the soil when the locust leaves fall and decay (Boring & Swank 1984b). Nitrogen within the fallen biomass is not immediately released into the soil but is retained due to the high amount of lignin found within the leaves (White *et al.* 1988). Young locust stands have been observed to fix approximately 30-kg N ha⁻¹ year⁻¹ (Boring & Swank 1984a). This large collection of nitrogen on the ground gradually aids in the replacement of black locust trees by trees typical of later successional stages (Chapman 1935; White *et al.* 1988; Dzwonko & Loster 1997).

1.4 Competition between species

Greenhouse replacement and additive series have commonly placed invasive plant species against native plant species to indicate potential interference between the two. For example, seedlings of the invasive Australian plant *Chrysanthemoides monilifera* (DC). T. Norl (bitou bush) were placed in a study with seedlings of the native *Acacia longifolia* var. *sophorae* (Labill.) F. Muell (coast wattle) to analyze competition between the two plants (Weiss & Noble 1984). This replacement series was able to identify that the invasive *C. monilifera* had a competitive advantage over the native *A. longifolia* because of its rapid root growth, large leaf area, and high use of water.

Further research has examined the effects of invasive plants, including allelopathic ones, upon native plants. Invasive plants such as *Carduus nutans* L. (nodding or musk thistle) have decomposing rosettes that can inhibit nitrogen fixation of the native *Trifolium repens* L. (white clover) (Wardle *et al.* 1994). The process of

decreasing the soil nitrogen input is likely an advantage for *C. nutans* in competing with the native plant population. In another competition study, the weedy and aggressive *Agropyron repens* (L.) P. Beauv (quackgrass) was grown with common crop legumes (Weston & Putnam 1985). The allelopathic qualities of *A. repens* inhibited the number of nodules produced in the legumes. Another study of allelopathy found chemical exudates to be a factor in a competition between *Centaurea diffusa* (Lam.) (diffuse knapweed), an invasive weed in North America, and three native bunchgrasses. This study indicated that *C. diffusa* was capable of producing root exudates that were able to suppress the growth of the native bunchgrasses (Callaway & Aschehoug 2000).

1.5 Objectives

Numerous ecological traits are comparable between *A. altissima* and *R. pseudoacacia*. Both species establish in disturbed sites, and early in the century in Pennsylvania, *R. pseudoacacia* was frequently observed to be associated with *A. altissima* (Illick & Brouse 1926). Both trees have been observed to share the upper canopy (Kowarik 1995), have aggressive reproductive qualities, and exhibit rapid growth. Thus, it is no surprise that these qualities place these two species on the list of forty of the most invasive woody angiosperm species from forty different genera (Rejmánek & Richardson 1996).

However, each of these tree species has a different functional attribute that is critical to succession and ecosystem processes, allelopathy of *A. altissima*, and nitrogen fixation in *R. pseudoacacia*. The allelopathic qualities of *A. altissima* can suppress the growth of replacement successional species and possibly inhibit nitrogen-fixing bacteria (Rice 1984). *Robinia pseudoacacia* adds advantageous fixed nitrogen to the soil to aid in the establishment of replacement species and stimulates growth of nearby species (Chapman 1935). This is an important difference because studies have shown that the functional characteristics of the component species, rather than total species richness in an ecosystem, have a large impact upon ecosystem processes such as nutrient cycling (Hooper & Vitousek 1997).

It is likely that there is interference between these two species (based on their similarities). The analysis of this interaction will reveal insight into the effect that *A. altissima* has upon *R. pseudoacacia* and the

potential indirect effect on larger ecosystem processes such as productivity, decomposition, succession, and nutrient cycling.

The term interference was used in this study as a large category that includes the deletion reaction of competition (removal of a resource by one organism) and the addition reaction of allelopathy (addition of an inhibitory compound to a plant's environment) (Tinnin 1972; Harper 1977). Interference was used in this situation because the mechanisms of the plant interactions were unknown and difficult to determine (Wilson 1988).

This goal of this research was to determine if the invasive exotic *A. altissima* negatively interacts with the native *R. pseudoacacia*, indicating its potential for displacing the native black locust in the ecosystem. Experimental approaches for studying plant interactions were used to determine potential interference between the two species. A classical greenhouse experiment analyzed the interspecific and intraspecific interference between the two species competing for resources. Spatial pattern analysis in the field evaluated the dispersion and association of the two species as indicators of competitive interactions.

The main goal of the greenhouse study was to determine if there was interference between *A. altissima* and *R. pseudoacacia* seedlings, and if this interference favored *A. altissima* over *R. pseudoacacia*. The unifying hypotheses were: 1) Interspecific interference of *A. altissima* seedlings and *R. pseudoacacia* seedlings would be greater than the intraspecific interference within either species and, 2) In the majority of the mixtures, *A. altissima* would have a greater performance compared to *R. pseudoacacia*. We used combined additive and replacement designs where the relative proportions of each tree species were varied over a range of densities. Total biomass and biomass allocation were used as measures of plant interference.

In the field, the main goal was to determine if there was interference between *A. altissima* and *R. pseudoacacia*, and if this interference was evident in the spatial patterns of *A. altissima* and *R. pseudoacacia*. The hypotheses were: 1) The two species would have a clumped spatial pattern due in part to their reproductive characteristics and to weak intraspecific interactions and 2) The two tree species would be negatively associated with each other suggesting potential competitive interspecific interactions between the two. Spatial

association analysis was used to determine whether the presence of one species was associated with the presence of the other.

Fig 1.1 Illustration of *A. altissima*. A) pistillate flower, B) staminate flower, C) unopened flower bud, D) samaras, E) individual seed, F) leaflet, and G) gland underneath leaflet.

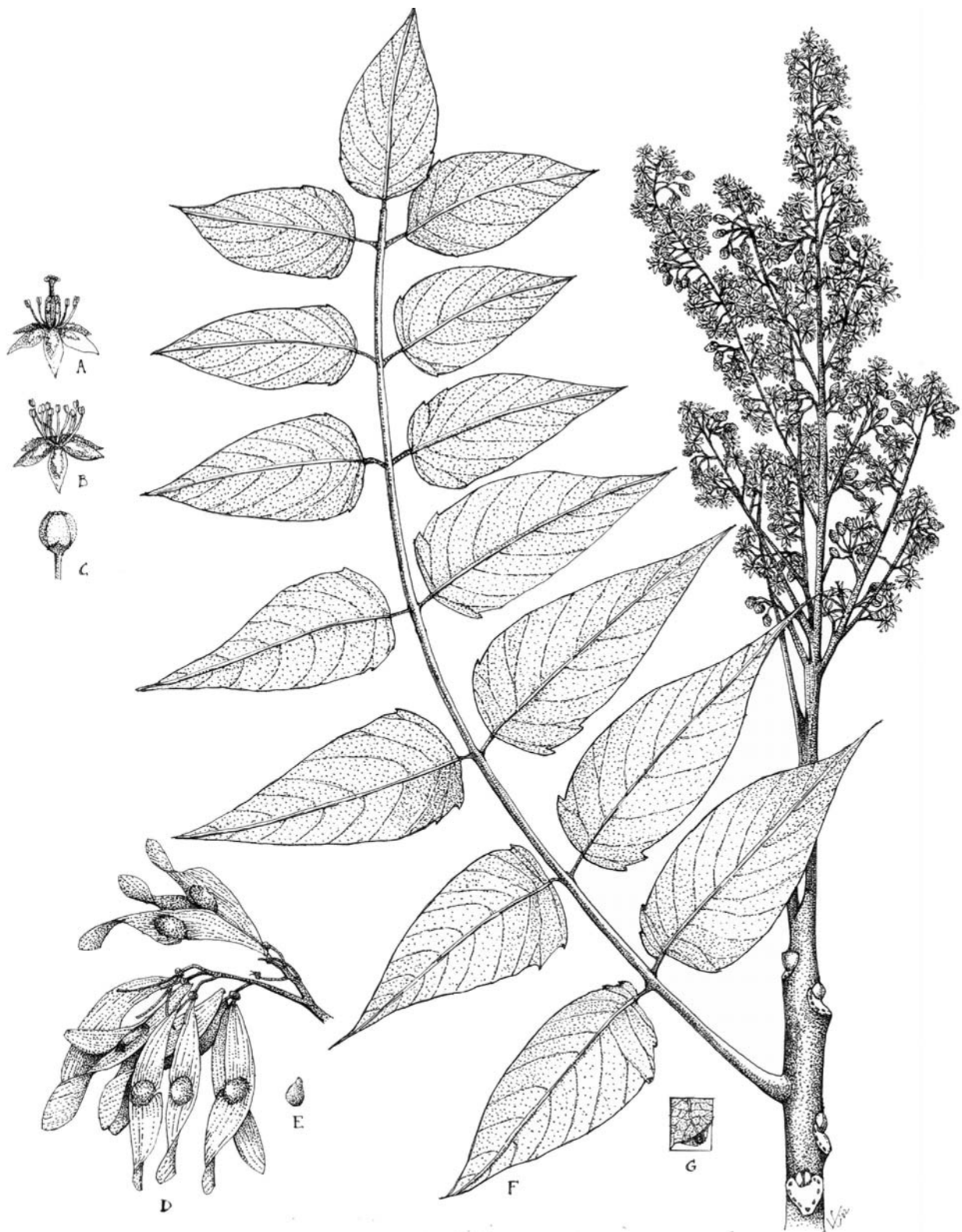


Fig 1.2 Illustration of *R. pseudoacacia*. A) front view of flower, B) side view of flower, C)) longitudinal section of flower showing diadelphous pistils, D) legumes, E) seed, F) leaflet, and G) stipules.



2.0 GREENHOUSE STUDY Analysis of intraspecific and interspecific interference between *Ailanthus altissima* and *Robinia pseudoacacia*

2.1 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 & 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 & Walker 1989), fire frequency and intensity (D'Antonio & Vitousek 1992), and recruitment of native species (Mooney & 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 & Vitousek 1992). Estimated extinction of native species due to biotic invasions is greater than that resulting from climate or atmospheric changes (D'Antonio & Vitousek 1992). Therefore, competition between invasive and native species is an important issue that merits attention.

This research focused on the invasive exotic *Ailanthus altissima* (Miller) Swingle (Simaroubaceae) and its interaction with the native *Robinia pseudoacacia* L. (Fabaceae). Numerous ecological traits are comparable between *A. altissima* and *R. pseudoacacia*. Both species establish in disturbed sites, have aggressive reproductive qualities, and exhibit similar growth habits. Thus, it is no surprise that these qualities place these two species on the list of the forty most invasive woody angiosperm species (Rejmánek & Richardson 1996). However, each of these tree species has different functional attributes that are critical to succession and ecosystem processes. *Ailanthus altissima* can potentially inhibit post-disturbance successional sites by creating a relatively toxic soil environment (Lawrence *et al.* 1991) and *R. pseudoacacia* promotes post-disturbance succession by enriching soil with nitrogen from nitrogen fixation (Boring & Swank 1984a). This difference is important because the functional characteristics of component species, rather than species richness, can have a large impact on ecosystem processes (Hooper & Vitousek 1997; Schwartz *et al.* 2000).

It is likely that interference occurs between these two species based on their similarities. The analysis of this interaction will reveal insight into important potential indirect effects on post-disturbance succession and larger ecosystem processes. The term interference was used in this study as a large category that includes

competition (removal of a resource by one organism), allelopathy (addition of an inhibitory compound to a plant's environment), or facilitation (Tinnin 1972; Harper 1977). Interference was used in this situation because the mechanisms of the plant interactions were unknown and difficult to determine (Wilson 1988).

The main goal of this study was to determine if there was interference between *A. altissima* and *R. pseudoacacia*, and if this interference favored *A. altissima* over *R. pseudoacacia*. The unifying hypotheses were: 1) Interspecific interference of *A. altissima* seedlings and *R. pseudoacacia* seedlings would be greater than intraspecific interference within either species and, 2) In the majority of the mixtures, *A. altissima* would have a greater performance compared to *R. pseudoacacia*. We used a combined additive and replacement design to generate a response plane 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 these two species, the specific questions we addressed (generated from Connolly *et al.* 2001) were: 1) Which species dominated (total biomass) at the time of harvest? and, 2) Was there an effect of one species on the other species' performance when comparing the total biomass and biomass allocation in mixtures to that in the monocultures over multiple densities? Biomass at the time of harvest was used as a measure of resource capture and, thus, interference between these two species. Total biomass is considered to be a good measure of plant interactions and competitive abilities (Gaudet & Keddy 1988). The general trend of root and shoot responses was also considered because allocation among plant growth compartments in the species mixtures compared to that in monocultures may indicate the location of most intense interference (Brouwer 1962; Chapin 1980).

2.2 Materials and Methods

2.21 Species Descriptions

Ailanthus altissima (Tree of Heaven) was introduced to the United States in 1784 (Hu 1979). Today, *A. altissima* is considered a “weed” tree because of its capabilities 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 from the female tree falls to the ground to

germinate in one location (Pan & Bassuk 1986), which is further enhanced when stump sprouts grow from the original stem of the tree and suckers originate from the roots (Illick & 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 *Ailanthus altissima* to adapt to a wide range of soils (Pan & Bassuk 1985). The roots of *A. altissima* are comparably longer, more extensive, less branched and wider spreading than other trees in similar urban environments (Pan & Bassuk 1986). There is also evidence that the roots and stems of *A. altissima* exude chemicals that can negatively affect nearby plants (Heisey 1990a; Heisey 1996). High amounts of chemicals produced by *A. altissima* are found in the young invading trees that likely aid in early establishment into the ecosystem. Older, well-established stands of *A. altissima* do not produce as much chemical compounds as do the younger ramets (Lawrence *et al.* 1991). 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 *Robinia pseudoacacia* L. (Black Locust). *Robinia pseudoacacia* is native to the Appalachian region of Eastern North America (Young & Young 1992). It is typically found in open disturbed areas such as roadsides, can tolerate a range of pH levels in the soil (Bossard *et al.* 2000), and has been planted on reclaimed surface mines (Zeleznik & Skousen 1996). It is an important species because it actively fixes nitrogen, which helps prepare the soil for incoming late successional species (Boring & Swank 1984b). Cumulative fixation of nitrogen by *R. pseudoacacia* replaces nitrogen lost following forest disturbances (Boring & Swank 1984a). Young locust stands have been observed to fix approximately 30 kg N ha⁻¹ year⁻¹ (Boring & Swank 1984a). This gradually aids in the replacement of black locust trees by trees typical of later successional stages (White *et al.* 1988; Dzwonko & Loster 1997), and enhances the growth of adjacent trees (Chapman 1935).

2.22 Experimental Design

Ailanthus altissima seeds were collected from a single tree in Giles County, VA in order to minimize genetic variability (Feret *et al.* 1974) during fall 2000. The seeds were spread out to dry and were not stratified

(Graves 1990). The wings of the samaras were removed and the pericarp was left intact. The seeds were placed on saturated blotting paper in closed petri dishes. These dishes were placed into a dark incubator with temperatures alternating diurnally from 30°C ($\pm 0.5^\circ\text{C}$, 16 hr) to 20°C ($\pm 0.5^\circ\text{C}$, 8 hr). *Ailanthus altissima* seeds germinated within 7 days.

Robinia pseudoacacia seeds were collected from several roadside trees in close proximity in Montgomery County, VA in 1999. These seeds were stratified for 60 days, soaked in a 10% bleach solution for several minutes, and mechanically scarified (Sadhu & Kaul 1989). The seeds were placed in vermiculite on a heating pad at 20° C until germination. Germination of *R. pseudoacacia* occurred within 4-7 days and was started two days after the *A. altissima* seeds were planted. Seedling germination was coordinated so that the initial sizes of seedlings of both species were comparable.

After germination, each seedling was transplanted to a 2.54 cm seedling cell with Metro Mix®. Greenhouse day: night temperatures and hours varied between 21-32°C : 32°F and 10h : 14h throughout the experiment. After germination and early establishment, seedlings were randomly planted in masonry sand in 5-gallon pots (approximately 34 cm in diameter) according to a numbered grid on the pot surface (Fig 2.1).

Each square in the grid was 6.35 cm² and the areas near the edges of the pot (gray areas) were excluded from planting (Fig 2.1). The seedlings were placed in the middle of the selected squares. Every pot had a random spatial arrangement of seedlings. Masonry sand was chosen as the potting mixture to aid in the collecting and cleaning of roots during the harvest. Cheesecloth was inserted into the drainage holes in the pots to minimize sand loss.

Mixtures consisted of various proportions of 1, 2, 3, 5, 6, 7, 10, and 14 plants (Fig 2.2). Total pot density did not exceed 14 plants. This experiment had combined aspects of a De Wit (1960) replacement and additive series. This design consisted of thirty-two different “treatments” (the different proportions and densities of species) that were replicated three times for a total of 96 pots in the experiment. For each species, there were a total of 336 seedlings. The three replications were randomly labeled A, B, and C when they were planted. Each pot name included the following information: replication, density of *A. altissima*, and density of

R. pseudoacacia (e.g., A 5:3 was a pot in replication A that consisted of 5 *A. altissima* plants and 3 *R. pseudoacacia* plants).

Sixty-four grams of Osmocote® – (15-9-12) 8-9 month release at 70°F were added to each pot as a low measure of nutrients according to Osmocote® suggestions. The fertilizer was evenly spread and pressed into the sand to minimize unequal accumulations during watering. After 91 days of growth, since *R. pseudoacacia* plants appeared to be lacking in nutrients (yellow leaves), 27 g of Osmocote® was added to each pot. This addition placed the total nutrient level at 91 g, which was a medium level of nutrients for plants according to the Osmocote® instructions.

Initially the pots were watered to field capacity once a day until a fungus attack on *A. altissima* increased seedling mortality, and the water regime was reduced to once a week. However, after 2 ½ months of growth in the greenhouse, the watering schedule was increased to a daily watering regime because of the increased temperature, sun exposure, and large plant sizes.

To minimize the effect of the spatial variation in greenhouse microclimate, the pots were rotated along the benches every other week (the row farthest north was moved to the south front of the table), and each pot was rotated 180° when moved. The first pot rotation did not occur until 41 days after planting.

The largest seedling mortality for both species occurred 34 days after planting. A questionable fungus attack (*Fusarium sp.*) was found on *A. altissima* that was remedied with a fungicide drench. The mortality of *R. pseudoacacia* tended to be a result of stunted growth due to the viability of the collected seeds. *Robinia pseudoacacia* was also the target of mites, thrips, and leaf margin damage. There is evidence that this species is susceptible to damping off in the greenhouse (USDA 1965), which was evident in some of the seedlings.

After 139 day (4 ½ months), the plants were harvested. Pots were haphazardly selected and harvested over 14 consecutive days. From each pot, the plants were collected, dried, and weighed. The tissues were dried in a forced air oven approximately 48 hours to constant weight. Above ground parts were separated into stems and leaves.

The following measurements were made for each seedling in the pots: number of leaves, number of branches, stem height (cm), stem basal diameter (cm), total leaf area (cm²), root dry weight (g), stem dry weight (g), and leaf dry weight (g). Presence or absence of nodules in *R. pseudoacacia* was also observed even though this was not expected, because of the addition of nutrients and the lack of inoculated plants. Sand around the roots was gently removed without water to minimize root loss. Each root was gradually separated from nearby roots and rinsed in a sieve to collect any significant root loss. Leaf area was measured with a LI-3100 Area Meter (LiCor Inc., Lincoln, Nebraska, USA). The leaves of *R. pseudoacacia* tended to wilt, leading to an underestimation of the leaf area. The leaves of *A. altissima* did not have the wilting tendency that was evident with *R. pseudoacacia*. Stem and root weight was measured within an enclosed digital scale (Mettler Toledo PG503 Delta Range) measuring to the nearest milligram. Leaf weight was measured on a larger scale (Mettler Toledo PG 5002 Delta Range) measuring to the nearest decigram.

2.23 Data Analysis

The results from the three replications were not significantly different and were therefore pooled for all further analyses. 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 interactions between *A. altissima* and *R. pseudoacacia*.

Multiple linear regression

A multiple linear regression of the reciprocal of biomass per plant for each species on the mixture densities for *A. altissima* and *R. pseudoacacia* was generated, a method commonly used to describe plant yield/density relationship (Shinozaki & Kira 1956; Willey & Heath 1969; Spitters 1983). The equations were:

$$1/(\text{biomass per plant (g) } A. \textit{altissima}) = B_0 + B_{AA} (D_{AA}) + B_{AARP} (D_{RP})$$

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

B_{AA} represents the intraspecific effect of *A. altissima* on itself, B_{AARP} indicates the interspecific effect of *R. pseudoacacia* on the biomass of *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 for each species. B_0 is the intercept and the reciprocal of the biomass of an isolated plant experiencing no competition (Spitters 1983).

From the slopes of the regression analysis, substitution rates, also known as “competition coefficients” (Firbank & Watkinson 1985), were calculated to measure the influence of each species on itself and on the other component species (Spitters 1983; Connolly 1987). This 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:

$$\begin{aligned} S_{AA} &= B_{AARP} / B_{AA} \\ S_{RP} &= B_{RPAA} / B_{RP} \end{aligned}$$

The responses of plant parts to the density of the two species were also included in the analysis. The log of the mean weight of plant parts (shoots, roots, etc.) was regressed on the log of the weight of the entire plant to show the linear relationship below (Kira *et al.* 1956). This follows Huxley’s law of allometry, which was used to analyze growth rates of organs (Gayon 2000).

$$\log w_p = \log k + b \log w$$

w_p represents the weight of the plant part per plant, w is the total biomass of the plant, $\log k$ is the intercept, and b 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 & Kira 1956):

$$\begin{aligned} 1/(\text{plant part (g) } A. \textit{altissima})^{1/h} &= B_0 + B_{AA}(D_{AA}) + B_{AARP}(D_{RP}) \\ 1/(\text{plant part (g) } R. \textit{pseudoacacia})^{1/h} &= B_0 + B_{RP}(D_{RP}) + B_{RPAA}(D_{AA}) \end{aligned}$$

Relative Yield Total (RYT)

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 & Van der Bergh 1965; Harper 1977; Snaydon 1991).

$$\text{Relative yield total (RYT)} = \frac{W_{AARP}}{W_{AA}} + \frac{W_{RPAA}}{W_{RP}}$$

W_{AA} and W_{RP} were the mean dry weights per pot (g) of *A. altissima* and *R. pseudoacacia*, respectively, in monoculture, and W_{AARP} and W_{RPAA} 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, above ground, and below ground responses at densities of 2, 6, 10, and 14 total plants were calculated. RYT was also calculated for stem volume per pot (cm³) but was not interpreted with regards to resource use since this definition has only been applied to total biomass per pot (Harper 1977).

Relative Crowding Coefficient (RCC)

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).

$$\text{Relative crowding coefficient (RCC)} = \frac{W_{AARP}}{W_{RPAA}} \div \frac{W_{AA}}{W_{RP}}$$

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.

2.3 Results

Data from all the combined pots showed that *R. pseudoacacia* had significantly larger mean total biomass (g), shoot biomass (g), stem biomass (g), leaf area (cm²), number of leaves, and stem volume (cm³) per seedling than did *A. altissima* (Table 2.1). The mean root and leaf biomass per seedling (g) for *A. altissima* and *R. pseudoacacia* were not significantly different.

For both species, an increase in density of the other species caused a significant decrease ($p < 0.05$) in the total biomass response per plant as seen by the positive slopes for the interspecific term in the regression (Table 2.2). Increases in density within a species were associated with a slight but not significant increase (negative slope) in the mean total biomass response per plant, an indication that intraspecific interactions were weak or absent. This could have also been an indication of facilitation instead of competition.

Plots of predicted values in three dimensions showed negative influences of interspecific interference (gray lines) and less evidence of intraspecific interference (monoculture and black lines) in both species (Fig 2.3A, 2.3B). The same can be seen when the predicted planes for both species are plotted together in the same diagram (Fig 2.3C).

The substitution rates for total biomass responses were greater than one (Table 2.2). The substitution rate (S_{RP}) for *R. pseudoacacia* was slightly greater than the substitution rate for *A. altissima* (S_{AA}).

Multiple regressions of above ground biomass, stem biomass, and below ground biomass indicated significant above ground interspecific interference for both species (Table 2.2). However, root and leaf biomass showed significant interspecific responses only for *A. altissima*.

Relative Yield Total (RYT) (De Wit 1960) for total biomass and root biomass per pot were the largest at a total pot density of 2 plants (Fig 2.4A, 2.5A). *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 6 and 10 plants (Fig 2.4B-C, 2.5B-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 (Fig 2.4D, 2.5D), the RYT of *A. altissima* and *R. pseudoacacia* was close to one. In the mixtures at this density, the relative total biomass per pot (g) of *R. pseudoacacia* was greater than that of *A. altissima* while the relative belowground biomass per pot (g) at this density was greater for *A. altissima*. RYT for total biomass, above ground biomass, and below ground biomass decreased towards one at high densities (Table 2.3). The replacement diagrams of aboveground biomass, stem biomass, and leaf biomass responses per pot were similar to the total biomass responses and are not shown. The replacement diagram for the stem volume per pot (Fig 2.6) indicated that *R. pseudoacacia* produced the greater relative stem yield per pot in the majority of the mixtures.

The Relative Crowding Coefficient (RCC) for total biomass and above ground biomass per pot was dominated by *A. altissima* at lower density levels and by *R. pseudoacacia* at the highest density level (Table 2.4). Below ground RCC responses consistently indicated a greater aggressiveness of *A. altissima* on *R. pseudoacacia* at all density levels.

2.4 Discussion

2.41 Intraspecific and Interspecific Interactions

In accordance with the main hypothesis, the interspecific interference between species had a greater negative effect than intraspecific interference upon multiple biomass responses for both species (Table 2.2). The interspecific slopes were similar for both species, indicating comparable biomass responses to the presence of the other component species (Table 2.2, Fig 2.3C). The substitution rates also showed that the interspecific interference played a larger role on total biomass production than intraspecific interference. One

R. pseudoacacia seedling “perceived” one *A. altissima* to be like 2.03 *R. pseudoacacia* plants, and one *A. altissima* “perceived” one *R. pseudoacacia* to be like 1.92 *A. altissima* plants.

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 (Table 2.3). Very likely, the two species were 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 & Watkinson 1990).

On the other hand, RYT values greater than one, at low pot densities, indicated that the two species were not fully sharing or competing for the same resources (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, although this was a very slight response for *R. pseudoacacia* (Fig 2.4A). Overall, *A. altissima* was the better interspecific competitor at the majority of pot densities, yet *R. pseudoacacia* had a larger competitive advantage at the highest pot density (Fig 2.4D, Table 2.4). It is also evident that *R. pseudoacacia* had the overall greater advantage by looking at its significantly larger mean responses per seedling (Table 2.1).

2.42 Above ground interference

Analysis of the yields of plant parts revealed different allocation patterns and different competitive attributes for *A. altissima* and *R. pseudoacacia*. Both the mean above ground biomass per plant and the mean stem biomass per plant for both species were negatively affected by the presence of the other species yet interspecific interference for mean leaf biomass per plant was only significant for *A. altissima* (Table 2.2).

In most mixtures of above ground biomass, *A. altissima* performed better in mixture than did *R. pseudoacacia* (Table 2.4). Having greater above ground biomass, like *A. altissima* did in the mixtures relative to its monocultures, is a good indicator of competitive ability (Gaudet & Keddy 1988). A competitive above ground advantage is important since above ground interactions are intense as each individual attempts to obtain limiting light resources (Weiner 1990).

However, not all components of above ground biomass were dominated by *A. altissima*. For instance, mean leaf biomass per plant of *A. altissima* was negatively affected by interspecific interference (Table 2.2) whereas the mean leaf biomass of *R. pseudoacacia* was not. The leaf biomass of *A. altissima* was more closely related to the number of leaves it produced compared to that of *R. pseudoacacia* (Table 2.1). An individual leaf of *A. altissima* was thicker and heavier than one leaf of *R. pseudoacacia* by looking at the relationship of leaf number and leaf biomass (Table 2.1). There was also less variation around the number of leaves and leaf area produced by *A. altissima* compared to *R. pseudoacacia* (Table 2.1) due to *A. altissima*'s limited stem height, lack of branches, and overall less leaf plasticity. Thus, a negative effect on leaf production led to a greater negative effect on the leaf biomass response for *A. altissima* than for *R. pseudoacacia* (Table 2.2). Leaf number and leaf biomass were not strongly correlated in *R. pseudoacacia* and there was greater variability in the number of leaves and leaf area per seedling than for *A. altissima* (Table 2.1).

Robinia pseudoacacia produced stem volumes per pot in the 50:50 mixtures that were consistently greater than those of *A. altissima* (Fig 2.6). The overall mean stem volume per seedling of *R. pseudoacacia* was twelve times the mean stem volume per seedling of *A. altissima* (Table 2.1). The vertical stem growth of several *R. pseudoacacia* individuals was also faster than *A. altissima* individuals early in the experiment (Call, personal observation). Similarly, 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. These tall dominant *R. pseudoacacia* individuals with significantly larger leaf area, more leaves, greater stem volume (Table 2.1), and multiple branching likely reduced multiple biomass traits of *A. altissima* by increasing competition for light (Table 2.2). 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 & Weiner 1989).

These above ground traits of *R. pseudoacacia* enabled it to have an above ground advantage over *A. altissima* at high-density levels (Table 2.4) where asymmetric competition can be intense (Weiner 1985). The coefficient of variation of the mean total biomass responses per seedling of *R. pseudoacacia* increased with total

density whereas no increase was found in *A. altissima* (Fig 2.7). An increase in size variability of seedlings with increasing density can suggest asymmetric or one-sided interactions, where few individuals obtain a disproportionate amount of resources compared to other individuals in the mixture (Weiner 1990). Increased total density, and therefore increased competition, can exaggerate these above ground size inequalities (Weiner 1985).

The observed size variability and size inequalities of *R. pseudoacacia* were likely due to multiple factors. Since the seeds were collected from several individual trees, there was potentially more genetic variation among the seedlings compared to the half-sib population used for *A. altissima*. In pots with an increasing proportion of *R. pseudoacacia* individuals, there was a greater probability of having an individual seedling with a particular genetic advantage for rapid and dominant biomass production. Another reason for several large *R. pseudoacacia* plants resulted from random root nodulation. Three percent of all *R. pseudoacacia* seedlings in the experiment had root nodules and several of these plants produced unexpectedly large individuals, particularly in mixtures that had a greater proportion of *A. altissima* than *R. pseudoacacia*. The nodulation of *R. pseudoacacia* was likely a result of nutrient limitation at high mixture density. This suggests that when nodulated, *R. pseudoacacia* might be a better interspecific competitor with *A. altissima*.

2.43 Below ground interference

The below ground biomass of *A. altissima* was reduced by interspecific interference (Table 2.2). 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). Thus, it is likely that the presence of *R. pseudoacacia*, particularly the large dominant individuals discussed earlier, with extensive height, branching, and leaf area could have inhibited root production of *A. altissima*. The negative interspecific effect that *R. pseudoacacia* had upon the below ground response of *A. altissima* could have also been related to water use patterns. *Ailanthus altissima* likely demands much water due to its large leaf area and light wooded stem (Table 2.1) whereas *R. pseudoacacia* has been shown to have high conductance rates (Mebratu & Hanover 1991). Thus, below ground competition for water was possibly intense.

However, compared to its monoculture, the below ground performance of *A. altissima* in mixture was greater than that of *R. pseudoacacia*. RCC for mean root biomass per pot (Table 2.4) revealed that *A. altissima* had the competitive below ground advantage in the mixtures. Below ground competitive ability is an important plant trait because competition for below ground resources can negatively affect plant growth and establishment (Donald 1958; Casper & Jackson 1997), which can have a greater negative effect on mean plant biomass compared to only above ground competition (Wilson 1988; Weiner 1986). Below ground interactions can be intense when roots overlap and increase in abundance. Since *A. altissima* consistently generated a larger below ground biomass, it was likely a strong competitor for *R. pseudoacacia* since root biomass is related to competitive intensity (Cahill & Casper 2000).

The apparent below ground advantage of *A. altissima* in this experiment (Table 2.4) 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 with extensive lateral roots to aid in establishment at a site (Davies 1943-44). This was evident during the harvest when the roots of *A. altissima* were extensively spread throughout the pot, sometimes penetrating into the root mass of *R. pseudoacacia*. This suggested that *A. altissima* has aggressive roots that are nutrient demanding and can rapidly obtain resources, an attribute for a strong competitor for resources (Grime 1977). Due to its larger relative root biomass, *A. altissima* had a greater advantage than *R. pseudoacacia*, because it was also able to obtain more of the below ground space in the pots. In an experimental pot design, space can be considered a limited resource for both species and can negatively affect the performance of plants (McConnaughay & Bazzaz 1991).

The exudation of inhibitory compounds from the roots of *A. altissima* might have aided in its apparent below ground superiority (Heisey 1990a, 1990b). Plants that release inhibitory compounds have been shown to reduce root elongation of neighboring plants and thus affect plant distributions (Mahall & Callaway 1992). Cahill and Casper (2000) suggested that allelopathic roots could potentially prevent a neighbor's roots from obtaining resources, thus creating an asymmetric situation, with one species obtaining more than its proportional share of resources. In another competition study, the weedy and aggressive *Agropyron repens* (quackgrass) was grown with common crop legumes (Weston & Putnam 1985). The

allelopathic qualities of *A. repens* inhibited the number of nodules formed on the legumes. Although our study did not look at the effect of *A. altissima* on nodule activity in *R. pseudoacacia*, our results suggest that chemical exudates from *A. altissima* roots could inhibit root growth and nodulation of neighboring *R. pseudoacacia* plants. This inhibition would favor the growth of *A. altissima* over a longer time period and potentially result in a decrease in nitrogen accretion in post-disturbance sites.

However, one must be cautious of using below ground and above ground biomass responses as an indicator of mechanisms of interference. Root and shoot responses can fluctuate under different conditions (Brouwer 1962; Chapin 1980) and can reflect both the optimal partitioning of resources (Bloom *et al.* 1985) and the ontogenetic morphology of a particular species (Aerts *et al.* 1991; Gedroc *et al.* 1996). Moreover, above ground and below ground parts of plants are interrelated and negative effects on the aboveground organs can reduce belowground growth and alter nutrient uptake (Massimino *et al.* 1981; Caldwell *et al.* 1987). Also, the combination of both belowground competition and above ground competition is more intense than either by itself (Donald 1958; Weiner 1986).

2.44 *Analysis of experimental design*

Recent articles have criticized traditional replacement and additive designs used in greenhouse studies to assess interspecific competition (Jolliffe 2000; Connolly *et al.* 2001). The experimental design used in this study has been referred to as a full additive series, a bivariate factorial design, or a response surface design (Spitters 1983; Snaydon 1991; Connolly *et al.* 2001) and avoids most of the faults inherent in the replacement and simple additive series. The response surface generated from this experiment had the advantage of describing the yields of the plants over a range of frequencies and densities.

Because of the low R^2 values (e.g., 0.09, 0.14), it is clear that this regression analysis did not explain much of the variation in the experiment regarding the interactions between these two species, particularly for *R. pseudoacacia*.

Much of the observed variation resulted from pot location on the greenhouse bench, pot edge effects, genetics of the seed lot, unequal access to fertilizer, different degrees of herbivory, and unexpected

root nodulation in some *R. pseudoacacia* plants. Due to limited space on the bench and the rapid growth of the plants, there were unavoidable interactions between plants in neighboring pots. Also, final seedling mortality at the time of harvest (13% for *R. pseudoacacia* and 1% for *A. altissima*) caused the densities at the harvest to slightly deviate from the planted densities, thus creating errors around the means per plant when regressed on density (Firbank & Watkinson 1990).

The indices have faults for a number of reasons. The replacement series were compared to a selected monoculture that did not have a constant yield across different densities, did not include a factor for the spatial arrangement of the component species, were density dependent, and were unable to be statistically interpreted (Connolly 1986; Connolly 1988; Firbank & Watkinson 1990; Snaydon 1991). The indices showed that *A. altissima* was the “winner” in mixture due to the smaller difference between its yield in mixture relative to its yield in monoculture. *Robinia pseudoacacia* did not appear to be the “winner” in the indices because the large variation around its mean responses that led to a highly variable response in its mixtures and monoculture. Similarly, overall mean values per seedling indicated that *R. pseudoacacia* was the greater competitor in the experiment (Table 2.1). Moreover, when using any of these analyses, there is some loss of detail compared to the original data.

The interpretation of RYT assumed that resource exploitation was the only competitive mechanism that occurred and disregarded other possible interactions such as allelopathy or facilitation (Jolliffe 2000). Also, the species with the greater relative yield in the replacement series might not have been the better competitor. For example, the “losing” species, although its relative yield was negatively affected by the other species in the mixture, could have had an absolute yield in mixture that outperformed its competitor (Connolly 1997). RYT calculations can also be misleading because in the absence of interspecific competition, RYT can vary between one or two, depending on the density of the monoculture (Snaydon & Satorre 1989).

It is also important to note that due to the physical limitations of replicating this experiment, measurements had to be made on both species within one pot, thus disregarding statistical independence of errors. This experiment also lacks the reality of a natural situation in which herbivory, spatial components, a

reproductive generation, and a longer temporal scale could be important factors affecting biomass production in plants. For example, the spatial density of the individual plants in this experiment was greater than natural population densities and the limited pot size potentially inhibited the performance of the individual plants (McConnaughay & Bazzaz 1991). Similarly, the level of nitrogen in the pots provided to the plants was approximately three times the amount found in the natural environment (Boring & Swank 1984b), thus providing an advantage to the nutrient demanding *A. altissima*. In the experiment, *R. pseudoacacia* had an unnatural disadvantage since it was not nodulated like it is during natural field conditions. Also, the results from this experiment cannot be directly extrapolated to field conditions because of the unnatural even-aged population within the pots, compared to the size and age variability found in seedlings in the field (Goldberg & Werner 1983). Similarly, the commonly occurring locust herbivores, the locust stem borer, *Megacyllene robiniae* Forst. (Chittenden 1904; Boring & Swank 1984b; USDA 1999), or the leaf miner, *Odontata dorsalis* Thunb. (Chittenden 1904; USDA 1999) were not considered. These herbivores can negatively affect growth characteristics of *R. pseudoacacia*, (Echaves *et al.* 1998), reducing its competitive abilities against *A. altissima*.

2.45 Summary

Despite faults inherent in plant greenhouse competition studies, this analysis showed that the presence of both *A. altissima* and *R. pseudoacacia* negatively affected the performance of the other and could potentially lead to the competitive exclusion of one of the species over time, depending on the particular conditions. However, this is difficult to predict, since competition between similar species does not always lead to competitive exclusion (Ågren & Fagerström 1984). Due to the randomness inherent in seed dispersal, germination, establishment, and timing of disturbance in natural conditions, these two species might enter into the community at different ages and times and be able to coexist (Ågren & Fagerström 1984; Bazzaz 1990).

Each species exhibited strong competitive attributes enabling each to occasionally dominate in the mixtures. 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 & Tilman 1993). *Ailanthus altissima* could have

an advantage over *R. pseudoacacia* by becoming established and dominating 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).

However, since *A. altissima* was a comparable competitor to *R. pseudoacacia* in this experiment, it is likely that with increasing propagule pressure and increased disturbances in the natural environment (Lonsdale 1999), *A. altissima* could become frequently established in habitats that are occupied by *R. pseudoacacia* and play a role in native species displacement. Studies of how these two species are naturally dispersed and associated in the field under different degrees of disturbances (Chapter 3.0) 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* negatively interact with each other, suggesting possible competitive interactions, although the mechanisms are unresolved. Further studies should examine the specific interactions between root nodulation of *R. pseudoacacia* and interactions with *A. altissima* since this study indicated a great positive benefit for *R. pseudoacacia* when nodulated.

Table 2.1. Mean responses per seedling for each species; data pooled across all pots (n=336 per species).

Response variable	Species	Mean *	Standard Dev
TOTAL BIOMASS (g)	<i>A. altissima</i>	15.34 a	20.00
	<i>R. pseudoacacia</i>	20.27 b	37.91
ROOT BIOMASS (g)	<i>A. altissima</i>	2.83 a	3.94
	<i>R. pseudoacacia</i>	2.63 a	5.56
SHOOT BIOMASS (g)	<i>A. altissima</i>	12.52 a	16.42
	<i>R. pseudoacacia</i>	17.66 b	32.65
LEAF BIOMASS (g)	<i>A. altissima</i>	8.74 a	11.32
	<i>R. pseudoacacia</i>	9.15 a	16.77
STEM BIOMASS (g)	<i>A. altissima</i>	3.78 a	5.29
	<i>R. pseudoacacia</i>	8.49 b	16.31
LEAF AREA (cm ²)	<i>A. altissima</i>	2483.12 a	2871.99
	<i>R. pseudoacacia</i>	3350.75 b	5545.40
NUMBER of LEAVES	<i>A. altissima</i>	7.98 a	3.34
	<i>R. pseudoacacia</i>	38.82 b	54.76
STEM VOLUME (cm ³)	<i>A. altissima</i>	24.68 a	36.23
	<i>R. pseudoacacia</i>	296.17 b	3343.04

* Means for each response followed by the same letter are not significantly different at the $\alpha=0.05$ level using a student's t-test.

Table 2.2. 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 for each species are included for total biomass responses. Means with SD greater than 1.0 were excluded. Equations for the regressions are included in the text.

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

Table 2.3. Relative Yield Total (RYT) of the mean relative yield for total biomass (g), aboveground (g), and belowground (g) responses per pot for the two species with increasing total density. The density of each species in the mixture are indicated in parentheses, with the density of *A. altissima* listed first.

Total density	Total biomass (g) per pot	Above ground biomass (g) per pot	Below ground biomass (g) per pot
2 (1:1)	2.47	2.27	3.77
6 (1:5)	1.37	1.23	2.64
6 (3:3)	1.02	0.99	1.20
6 (5:1)	1.20	1.14	1.67
10 (3:7)	0.96	0.95	1.01
10 (5:5)	1.55	1.57	1.53
10 (7:3)	1.33	1.27	1.90
14 (7:7)	1.04	1.02	1.14

Table 2.4. Mean Relative Crowding Coefficient (RCC) of the biomass responses of *A. altissima* against *R. pseudoacacia*. RCC values for mean aboveground, belowground, 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 density	Total biomass (g) per pot	Above ground biomass (g) per pot	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

Fig 2.1. Seedling planting arrangement. Seedlings were randomly placed into the numbered squares assigned from selecting a numbered piece of paper from a pool.

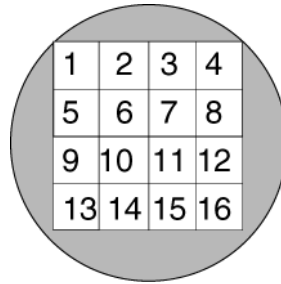


Fig 2.2 Greenhouse Experimental Design. Full additive design for the greenhouse experiment. Each square represents a treatment (n=32). The density (number) of *R. pseudoacacia* and *A. altissima* seedlings in each pot are indicated (n = 336 per species).

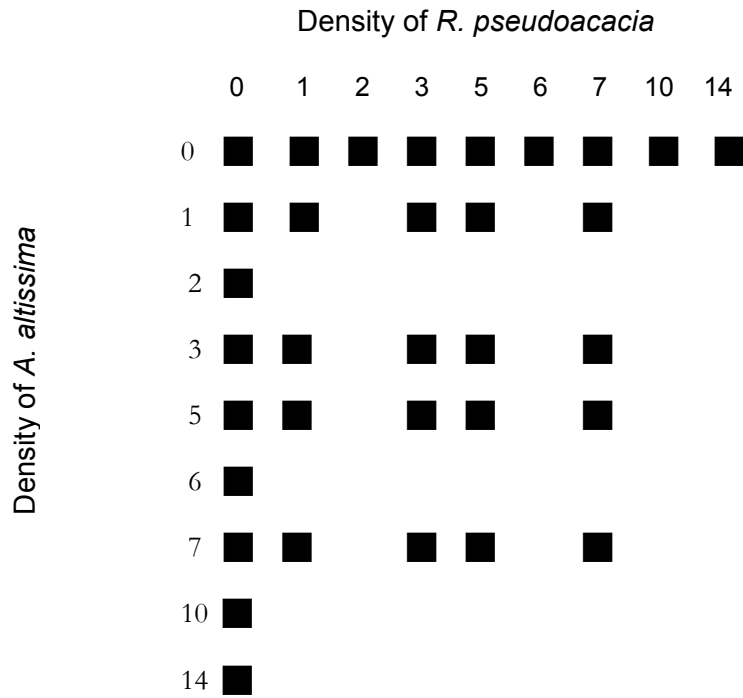
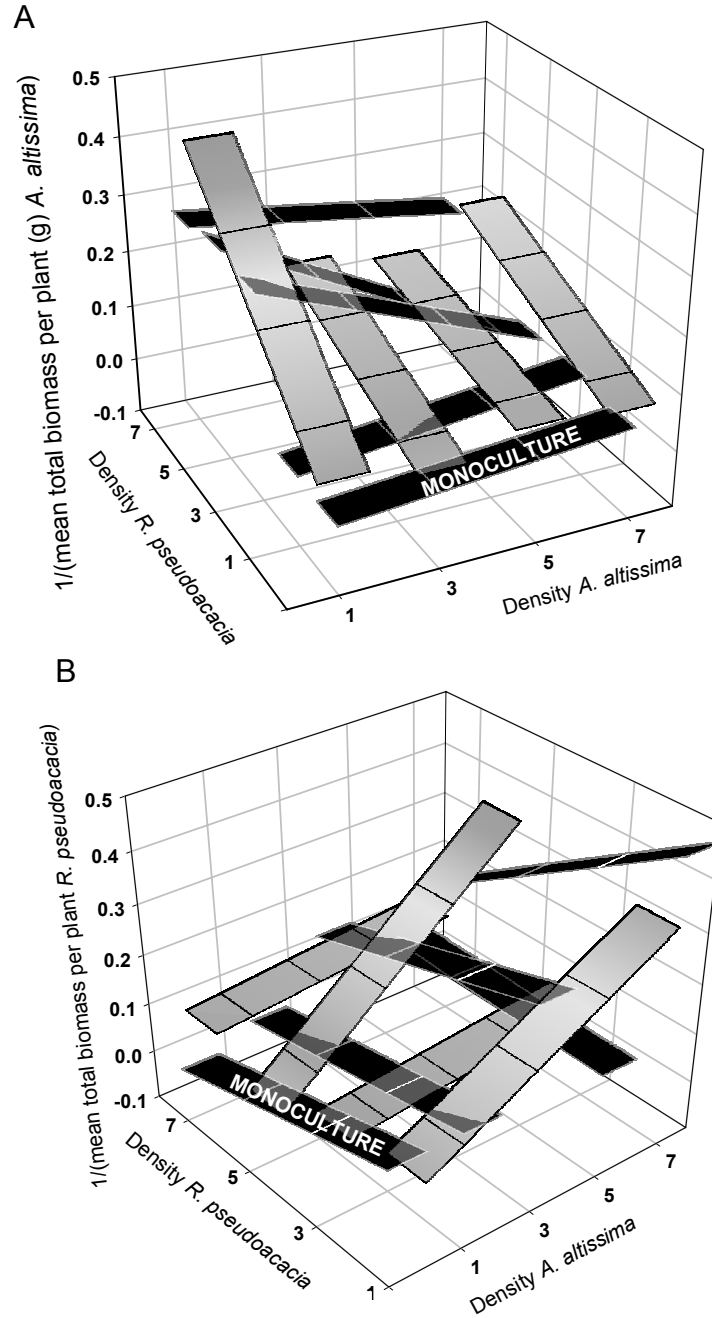


Fig 2.3. Reciprocal simple linear regression “lines” for the interspecific (gray lines) and intraspecific (black lines) additive series in the experiment for the reciprocal mean total biomass responses (g) per plant for (A) *A. altissima* and (B) *R. pseudoacacia*. Each “line” consists of the mean of the three replications. C) The predicted plane for both species (*R. pseudoacacia* = light gray plane, *A. altissima* = dark gray plane) generated from the regression line for all densities and frequencies.



C

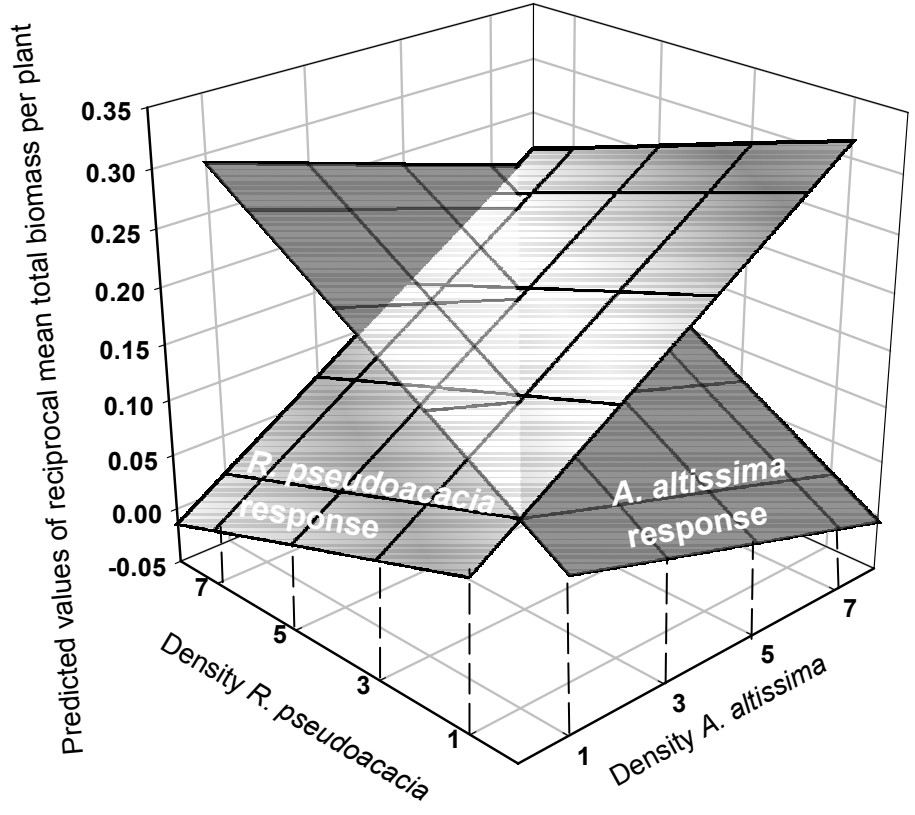


Fig 2.4. Replacement diagrams indicating the mean relative yield total biomass (g) per pot for *A. altissima* (closed circles), *R. pseudoacacia* (open circles), and Relative Yield Total (long dashed lines) at different constant densities and proportions of species. A) Total density of 2 plants, B) Total density of 6 plants, C) Total density of 10 plants, and D) Total density of 14 plants. The numerator in the ratios indicates the density of *A. altissima* and the denominator indicates the density of *R. pseudoacacia*.

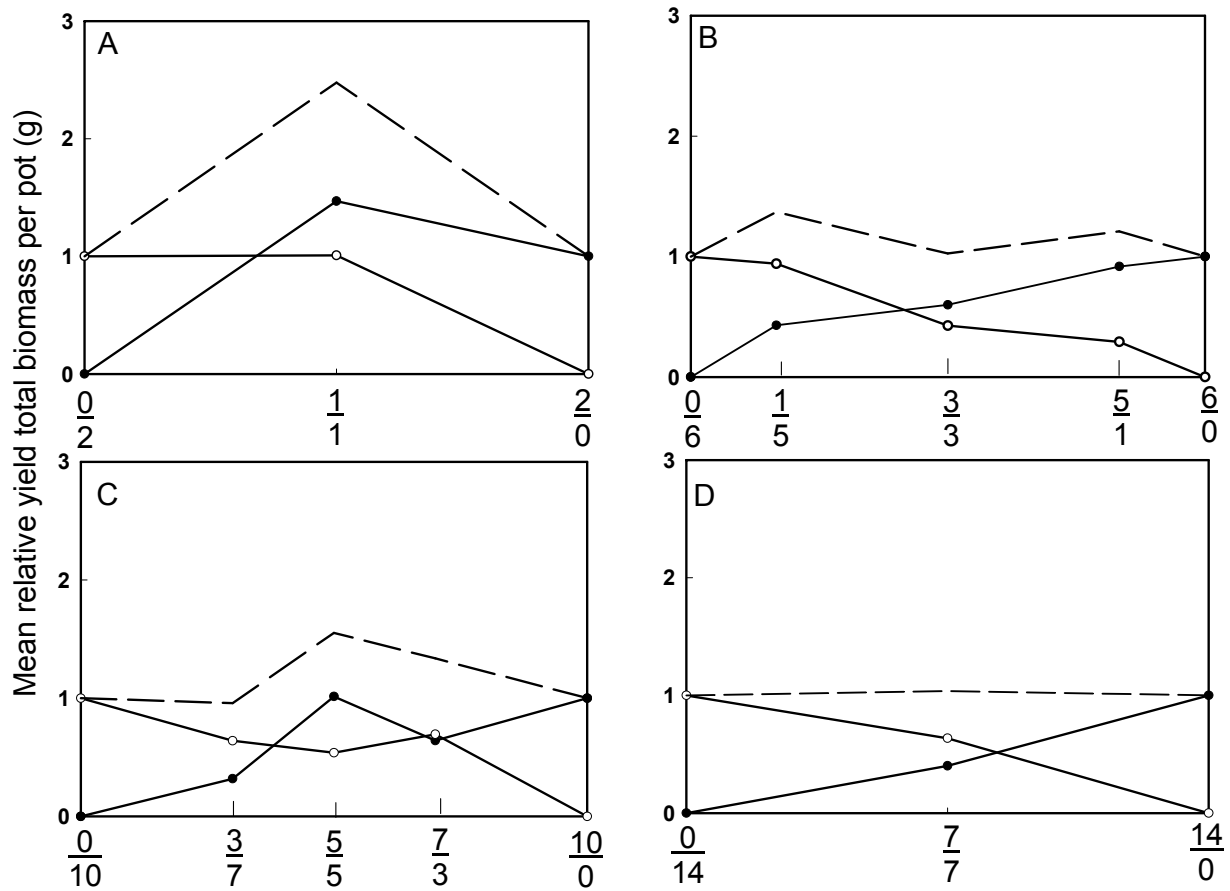


Fig 2.5. Replacement diagrams indicating the mean relative yield below ground biomass (g) per pot for *A. altissima* (closed circles), *R. pseudoacacia* (open circles), and Relative Yield Total (long dashed lines) at different constant densities and proportions of species. A) Total density of 2 plants, B) Total density of 6 plants, C) Total density of 10 plants, and D) Total density of 14 plants. The numerator in the ratios indicates the density of *A. altissima* and the denominator indicates the density of *R. pseudoacacia*.

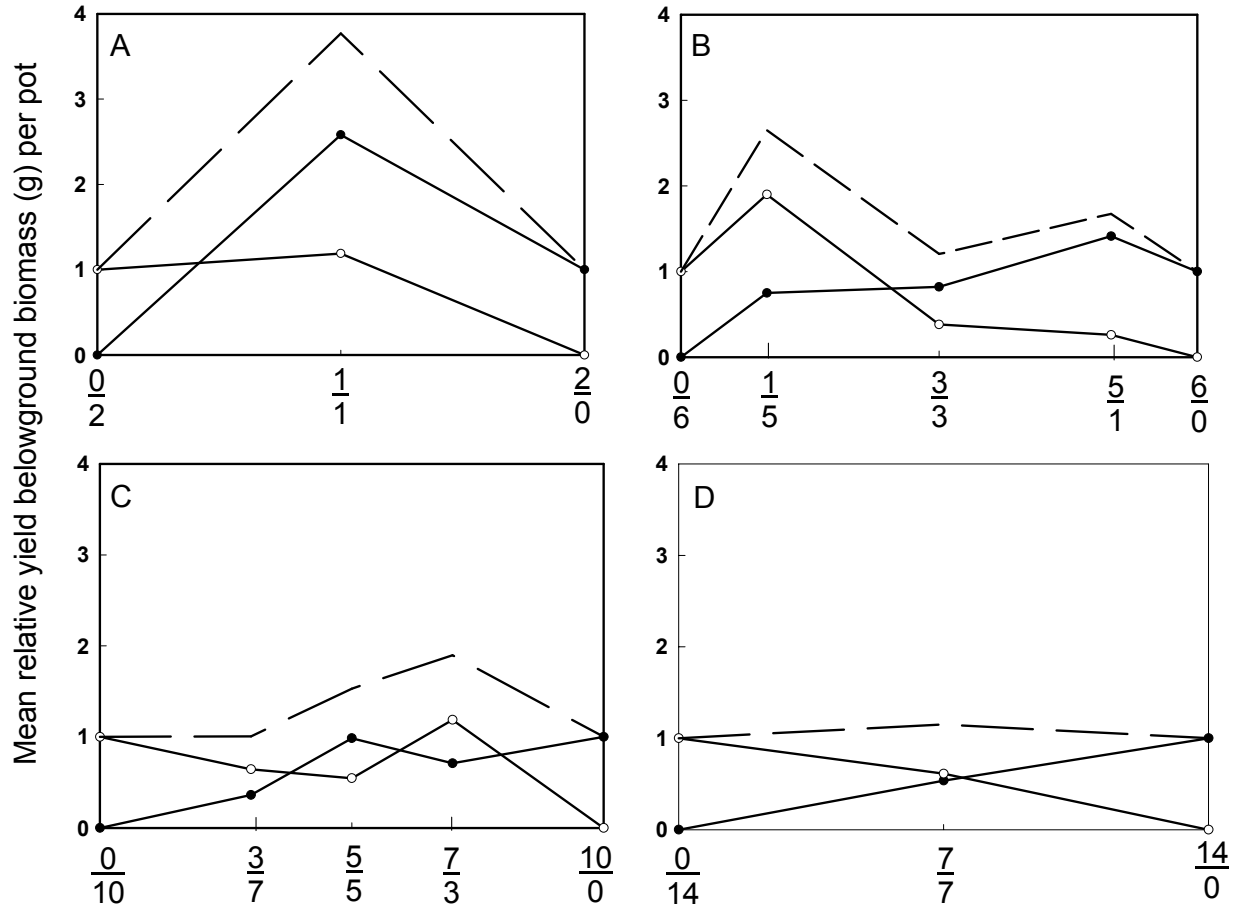


Fig 2.6. Replacement diagrams indicating the mean relative yield stem volume (cm^3) per pot for *A. altissima* (closed circles), *R. pseudoacacia* (open circles), and Relative Yield Total (long dashed lines) at different constant densities and proportions of species. A) Total density of 2 plants, B) Total density of 6 plants, C) Total density of 10 plants, and D) Total density of 14 plants. The numerator in the ratios indicates the density of *A. altissima* and the denominator indicates the density of *R. pseudoacacia*.

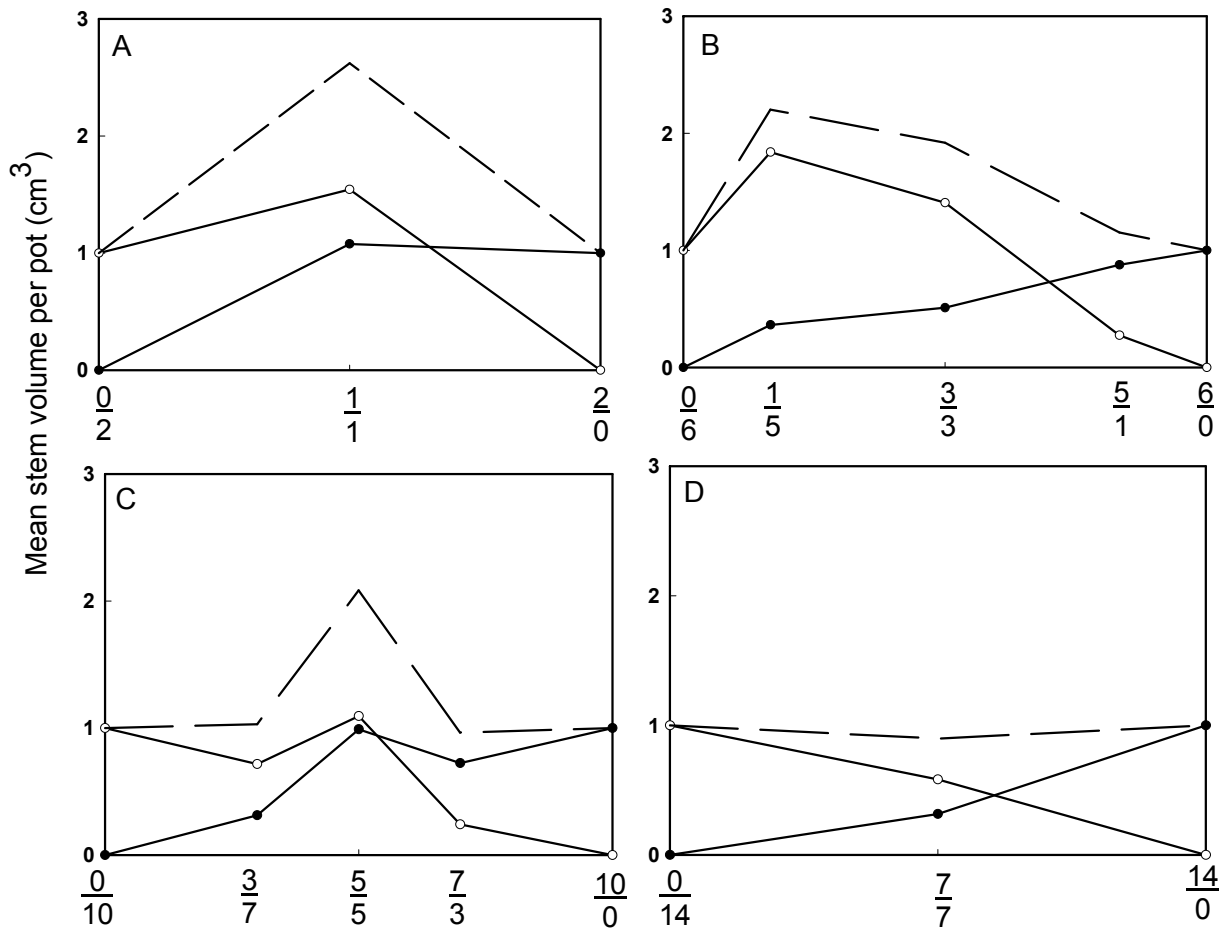
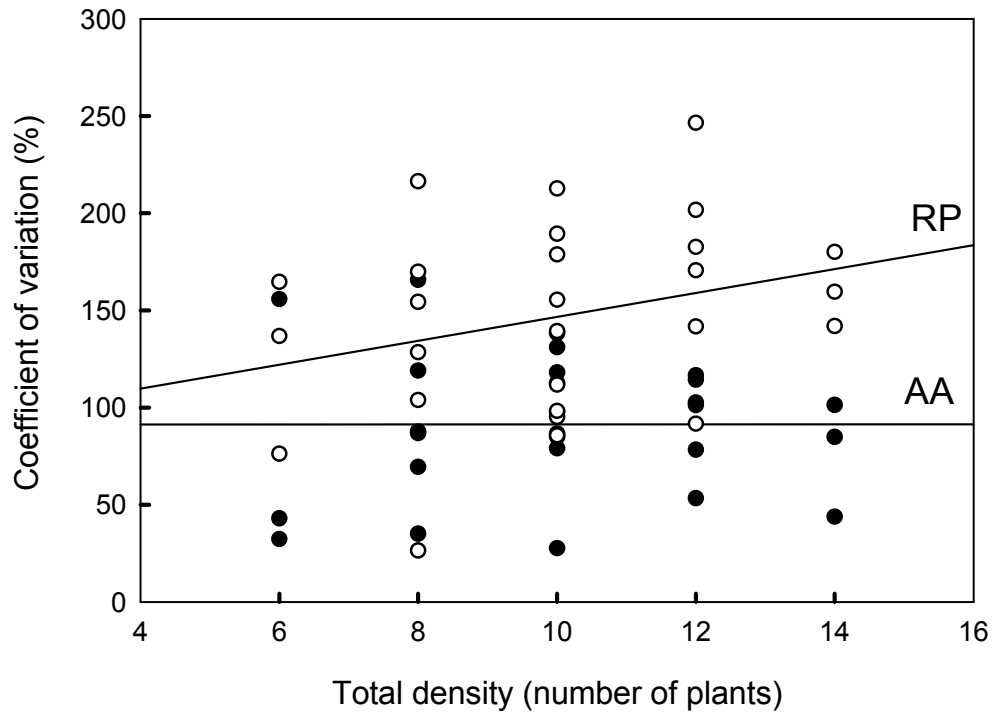


Fig 2.7. The coefficient of variation (%) for total biomass response (g) per seedling at increasing total pot density. *A. altissima* is represented by the closed circles (●) and *R. pseudoacacia* is represented by the open circles (○). This analysis only includes the 1:1 mixtures.



3.0 FIELD STUDY - Analysis of spatial point patterns of *Ailanthus altissima* and *Robinia pseudoacacia*

3.1 Introduction

Today, as the landscape continues to be altered by human influences, frequent invasions of exotic species have impacted and altered plant community processes (D'Antonio & Vitousek 1992). Invasive exotic plants can have competitive attributes that are not prevalent in the invaded community, which can result in dominance over native plant species (Callaway & Aschehoug 2000). Also, invasive species have been shown to compete with native species and negatively affect their recruitment (Mooney & Drake 1989), leading to a homogenized ecosystem and a decrease in regional diversity (D'Antonio & Vitousek 1992). Moreover, invasive exotic species can affect the fitness of native plants (Gould & Gorchov 2000) and can alter basic ecosystem processes (Vitousek & Walker 1989; D'Antonio & Vitousek 1992).

Plants most likely to compete with each other are those that occur in the same seral stages of succession and require the same habitat conditions. Numerous ecological traits are comparable between the invasive exotic *Ailanthus altissima* (Miller) Swingle and the native *Robinia pseudoacacia* L., two species that can be found in early successional seral stages of the eastern deciduous forest and in other disturbed areas, ranging from old-fields, roadsides, and forest edges. Each species has aggressive reproductive qualities (heavy seed set and vegetative reproduction) and similar growth traits. However, each of these tree species has a different functional attribute that has an important bearing on succession and ecosystem processes; allelopathic compounds emitted from *A. altissima* (Heisey 1990), and nitrogen fixation in *R. pseudoacacia* (Boring & Swank 1984a). Invasive species that produce allelopathic compounds not only have been shown to affect other nearby organisms, but also to alter key ecosystem processes and the structure of the plant community (Wardle *et al.* 1998). *Robinia pseudoacacia* adds advantageous fixed nitrogen to the soil to aid in the establishment of replacement species and stimulates growth of nearby species (Chapman 1935). Other studies have shown that the functional characteristics of the component species, rather than species richness in a community, regulate ecosystem processes such as nutrient cycling (Hooper & Vitousek 1997; Schwartz *et al.* 2000). Therefore, negative influences of *A. altissima* on *R. pseudoacacia* could have significant long-term effects on succession in eastern deciduous forests.

Although it is difficult to analyze competition between species in the natural environment and to explain the mechanisms of the interactions, the observed spatial pattern, consisting of the spatial distribution of a species and the spatial association between different species, can provide a basis for generating hypotheses about underlying processes. Spatial dispersion of an individual species (intraspecific interaction) ranges from being clumped, random, to regular depending on strength of the intraspecific interactions, reproductive traits (clonal reproduction or seed dispersal), and the environmental conditions (Pielou 1960, Whittaker 1975). Spatial association between two species (interspecific interaction) can range from positive, independent, to negative associations. These associations can be positive when species are dependently linked to each other or if they both respond to the environment in similar ways (Whittaker 1975). On the other hand, negative associations can imply that one species is excluding the other or that each species responds to the environment differently.

In order to examine if there was evidence of negative interactions between *A. altissima* and *R. pseudoacacia*, the spatial patterns of these two species was evaluated in early post disturbance (logging) sites. Measurements of spatial dispersion for each species and spatial association between *A. altissima* and *R. pseudoacacia* were used to evaluate two hypotheses: 1) Each individual species would have a clumped spatial distribution, due to their reproductive characteristics (vegetative reproduction) and to weak intraspecific interactions, and 2) The two species would have a negative spatial association with each other, indicating that one species was competitively excluding the other. Negative interspecific interactions could be due to many interactions such as the release of inhibitory compounds from *A. altissima*. Inhibitory compounds can alter the biomass of neighboring plants (Mahall and Callaway, 1992; Callaway and Aschehoug, 2000) and can potentially affect the structure and functioning of the plant community (Wardle *et al.* 1998).

3.20 Materials and Methods

3.21 *Species description*

Ailanthus altissima (Tree of Heaven) in the Simaroubaceae (Quassia Family) was introduced into the United State in 1784 (Davies 1942). As early as 1888, the invasive *A. altissima* was recorded to have spread through Virginia and neighboring states (Curtiss 1888). Today, *A. altissima* is considered a “weed” tree because of its rapid growth and efficient production of thin papery samaras, stump sprouts, and root suckers (Brizicky 1962). Allelochemicals produced in relatively large amounts by young invading *A. altissima* aid initial establishment into an ecosystem (Lawrence *et al.* 1991). The allelopathic qualities and clonal reproduction of *A. altissima* enable this species to create dense stands that dominate an area and curb growth of other plant species (Mergen 1959).

Robinia pseudoacacia (Black Locust) in the Fabaceae (Pea Family) is native to the Appalachian region of Eastern North America (Young & Young 1992). The tree has been cultivated and used frequently for its valued resistant wood, fragrant flowers, nitrogen-fixing root nodules, and ability to grow quickly (Young & Young 1992). Like *A. altissima*, it produces numerous seeds and root sprouts. It is considered an opportunistic species that aggressively enters into a disturbed area and grows comparatively faster than other trees for 10-20 years (Boring & Swank 1984b; Elliot *et al.* 1997). Cumulative nitrogen fixation by *R. pseudoacacia* not only enhances growth of adjacent trees (Chapman 1935), but also replaces nitrogen lost following disturbances (Boring & Swank 1984a), facilitating the replacement of *R. pseudoacacia* by later successional species (White *et al.* 1988; Dzwonko & Loster 1997).

3.22 *Study site*

The study sites were located in the Jefferson National Forest Blacksburg Ranger District near Craig Creek north of Blacksburg (Longitude = 37° 17' 30"; Latitude = 80° 27' 30"). These sites were established for a long-term investigation of the effects of different logging treatments on forest development. See (Wender 2000) or (Hood 2001) for more specific details regarding these sites. The sites are typical of low elevation Appalachian oak-hardwood forests that were heavily logged in the early 20th century and minimally

disturbed since. Each site consists of seven 2-ha treatment plots with no buffers between treatments. The applied treatments were control, understory control, group selection, leave tree, high-leave shelter wood, low-leave shelter wood and clear-cut. The treatment sites were established in two parallel rows. These particular treatments were applied to Blacksburg site one (BB1) November 1994-March 1995 and to Blacksburg site two (BB2) from November 1995-June 1996. Therefore, at the time of our measurement in 2001, it was seven and six years post-logging for BB1 and BB2, respectively.

These two Blacksburg sites were chosen because they both contained the same replicated treatments and both *A. altissima* and *R. pseudoacacia* were observed in the selected treatment plots. Moreover, clear-cut, low-leave shelter wood and high-leave shelter wood were selected at BB1 and BB2 to represent a gradient of disturbance across the treatments from high to low, respectively. The clear-cut treatment removed all large trees, the low-leave shelter wood treatment retained 4-7 m² basal area/hectare, and the high-leave shelter wood treatment retained 12-15 m² basal area/hectare distributed evenly over the treatment. The two Blacksburg sites were at similar elevations (BB1- 710 m and BB2- 730 m), had southern exposures, similar aspect (BB1 - 153°, BB2 – 151°), but differed slightly in their slopes (BB1 – 16%, BB2 – 21%). The two sites, surrounded by a forested area, were approximately 0.5 miles apart and were exposed to similar weather patterns.

3.23 Sampling

In August and September of 2001, a temporary 50 x 50 m quadrat was created within each of the selected treatments. The edge of each treatment was located and the corner of the quadrat was established 10 m in from the edge towards the center of each treatment plot. A 50 m measuring tape was extended through the site, usually from west to east or vice versa. A point 90° N and 10 m from the end of the 50 m tape was located. The second 50 m tape was stretched parallel with the first line so that two parallel 50 m lines were placed in the treatment plot with a distance of 10 m between the two. Two persons walked along each tape sighting for the tree species within the temporary 10 m boundary. This was walked twice, once each direction, to insure that all trees were counted. Typically either the southernmost or northernmost tape was

used throughout a line for all the tree calculations to minimize errors. Coordinate point measurements to the center of each living *R. pseudoacacia* and *A. altissima* trees (stem basal diameter >2.5 cm) between each tape were measured perpendicularly from the 50 m tapes.

3.24 Data Analysis

There are currently several methods used to analyze spatial patterns using distance measurements between points (Clark & Evans 1954; Diggle 1983; Barot *et al.* 1999). In this study, Ripley's K (1977) was used because it describes spatial patterns simultaneously at different scales when all spatial points within the plot are known. As a second order statistic, it analyzes the variation of the cumulative distances from all trees to all other trees in the plot. Ripley's K has the advantage of describing spatial dynamics of the observed patterns since it is a function of distance (Moeur 1993).

X and Y coordinate data was collected for every tree, to determine 1) The univariate spatial pattern (distribution) for each species, and 2) The bivariate spatial pattern (association) between *A. altissima* and *R. pseudoacacia* at each site using a modified version of Ripley's K (Lotwick & Silverman 1982). The univariate spatial pattern was calculated for each individual species since the bivariate spatial pattern between two species can depend upon their individual spatial patterns (Barot *et al.* 1999). The Ripley K (d) statistic was calculated with SAS (SAS Institute 1999-2001) according to the following equation(s).

$$K(d) = \left(\frac{A}{n^2} \right) \sum_{i=1}^n \sum_{j=1}^n \frac{I_d(u_{ij})}{w_{ij}} \quad i \neq j$$

The counter variable, $I_d(u_{ij})$, was calculated for every distance between all the points and was summed. If the distance between point i and j , u_{ij} , was less than d , then $I_d(u_{ij})$ was 1; otherwise it was 0. A was the area of the plot in m^2 , n was the number of trees in the plot, and w_{ij} was a weighting factor to correct for edge effects.

Edge effects occur when the distance between two points is greater than the distance to the nearest boundary of the plot. This leads to a biased estimate of $K(d)$ when points outside of the boundary are not

included (Moeur 1993). In this study, w_{ij} was equal to the proportion of the circle's circumference within the plot with radius u_{ij} , centered on tree i , and passing through tree j (Ripley 1977; Getis & Franklin 1987; Moeur 1993). The edge correction in the 50 x 50 m plots in this study were generated for distances up to 25 meters, half of the shortest boundary of 50 meters in the site as suggested by Moeur (1993) and Diggle (1983).

The edge correction was applied according to three conditions (Fig 3.1). If the circle with the radius of the distance between tree i and j was entirely within the plot boundary (the distance between the two points was less than the distance to the nearest boundary), then w_{ij} was 1 (scenario 1.). In scenario 2., if the distance between tree i and tree j was greater than the distance between i to the nearest boundary, e_1 , then w_{ij} was:

$$1 - \left(\cos^{-1} \left(\frac{e_1}{u_{ij}} \right) \div \pi \right)$$

In case 3, if the distance between tree i and tree j was greater than the distance to both boundaries, e_1, e_2 , then w_{ij} was:

$$1 - \left(\cos^{-1} \left(\frac{e_1}{u_{ij}} \right) + \cos^{-1} \left(\frac{e_2}{u_{ij}} \right) + \frac{\pi}{2} \right) \div 2\pi$$

A linear plot of $K(d)$ versus d compared the observed values to a random dispersion of the points representing the null of complete spatial randomness, known as CSR (Ripley 1977; Haase 1995; Dale 1999). CSR is a homogenous random distribution that is regarded as the null hypothesis or the Poisson distribution (Diggle, 1983). The definition of CSR states that 1) An n event is as likely to occur at a point in area \mathcal{A} as any other of n possible events and 2) The n events are located independently of each other (Clark & Evans, 1954; Diggle 1983). CSR provides a good test to use when analyzing plant dispersion patterns by distinguishing between “clumped” or “regular” spatial patterns (Diggle 1983). Clumped patterns occur when the presence of

an individual increases the probability of finding another individual and regular patterns occur when the presence of one individual reduces the probability of finding other individuals (Whittaker 1975; Dale 1999). $K(d)$ was standardized with the following equation (Moeur 1993):

$$L(d) = \sqrt{\frac{K(d)}{\pi}} - d$$

This transformation made $K(d)$ linear, reduced variance, and facilitated testing against the null of zero when plotted against d (Moeur 1993). $L(d)$ values >0 indicated a clumped spatial arrangement and $L(d)$ values <0 suggested regular spacing. A confidence interval was defined to test statistically significant departures from the CSR. Approximate 95% confidence intervals were calculated as

$$CI = \pm 1.42 \sqrt{\frac{A}{n-1}}$$

A was the area of the plot (2500 m²) and n was the total number of trees in the plot (Ripley 1979). Values of $L(d)$ above or below this confidence interval indicated a significant departure from CSR. Ripley's K was modified to analyze the interspecific association between the two species in the plots (Lotwick & Silverman 1982).

$$K_{12}(d) = \frac{n_2 K_{12}^*(d) + n_1 K_{21}^*(d)}{n_1 + n_2}$$

In this equation, n_1 and n_2 represented species one and species two, respectively. This intertype is calculated from summing the distance distributions $K^*(d)$ from species one and species two, and vice versa (Lotwick & Silverman 1982). These data were standardized according to the transformation described above.

The two tree species were independent of each other if $L(d)$ was close to zero. $L(d)$ was positive if the two species were positively associated (attraction) and negative if they were negatively associated (repulsion) (Duncan 1991; Moeur 1993). A 95% confidence interval was generated as explained above. Ripley's $K(d)$ statistic was calculated from distances of 1 to 25 m by 1 m intervals for all of the six treatment plots.

Contingency analysis, using number of stems in 5 m x 5 m and 10 m x 10 m subplots, was also used to confirm the association of the two species. Presence and absence data were generated and analyzed in a contingency table. Positive associations indicate that the two species were found spatially closer than expected and negative associations indicate a less than expected spacing of the species (Dale 1999).

$$X^2 = \sum (\text{Observed} - \text{Expected})^2 / \text{Expected}$$

	+ RP	-RP
+AA	<i>a</i>	<i>b</i>
-AA	<i>c</i>	<i>d</i>
	Total	<i>n</i>

Variable *a* (the number of quadrats with both species present), *b* (*A. altissima* present, *R. pseudoacacia* absent), *c* (*A. altissima* absent, *R. pseudoacacia* present) and *d* (neither tree species present) were collected from analysis in each of the defined 5 m and 10 m subplots. A Likelihood Ratio X^2 test was used to determine possible associations.

3.3 Results

Coordinate data for all trees in each plot are shown in Figure 3.2. In every plot, *R. pseudoacacia* had a greater actual and relative density (%) than did *A. altissima* (Table 3.1). Except for low leave shelter wood, the two species were spatially limited to linear-like corridors within the plots that corresponded to zones heavily impacted by machines during logging.

Univariate analysis of the dispersion patterns for *A. altissima* indicated a tendency for significant clumping in both low leave shelter wood treatment sites at distances greater than 4 m (Fig 3.3C) and 12 m (Fig 3.3D). However, dispersion of *A. altissima* at both clear-cut and high leave shelter wood sites was random (Fig 3.3A, B, E, F). *Robinia pseudoacacia* was significantly clumped at all of the treatment sites at a minimum distance of 1 m to a maximum distance of 25 m (Fig 3.4).

Bivariate point analysis revealed a significant attraction of the two species at four of the six treatment sites; BB2 clear-cut, BB1 low leave shelter wood, BB1 high leave shelter wood, and BB2 high leave shelter wood (Fig 3.5B, C, E, F). The minimum distance of significant attraction was approximately 2 m in plots that had defined skid trails (Fig 3.5B, E, F) and 12 m in the low leave shelter wood plot, which did not have obvious signs of skid trails (Fig 3.5C). In BB1 clear-cut and BB2 low leave shelter wood (Fig 3.5A, D); *A. altissima* and *R. pseudoacacia* were independently associated.

Contingency analysis indicated that *A. altissima* and *R. pseudoacacia* were positively associated at 5 m in BB1 low leave shelter wood, BB1 high leave shelter wood, and BB2 high leave shelter wood (Table 3.2). The contingency analysis at 10 m indicated positive associations between the two species at BB1 low leave shelter wood and BB1 high leave shelter wood (Table 3.2)

3.4 Discussion

Ailanthus altissima and *R. pseudoacacia* were positively associated in the majority of the field sites, a result not corresponding to our hypothesis. The spatial patterns for the species differed and ranged from apparently random to clumped. These spatial point associations and patterns were dependent upon the site and the individual species density.

3.41 Intraspecific spatial pattern

Ailanthus altissima generated a random spatial pattern in the majority of the plots when its actual density ranged from 2-4 individuals (Table 3.1). It is possible that the low density of *A. altissima* individuals in

the BB1 high leave shelter wood, BB2 high leave shelter wood, and BB2 clear-cut sites was below the sensitivity of the statistical pattern analysis and thus generated non-significant random patterns (Fig 3.3). *Ailanthus altissima* individuals at these low-density sites were usually solitary, small plants that had likely been established by seed instead of vegetative reproduction. The low density of *A. altissima* individuals in the high leave shelter wood sites could have also been due to the lower degree of disturbance applied to this site. Several additional *A. altissima* plants were not included in the analyses because their stem basal diameters were less than 2.5 cm. Perhaps, in a few years when the trees have grown, their pattern analysis will be similar to the sites with higher densities of *A. altissima*.

Even though *A. altissima* was not relatively abundant in these particular field sites and did not exhibit the expected clumped pattern, *A. altissima* has been observed to grow in large clonal groups. Despite being classified as shade-intolerant (Grime 1965), under the forest subcanopy, *A. altissima* can establish a ramet bank that can persist until a gap opens in the forest canopy (Kowarik 1995). Over time, the few *A. altissima* individuals located in the sites we measured could use this mechanism (advanced regeneration) to become abundant and create a pattern closer to clumping. Similarly, Knapp & Canham (2000) observed that once established and then exposed to light in a gap, *A. altissima* was capable of growing into the upper forest canopy. It can attain significantly greater vertical height, diameter increase, and extension growth when compared to the native species in the upper canopy. In contrast to these randomly dispersed individuals, significant clumping patterns were observed for *A. altissima* in the remaining sites (Fig 3.3C, D) suggesting vegetative reproduction in some cases.

Robinia pseudoacacia had a clumped distribution pattern within all the sites (Fig 3.4). The minimum distance for significant clumping of *R. pseudoacacia* was 1 m, smaller than that of the minimum clumping distance for *A. altissima* (Fig 3.3). This closer distance of clumping for *R. pseudoacacia* was due to the more abundant individuals (Table 3.1) and to the many root sprouts growing from individuals (Call, personal observation). It is possible that these individuals were producing seeds since *R. pseudoacacia* has been observed to produce seeds at 6 years of age (USDA 1965), therefore increasing its dispersal capabilities. Clumping also

suggests that intraspecific competition was not strong for these two species, a similar result obtained in a greenhouse competition study (Chapter 2.0).

3.42 Interspecific spatial pattern

Ailanthus altissima and *Robinia pseudoacacia* were positively associated in the majority of the observed plots (Fig 3.5). Analyzing the patterns of association of *A. altissima* and *R. pseudoacacia* from sites of high disturbance (e.g., clear-cut) to sites of less disturbance (e.g., high leave shelter wood) indicated that both species tended to be found along the skid trails, which may have followed old roads established before the most recent logging treatment, more so in the high leave shelter wood than in the more disturbed sites. There could have been skid trails in all of the sites, yet the area studied might not have included them. The distribution of these trees was associated with locations that had a history of multiple disturbances and apparent compaction compared with other locations within the study sites. This is not surprising since *A. altissima* has been observed to grow well with situations of high soil compaction and frequent disturbance such as in urban environments (Pan & Bassuk 1985).

The mutual affinity for the skid trails was most evident in BB2 clear-cut and at both high leave shelter wood sites (Fig 3.5D, E, F). Due to the attraction for the skid trails, in these sites the two trees were associated at small minimum distances of 2 meters. Since *A. altissima* and *R. pseudoacacia* were able to thrive along the disturbed trails, they were most abundant there compared to other successional species within these sites. In the high leave shelter wood sites, *A. altissima* and *R. pseudoacacia* individuals along the trails in the high leave shelter wood sites could eventually be replaced by more abundant shade-tolerant species found in the high leave site.

Although defined skid trails were not strongly evident in the BB1 low leave shelter wood site (Fig 3.2C), the two species were spatially attracted in this site (Fig 3.5C). These two species were positively attracted at larger distances here than in the other sites. It is clear that both *A. altissima* and *R. pseudoacacia* were able to occupy and become established at high densities and with larger distances between stems in both low leave shelter wood sites. There is pre-harvest evidence that numerous *R. pseudoacacia* individuals were

present in BB1 low leave shelter wood, which led to the numerous remnants of *R. pseudoacacia* observed at this site in this study. There is no pre-harvest evidence of established *A. altissima* in these sites (Wender 2000; Hood 2001).

The two species were not positively associated in the remaining field sites. In BB1 clear-cut, the two species were independently associated at the majority of the distances (Fig 3.5A). The affinity for a skid trail was not evident since a defined trail was not present in this selected part of the treatment site. Similarly, within the BB2 low leave shelter wood site, the two species were independently associated (Fig 3.5D). Here, the intraspecific spatial pattern of *A. altissima* tended towards random, although there was some significant clumping (Fig 3.3D), and the association of the clumped *R. pseudoacacia* with this random pattern of *A. altissima* was not significant (Fig 3.5D). Both species were able to occupy space not inhabited by the other.

The contingency analysis supported the bivariate spatial point analysis in the majority of the treatment sites for *A. altissima* and *R. pseudoacacia* at distances of 5 m (Table 3.2). However, this analysis was limited because it was not able to assess association between the points at different distances and to include plants that might have occurred outside the edges of the plot.

Overall, the bivariate spatial patterns of these two species indicated that both *A. altissima* and *R. pseudoacacia* were positively attracted in the majority of the field sites, due to their mutual affinity for the disturbed and compacted skid trails. Although positively attracted, these two tree species were not strongly interacting since they were associated at minimum distances of 2 m when found along the skid trails (Fig 3.5), not close enough for interactions between trees of these small sizes and young ages.

As stated earlier, *A. altissima* and *R. pseudoacacia* have similar life history traits such as aggressive growth, multiple reproductive mechanisms, overall life span, and habitat preference. From this study, it is clear that both species exhibited a preference for establishing in heavily disturbed and compacted areas in the plots. These two species likely occupied the same broad niche, which is characteristic of early successional species. However, similar broad niche breadth in early successional species leads to intense interactions between species (Parrish & Bazzaz 1982), such as the negative interspecific interactions that was observed between these two species in a greenhouse experiment (Chapter 2.0). This intense competition can lead to

narrower niche breadth and reduced competition between late-successional species (Parrish & Bazzaz 1982). Thus, increased physical interactions between these two species as they continue to grow and disperse could lead to strong interference.

On the other hand, within the niche of the opportunistic species, each species can differ in the range of conditions where they can be the better competitor, depending upon the neighborhood or the physical conditions (Pickett & Bazzaz 1978). Due to the randomness inherent in seed dispersal, germination, establishment, and timing of disturbance, these two species might enter into the community at different ages and times and be able to coexist (Ågren & Fagerström 1984; Bazzaz 1990). Coexistence between plant individuals can occur because interactions between individual plants are diffuse and simultaneous and are not limited to only two species (Goldberg & Werner 1983; Bazzaz 1990). Thus, with more time, a combination of both increased competitive interactions and environmental variability will determine the species abundance within these communities (Freckleton *et al.* 2000).

3.43 *Limits on interpretation*

Measurements from one discrete moment in time limit the value of these data for projecting long-term interactions between *A. altissima* and *R. pseudoacacia*. Sequential measurements of the spatial patterns might indicate strong interactions between these two species as they increase in size, biomass, abundance, and physical contact. Increasing the selected area of the field sites could indicate patterns different than observed. A group of plant species randomly distributed in a selected area might be non-randomly distributed when the larger surrounding area is included (Dale 1999). Thus, it is possible that *A. altissima* would not be distributed randomly if the full treatment plot (approximately 2 ha) had been examined beyond the 2500 m² plots used in this study. Similarly, including a larger area would likely include more skid trails within these sites, possibly providing more evidence for positive spatial associations. Including dbh measurements would potentially indicate associations between individuals of different ages and sizes. Similarly, including a control site with no treatment would have provided a good comparison to these results.

Since these statistical analyses are viewed as primarily descriptive, caution should be used when making conclusions (Barot *et al.* 1999). There are numerous possible variables that affect plant-plant interactions and thus create the observed patterns. As mentioned above, seed dispersal, different germination times and requirements, strength of the inter- and intraspecific interactions, sizes of interacting plants, other competing species, or the heterogeneity within the site could be factors involved in the observed dispersions (Bazzaz 1990).

3.44 *Summary*

Both species occupied similar compacted and disturbed areas within each plot, yet also occupied most of the sites of intermediate disturbance (low leave sites). The presence of *A. altissima* and *R. pseudoacacia* were positively associated with the presence of the other in the majority of the sites (Fig 3.5), indicating a lack of negative interactions from the spatial patterns. However, due to the low abundances of *A. altissima* and the small sizes of the trees sampled, this spatial pattern analysis may not yet reflect competitive interactions.

Changes in the following factors could allow an invasive species, like *A. altissima*, to attain greater dominance in the ecosystem. The number of propagules in the disturbed system, the life history traits of the species, and the invasibility of the site affects the establishment of an invasive species in an ecosystem (Lonsdale 1999; Davis *et al.* 2000). The number of exotic species in a particular region is also due to propagule survival from native plant competition, herbivory and pathogens, or chance events in the ecosystem (Lonsdale 1999).

According to these predictions, since there was a greater number of propagules of *R. pseudoacacia* than *A. altissima* in these sites (Table 3.1), *R. pseudoacacia* would be more successful over time. The large abundance of *R. pseudoacacia* in the field sites was likely a result of asymmetric competition due to prior establishment in the site. However, continual disturbance within these sites would be an advantage to the establishment of *A. altissima*. A disturbance could lead to an increase in below ground competitive intensity when light is not limiting, enabling *A. altissima* to have an opportunity to establish. *Ailanthus altissima* has been shown to be a better below ground competitor compared to *R. pseudoacacia* (Chapter 2.0). Disturbances would also increase

the tendency for more clumping to occur for both species since they respond to disturbance with aggressive root sprouting and rapid growth. If the sites are left undisturbed, and succession continues, these two species will eventually be replaced by more shade-tolerant species.

It is clear that *A. altissima* is able to occupy and become established within these sites. Thus, further disturbance of these sites, could increase the abundance of this invasive exotic and lead to its dominance over some native plants within the local site. Continued analysis of spatial patterns between *A. altissima* and *R. pseudoacacia* in sites of different ages and disturbance types will help to provide a clearer view of the impact of *A. altissima* upon community structure in the eastern deciduous forest.

Table 3.1. Actual and relative density (%) of *A. altissima* and *R. pseudoacacia* at each 50 m² treatment plot. This only includes densities of these two species in the field. Plots were located near Blacksburg, Virginia as part of a larger study on the effects of logging procedures on forest development. Sites numbered as one or two represent the two treatment blocks. The treatments are listed for each site.

Treatment	Site	Actual density <i>A. altissima</i>	Actual density <i>R. pseudoacacia</i>	Rel. density (%) <i>A. altissima</i>	Rel. density (%) <i>R. pseudoacacia</i>
Clear cut	Blacksburg 1	10	11	47.6	52.3
Clear cut	Blacksburg 2	3	41	6.8	93.2
Low leave shelter wood	Blacksburg 1	14	88	13.7	86.3
Low leave shelter wood	Blacksburg 2	11	43	20.3	79.6
High leave shelter wood	Blacksburg 1	4	64	5.8	94.1
High leave shelter wood	Blacksburg 2	2	22	8.3	91.7

Table 3.2. Results from the Likelihood Ratio Chi-squared test of independence between *A. altissima* and *R. pseudoacacia* using presence/absence data. Data were obtained from 10 and 5 meter squares within each of the six 50 m² plots located near Blacksburg, Virginia.

Treatment	Site	Probability of larger X^2 value at::	
		10 meters	5 meters
Clear cut	Blacksburg 1	0.41	0.06
Clear cut	Blacksburg 2	0.95	0.12
Low leave shelter wood	Blacksburg 1	<0.05	<0.05
Low leave shelter wood	Blacksburg 2	0.87	0.24
High leave shelter wood	Blacksburg 1	<0.05	<0.001
High leave shelter wood	Blacksburg 2	<0.05	<0.05

Fig 3.1 Three different edge correction scenarios: 1) When the distance between the two points is entirely within the plot, 2) The distance between two points is greater than the distance to one boundary and 3) When the distance between the two points is larger than the distance to two boundaries. The weighted edge correction for each of these scenarios is described in Methods.

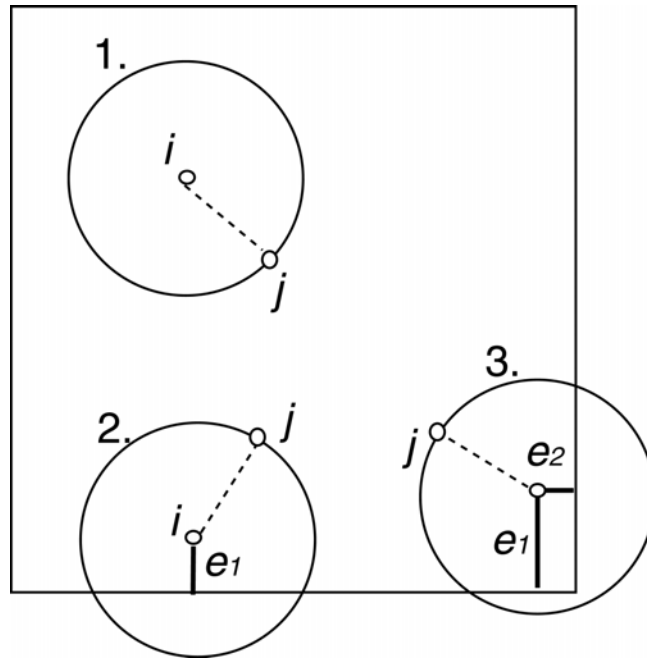


Fig 3.2 (A-F). Spatial point distributions for *A. altissima* (black circles) and *R. pseudoacacia* (gray circles) at six different sites near Blacksburg, VA. These plots consisted of three different logging treatments; A-B) clear cut, C-D) low leave shelter wood, and E-F) high leave shelter wood. They were replicated at the two different locations, Blacksburg 1 (BB1) and Blacksburg 2 (BB2). Straight lines indicate skid trails from the logging. Each tic mark represents 10 meters.

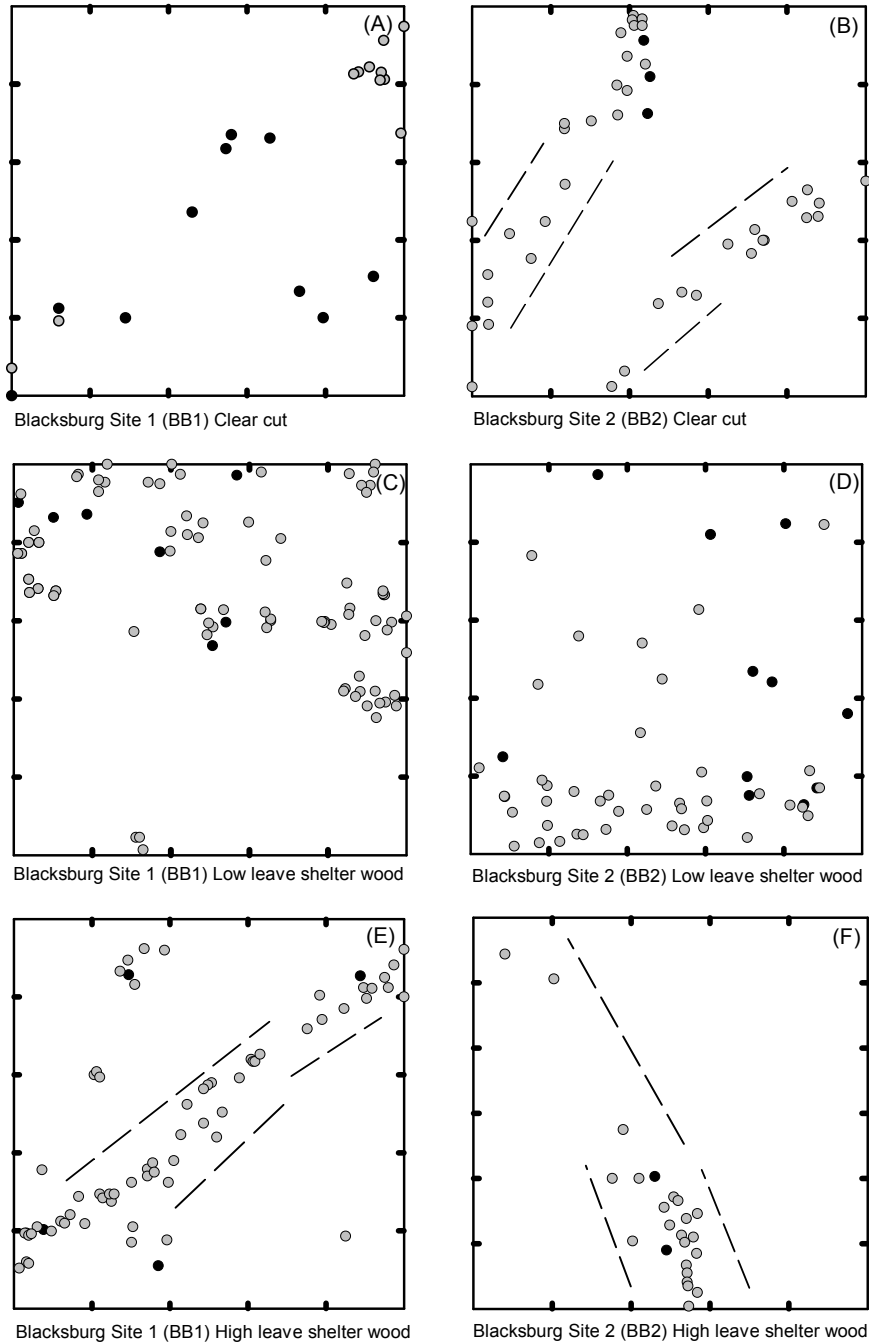


Fig 3.3 (A-F). Plot of $L(d)$, a modification of $K(d)$, against various distances d , showing the spatial dispersion for the individuals of *A. altissima* at Blacksburg 1 (BB1) and Blacksburg 2 (BB2) (see Methods). The dashed lines are the 95% confidence envelopes for spatial randomness at zero. $L(d)$ above the confidence envelope indicates a significant clumping while $L(d)$ below the envelope indicates a significant regular dispersion.

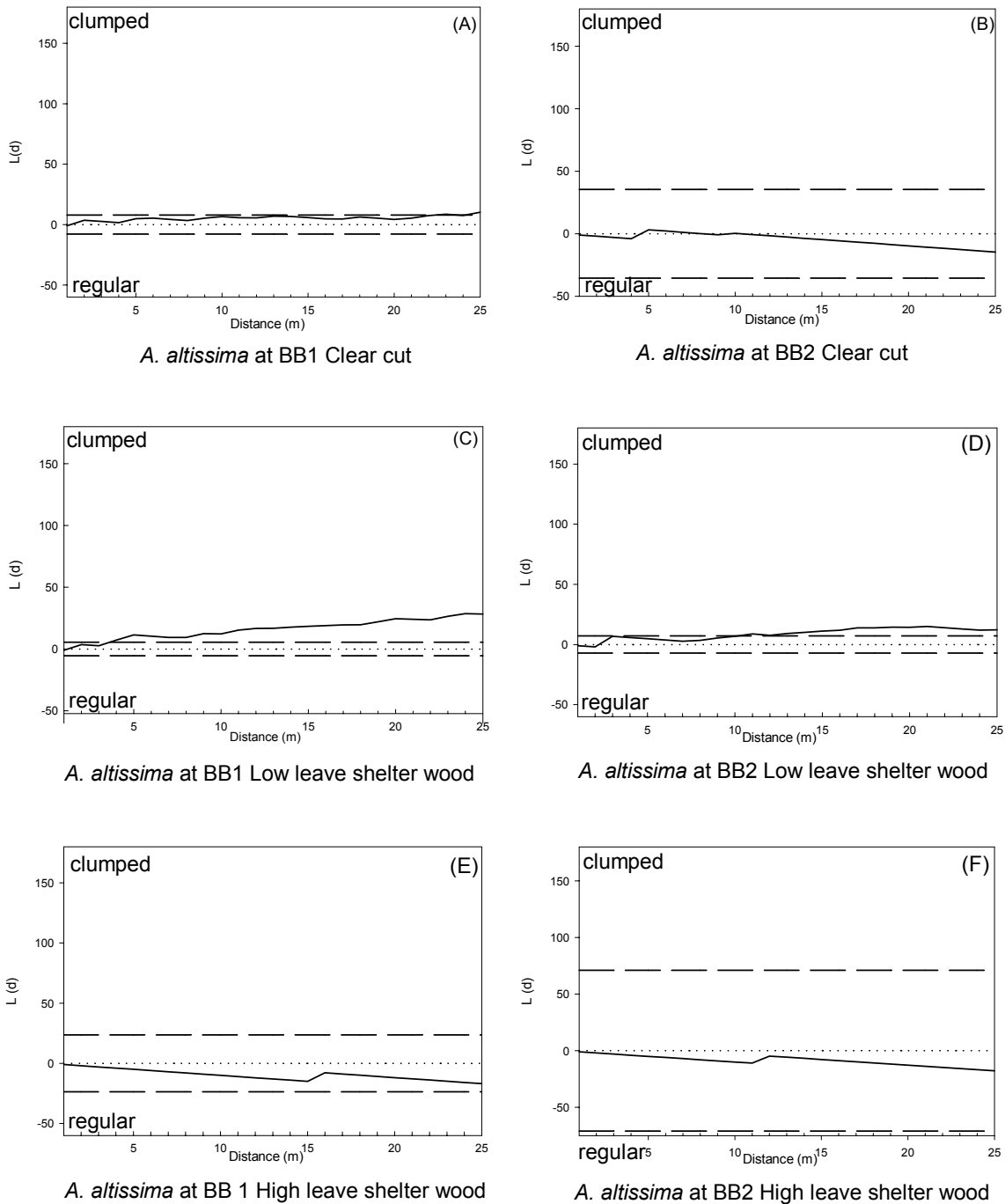
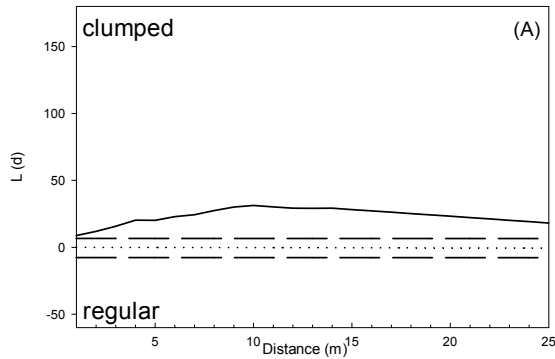
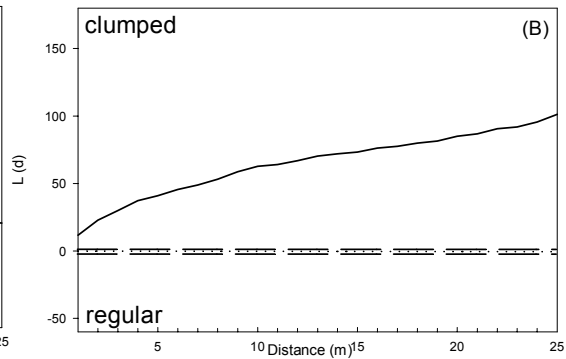


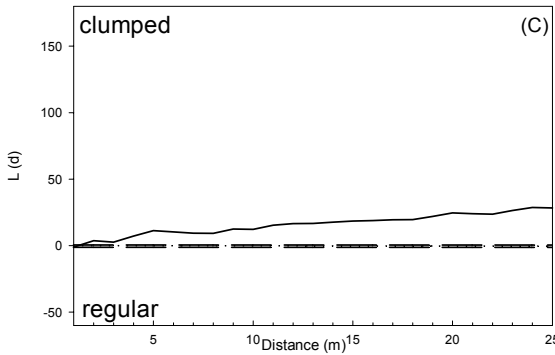
Fig 3.4 (A-F). Plot of $L(d)$, a modification of $K(d)$, against various distances d , showing the spatial dispersion for the individuals of *R. pseudoacacia* at Blacksburg 1 (BB1) and Blacksburg 2 (BB2) (see Methods). The dashed lines are the 95% confidence envelopes for spatial randomness at zero. $L(d)$ above the confidence envelope indicates a significant clumping while $L(d)$ below the envelope indicates a significant regular dispersion.



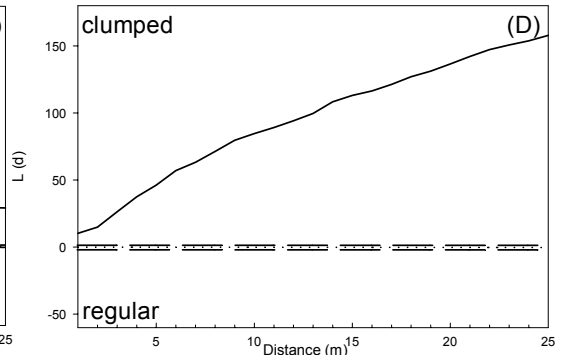
R. pseudoacacia at BB1 Clear cut



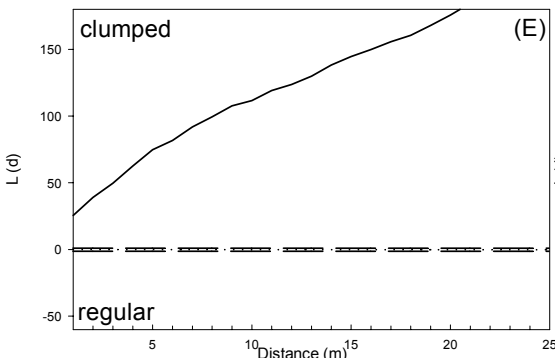
R. pseudoacacia at BB2 Clear cut



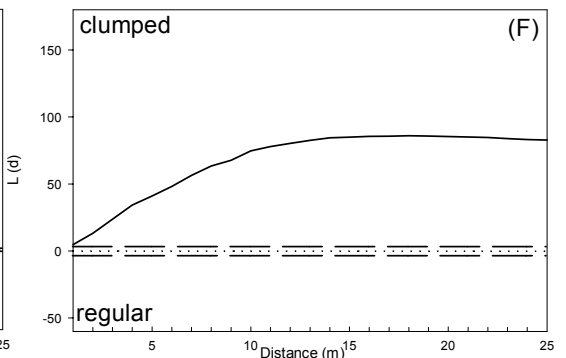
R. pseudoacacia at BB1 Low leave shelter wood



R. pseudoacacia at BB2 Low leave shelter wood

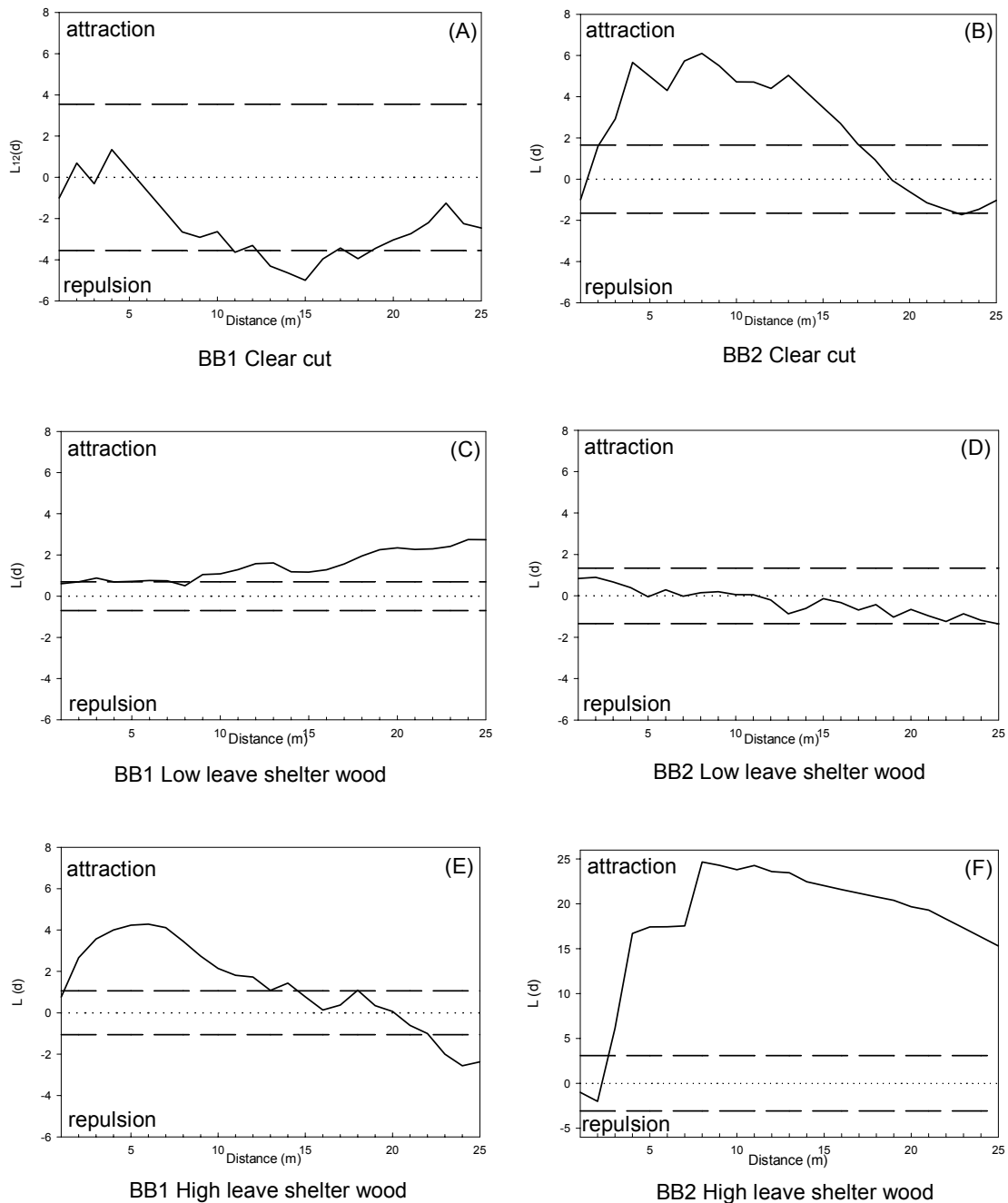


R. pseudoacacia at BB1 High leave shelter wood



R. pseudoacacia at BB2 High leave shelter wood

Fig 3.5 (A-F). Plot of $L_{12}(d)$, a modified version of $K_{12}(d)$, against various distances d , showing the spatial association between *A. altissima* and *R. pseudoacacia* at Blacksburg 1 (BB1) and Blacksburg (BB2) (see Methods). The dashed lines are the 95% confidence envelopes for spatial independence around the line at zero. $L_{12}(d)$ values above the confidence envelope indicate significant positive association between *A. altissima* and *R. pseudoacacia* while $L_{12}(d)$ values below the envelope indicate a significant negative association.



CONCLUSION

This study utilized two different experimental designs to analyze the interactions between *A. altissima* and *R. pseudoacacia*. We contrasted the competitive interactions in potted-plant experiments to the spatial point patterns in the field in order to determine if the invasive exotic *A. altissima* and the native *R. pseudoacacia* were negatively interacting.

The goal in the greenhouse study was to compare the strength of interspecific interference to intraspecific interference within these two species. This study defined competition as a measure of resource capture, although other interactions such as allelopathy or facilitation might have occurred. From this experiment, it was clear that interspecific interference significantly negatively affected the performance of both *A. altissima* and *R. pseudoacacia*. However, it was difficult to clearly state the better competitor from this study. *Ailanthus altissima* was the better competitor, according to the indices, for total biomass and below ground responses. Yet *R. pseudoacacia* revealed much variability in its responses, occasionally generating dominant individuals and overall having the greater absolute biomass. Thus, the species differed in their competitive abilities in different situations (Grime 1977).

In the field study, the spatial point patterns of *A. altissima* and *R. pseudoacacia* were analyzed to infer potential competitive interactions. The spatial patterns did not indicate negative interactions; instead they revealed positive associations between the two species. This was likely due to external factors such as historical establishment and environmental preference. However, with more time and growth of the plant individuals, there will likely be negative interspecific interactions occurring between these two species, as was observed in the greenhouse. Both increased competitive interactions and variability in the environment will affect the abundances of *A. altissima* and *R. pseudoacacia* in these sites.

Although the results from the greenhouse analysis indicated that both species had comparable competitive attributes, the patterns in the field revealed a greater abundance of *R. pseudoacacia* and very few *A. altissima* individuals. The greater abundance of *R. pseudoacacia* was likely due to its longer historical establishment at the sites. Similarly, in a competition study between two invasive C₄ grasses, *Melinis minutiflora* was competitively aggressive with *Schizachyrium condensatum* (Kunth) Nees in a potted experiment,

yet was not found in great abundance in field sites that had well-established *S. condensum* (D'Antonio *et al.* 2001). However, after a disturbance (fire), the priority effect of *S. condensum* was disrupted, increasing the opportunities for *M. minutiflora* to become more abundant in the field.

Thus, with continued disturbances in the field, *A. altissima*, being an aggressive species similar to *R. pseudoacacia*, will likely increase in abundance, benefiting from the disruption of *R. pseudoacacia* and other native species within the site. Within the disturbed local area, it is possible that *A. altissima* will be able to usurp space in the sites that might have been occupied by native plants. Since plant competitive interactions are not species specific, *A. altissima* will potentially displace any native species, including *R. pseudoacacia*, that frequents disturbed sites and this could include *R. pseudoacacia*.

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CURRICULUM VITAE

Lara J. Call

lcall@vt.edu Updated 05.15.02

Education

Virginia Polytechnic Institute and State University

Master's Degree in Plant Ecology – awarded May 2002. GPA: 4.0

University of Virginia

Bachelor of Arts in Biology, Architecture minor - awarded May 1998. GPA: 3.3

Rhode Island School of Design. Summer 1997.

Field Ecology and Drawing Program.

Cornell/University of New Hampshire Shoal's Marine Program. Summer 1996.

Summer Program in Biological Illustration.

Professional experience

Virginia Polytechnic Institute – Graduate Teaching Assistant. Fall 2000, Spring 2001, Fall 2001.
General and Biology Majors Laboratory.

National Wildlife Federation Summit Faculty Member. Summer 2001.
Taught a class on Field/Botanical Sketching.

Utah State University – Logan, Utah. Summer 1999.

Developed a GIS map of plant distributions for the web at <http://cc.usu.edu/~shultz/index.html>
and produced a promotional illustrated poster of endemic plant species in Logan Canyon.

Susan Nelson Warren Byrd Landscape Architects- Charlottesville, Virginia. 1998-1999 and
1999-2000. Computer Graphics/Marketing/Draftsperson/Plant research.

Scientific Illustration Projects and Commissions

Rhododendron sp. microscopic leaf cross-sections to be published. Summer 2001.

Public Art Show at the New Dominion Book Shop. Spring 2000.

Logan Canyon Endemic Plants Series. Summer 1999.

Moss Series for Ivy Creek Natural Area. Spring 1999-current.

Illustrations for Biology 204 Manual. Fall 1998, Fall 1996.

Published handbook for Richmond Science Museum. Spring 1998.

Grants

National Science Foundation Graduate Research Fellowship (declined) – Fall 2000.

Graduate Development Research Project Grant (funded) – Spring 2001.

Virginia Academy of Science Small Project Research Funds (funded) – Spring 2001.

Adkins Arboretum 2001 Research Support (declined) – Spring 2001

Publications (and illustrated works)

Illustrations in Wieboldt, T., 2000. A Report on New Jersey Rush (*Juncus caesariensis*) at Fort A.P. Hill, Virginia, for Management Purposes (in review).

Call, L., Elder, M., Johnson, J. and Maurakis, E. 1998. Teacher Curriculum Guides in Nutrition, Food Safety, and Biodiversity. Virginia Journal of Science. 49(2):81.

Presentations

“Analysis of intraspecific and interspecific interference between the invasive exotic *Ailanthus altissima* and the native *Robinia pseudoacacia*.”

Departmental Seminar (Botany Series) – Fall 2001.

Graduate Student Research Symposium – April 2002 – Poster presentation (Blacksburg, VA)

Atlantic Southeastern Biologists Conference - April 2002 – Paper presentation (Boone, NC.)

Masters Thesis Defense Seminar – May 2002 (Blacksburg, VA)

Virginia Academy of Science Meeting – May 2002 – Scheduled paper presentation (Hampton, VA)

Ecological Society of America Meeting – August 2002 – Scheduled paper presentation (Tucson, AZ)

Community/Service Activities

Botany Seminar Graduate Committee Chairperson – Fall 2001-Spring 2002.

Biology Graduate Student Association – Committee member – Spring 2001-Spring 2002.

New River Valley Women’s Resource Center – Marketing Designer - Spring 2001.

National Wildlife Federation Summit –North Carolina, New Hampshire, Colorado, New York, Michigan, West Virginia. Summers 1991-1994, 1997, 2000, 2001. Environmental conferences.

International Living Experience in Costa Rica at a Spanish Language School. Spring 1999.

Biology Undergraduate Assistant at the University of Virginia. Spring 1997.

Co-founder of Biology Society at University of Virginia. Fall 1997.

Marine Biology Course in San Salvador. Summer 1996.

Madison House volunteer. Accumulated over 100 hours of service. 1994-1998

Skills

Experienced in plant identification, plant taxonomy, and botanical illustration. Proficient with Arcview GIS, Word, Adobe Photoshop, Adobe Illustrator, Quark, and WWW. Partially fluent in Spanish.