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Comparative seed dispersal, seedling establishment and growth of exotic, invasive *Ailanthus altissima* (Mill.) Swingle and native *Liriodendron tulipifera* (L.)

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Comparative seed dispersal, seedling establishment and growth
of exotic, invasive *Ailanthus altissima* (Mill.) Swingle and
native *Liriodendron tulipifera* (L.)

Nathan L. Kota

Thesis submitted to the
Eberly College of Arts and Sciences
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Master of Science
in
Biology

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2005

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forest disturbance, seed dispersal, germination, seedling establishment

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ABSTRACT

Comparative seed dispersal, seedling establishment and growth of exotic, invasive *Ailanthus altissima* (Mill.) Swingle and native *Liriodendron tulipifera* (L.)

Nathan L. Kota

Ailanthus altissima (Mill.) Swingle (tree of heaven) is an exotic species from China that was intentionally introduced as an urban ornamental species but has since become naturalized throughout much of the U.S. This pioneer species appears poised to invade rural areas as current rates of human-induced forest disturbance lower dispersal barriers and increase available habitat, especially in eastern forests, where it will compete with pioneer native trees such as *Liriodendron tulipifera* (L.) (yellow poplar). To compare the invasion potential of exotic *A. altissima* and native *L. tulipifera*, my research focused on two objectives. First, I investigated characteristics that influence dispersal distance of the species' wind-dispersed samaras, and developed long distance seed dispersal curves from a forest edge into an open field. In the lab, *Ailanthus altissima* samaras exhibited features that suggest greater capacity to disperse long distances, such as lower wing loading and still air descent velocity. However, in the field there was no interspecific difference in relative densities with increasing distance into the open field. Factors such as tree height and seed cluster architecture appear to compensate for the difference in individual samara morphology, resulting in equal dispersal ability of *A. altissima* and *L. tulipifera*. The second objective addressed the response of seed germination and seedling growth of the two species to three levels of timber harvest on north and south-facing aspects.

Liriodendron tulipifera germination was negligible in all field treatment combinations, and in a growth chamber experiment, probably due to low seed viability. The combined field and growth chamber results demonstrated that *A. altissima* germinates in a variety of light conditions as long as sufficient moisture exists. However, *L. tulipifera* seedlings produced more biomass and leaf area after two growing seasons in the disturbed forest stands. The conclusions from these two studies are, first, that both species are equally likely to disperse into a site after large scale forest disturbance. Secondly, *A. altissima* is more likely to invade only in suitable microsites where sympatric native species such as *L. tulipifera* have not germinated. A reasonable solution to protect against *A. altissima* invasion requires the removal of mature females at least one year prior to timber harvest.

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CHAPTER 1

General Introduction

Species introductions to previously uninhabited areas are a global phenomenon that has increased throughout human history, given that humans are the most important facilitators of such introductions (di Castri, 1989; Heywood, 1989; Perrings et al., 2002). Deliberate introductions are potentially beneficial, for example as food sources and for ecosystem restoration and sport in the U.S. (Pimentel et al., 2000; Ewel and Putz, 2004), but not all species relocations are without potential harmful ramifications. Some nonnative species become invasive when they establish, reproduce and increase their range to the detriment of their new environment (Mack et al., 2000).

Although only 1% – 10% of introduced, nonnative species actually become naturalized and ultimately invasive (di Castri, 1989; Williamson and Fitter, 1996), those less frequent invaders can have profound and widespread effects. Pimentel et al. (2005) estimated that there are ca. 50,000 nonnative species in the U.S. alone that cause environmental damage costing nearly \$120 billion each year. Of the estimated 22,000 plants species in the U.S., ca. 5,000 are escaped, alien species (Morin, 1995; Morse et al., 1995).

Cronk and Fuller (1995) specifically define an invasive plant as “an alien plant spreading naturally (without the direct assistance of people) in natural or semi-natural habitats, to produce a significant change in terms of composition, structure or ecosystem processes.” Often referred to as “weeds,” current estimates suggest that invasive plants are spreading at a rate of nearly 700,000 ha per year in the U.S. (Babbitt, 1998). Negative effects occur on various scales (Gordon, 1998) from diminishing the survival of (Gould and Gorchov, 2000), and displacing native species (Morse et al., 1995) to altering whole ecosystem properties such as productivity, nutrient cycling and hydrology

(Vitousek 1995; Mack et al., 2000; Ehrenfeld, 2001).

Rejmanek and Richardson (1996) found similar features shared among invasive woody species such as recurrent, successful reproduction and seed qualities that allow quick movement and establishment. The propagule pressure exerted by invaders is an extremely important determining factor of the invasibility of a plant community (Williamson and Fitter, 1996), and species that can disperse long distances may have a relative advantage over natives with lower dispersal ability. However, the susceptibility of an environment to invasion also depends on characteristics of the threatened site (Lonsdale, 1999), such as resource availability (Davis et al., 2000).

A common attribute among invaded environments is the previous occurrence of a human-induced disturbance (Heywood, 1989). This may facilitate invasion by producing a novel habitat for a new species or simply by opening space for establishment and subsequent spread (Parker et al., 1993). Anthropogenic disturbance of vegetation communities also results in the breakdown of dispersal barriers (Heywood, 1989), which may be particularly important for regeneration, or invasion of wind-dispersed plants. Human-induced disturbance is rife throughout the U.S., particularly in the eastern forests (Morse et al., 1995) where increasing urban development and timber harvest may produce suitable habitat for invasion. However, despite the presence of many herbaceous plant invaders in the eastern deciduous forest, few exotic trees have become invasive. One nonnative tree that may benefit from anthropogenic environmental change in eastern forests is *Ailanthus altissima* (Mill.) Swingle (hereafter referred to by its genus name, *Ailanthus*).

Originally restricted to central China (Feret, 1985), *Ailanthus* was first imported to the United States in the late 19th century and was widely used as an urban ornamental (Hu, 1979), possibly due to its tolerance of pollutants (Kim, 1975; Davis et al., 1978, from the grant), dust (Klincsek, 1976) and drought (Trifilo et al., 2004). These characteristics may also contribute to its spread. *Ailanthus* is now naturalized throughout a large portion of the contiguous U.S. (Miller, 1990), reported as established in the wild and a potential problem in forty-two states (Swearingen, 1999).

Ailanthus is a dioecious species that also reproduces vegetatively via root sprouts (Miller, 1990). A single female may produce hundreds of thousands of samaras (Bory and Clair-Maczulajtys, 1980) that are wind-dispersed throughout the winter and often germinate the following spring (Miller, 1990). Rapid establishment and first year growth (Adamik and Brauns, 1957) even in harsh conditions, makes it a successful early colonizer especially in disturbed sites (Knapp and Canham, 2000; Miller, 1990). Even though *Ailanthus* is associated primarily with urban environments (Huebner, 2003) it has also been found in second and old growth forest in New York (Knapp and Canham, 2000) and West Virginia (Kowarik, 1995), affirming its potential to become a major invasive deciduous tree in the eastern forest. The combination of niche characteristics and the production of an allelopathic compound (ailanthone) (Heisey, 1990; Lawrence et al., 1991; Heisey, 1996) may contribute to the formation of dense, monotypic stands in invaded areas (Mergen, 1959) that would otherwise be habitat for native species.

Liriodendron tulipifera (L.) (tulip or yellow poplar) is a native tree of eastern forests that shares many ecological and life history similarities with *Ailanthus*. Reproduction occurs from wind-dispersed samaras that must overwinter prior to

germination, and seedlings grow rapidly in high light and mesic temperate environments (Della-Bianca, 1983; Beck, 1990; Kavanagh, 1990). Thus ‘gap obligate’ *L. tulipifera* (Orwig and Abrams, 1994) is an important early pioneer and early successional dominant species (Beck, 1990).

Since disturbed habitats are often invaded by both species (Beck, 1990; Miller, 1990), *L. tulipifera* and *Ailanthus* are likely to encounter one another after such events. A comparison of their dispersal into and relative performance within disturbed areas is therefore important to determine the likely outcome of stand initiation if these species are contributing to the propagule pool. Although many studies have investigated the performance of co-occurring native and invasive species in natural environments (Daehler, 2003), fewer have done so immediately after a disturbance event, and none have targeted these two tree species during important times in their life history. Therefore, the overall goal of my thesis work was to investigate elements of seed dispersal, germination and seedling growth of *Ailanthus* and *L. tulipifera* after anthropogenically-induced forest disturbance.

Seed dispersal is an important factor in alien plant invasion and spread (Greene and Johnson 1995, Ghera and Roush 1993), as well as for the persistence of native species. Although most seeds are deposited close to the parent (Horn et al., 2001), long distance dispersal (LDD) can quickly increase the range of a species (Cain et al. 2000; Nathan et al., 2002), even when the frequencies of LDD events are low (Higgins and Richardson, 1999; Nathan et al., 2001). To better understand the invasion potential of *Ailanthus* I first investigated both short and long distance seed dispersal patterns of *Ailanthus* and *L. tulipifera* from a forest edge into an adjacent field. Density distributions

of both species were measured out to 200 m to make inferences about the potential of one species to ‘out-disperse’ the other. Seed morphology and flight patterns were measured in the lab to examine dispersal mechanisms of each species. The results of this study are presented in Chapter 1, and are submitted for publication in the *American Journal of Botany*.

Not only is seed arrival in a new habitat central to range expansion, but subsequent germination and growth response of the species will also determine successful establishment. The second objective of this project was to examine the germination and growth response of *Ailanthus* and *L. tulipifera* in three levels of forest disturbance. Timber harvest is a type of anthropogenic disturbance that is increasing, particularly on private land in the eastern deciduous forest (Adams et al., 2000) and several methods of harvest exist. Seeds and seedlings of both species were placed in six sites representing three levels of disturbance: clearcut, selective cut and intact forest. Germination was examined in the first and second growing seasons after harvest, and seedling survival and growth were measured at the end of the two growing seasons. Different *Ailanthus* maternal seed sources were examined for differential germination potential. Systematic location of experimental plots allowed for investigation of aspect and distance effects on germination and growth. A growth chamber study was also performed to assess the specific role of light in germination. These results are addressed in Chapter 2 and will be submitted for publication in *Biological Invasions*.

The results of these studies enhance the understanding of two important, co-occurring exotic, invasive and native trees not only in human altered environments, but also to natural disturbances. Land managers and timber companies can benefit from this

information and use it as a tool to successfully manage regeneration of native pioneer species and suppression of invaders.

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CHAPTER 2

Comparison of seed dispersal of *Ailanthus altissima* (Simaroubaceae) and *Liriodendron tulipifera* (Magnoliaceae) from a forest edge.

Abstract

Seed dispersal profoundly influences the spread of plants and, in part, determines plant community composition and structure. Thus, it is useful to compare dispersal characteristics of sympatric native and exotic, invasive species to understand possible future plant community characteristics. I measured samara wing loading and descent velocity of exotic *Ailanthus altissima* and native *Liriodendron tulipifera* in the lab. I also measured long distance seed dispersal curves out to 200 m in the field, and mass, area and wing loading of field-collected seeds. Lower *Ailanthus* wing loading and still air descent velocity suggested that, under identical dispersal conditions, *Ailanthus* samaras should disperse greater distances than *L. tulipifera*. Field-collected *Ailanthus* samaras also had lower wing loading; however, there was no significant difference between relative seed densities of the species, and the ratio of invasive to native density did not change, with increasing distance from the source. *Liriodendron tulipifera* samara area significantly increased, and mass tended to increase, at greater distances from the parent plant. The majority of *L. tulipifera* samaras were captured in the first month of sampling while *Ailanthus* seeds were dispersed more evenly through the season. The species differ dramatically in their seed cluster architecture; this may account for the discrepancy in dispersal timing and the tendency for seemingly heavier and larger *L. tulipifera* samaras to travel farther from the source. Both species were capable of long distance dispersal, and height differences in favor of *L. tulipifera* may outweigh the effect of samara morphology characteristics in determining dispersal distance.

Introduction

Anemochorous (wind dispersed) seeds have evolved mechanisms that allow for dispersal both near the parent and at great distances. Although most seeds do not travel far from the parent (Horn et al., 2001) some fraction of seeds can be deposited outside the competitive sphere of the source plant (Matlack, 1992). This results in spatial separation of individuals that may diminish local intraspecific competition and predation or parasitism (Howe and Smallwood, 1982), and increases the probability of being deposited in an optimal site (Augspurger and Hogan, 1983; Greene and Johnson, 1992). Seed dispersal by wind is one method of spread that can quickly enhance the range of a species, particularly when long distance dispersal events occur. Therefore, it is important to quantify long distance dispersal of coexisting native and invasive species, as this may provide insight into future species composition and recruitment, especially after anthropogenic disturbance of an ecosystem.

Samaras are winged seeds that are evolutionarily specialized for flight. Despite distinct interspecific variation, the same factors of morphology, mass and wing area can greatly affect the dispersal distance of a propagule (McCutchen, 1977; Green, 1980; Guries and Nordheim, 1984; Augspurger, 1986; Greene and Johnson, 1993). Wing morphology, area and overall samara mass determine the specific descent patterns that create aerial drag and lift, influencing the rate of descent of a falling seed (Matlack, 1987) which is inversely related to potential dispersal distance (Augspurger, 1986). In general, seeds with lower rates of descent stay aloft longer, potentially increasing wind exposure and subsequent dispersal distance (Green, 1980). Furthermore, a great deal of experimental work (e.g. Guries and Nordheim, 1984; Augspurger, 1986) has

substantiated the findings of Green (1980), who empirically showed a strong positive correlation between samara rate of descent and the square root of wing loading (mass divided by area).

Quantification of the number of seeds versus distance from a parent source typically results in decreased seed density at increasing distances. Due to a predominant leptokurtic shape (Kot et al., 1996), seed dispersal data are commonly fit by negative exponential and negative power function models (Okubo and Levin, 1989; Portnoy and Willson, 1993; Williamson, 2002), often referred to as phenomenological models (Nathan and Muller-Landau, 2000). More complex mechanistic models that incorporate specific parameters known to influence dispersal distance have recently been developed in order to provide predictions depending on attributes of those parameters (see Greene and Johnson, 1989; Bullock and Clarke 2000; Nathan et al., 2001; Tackenberg, 2003). Although these and other multi-parameter models are more complex than the classical phenomenological models, they do not always provide a better fit to dispersal data (Clark et al., 1999; Greene et al., 2004).

Important ecological and evolutionary implications arise from the tail of any modeled dispersal distribution (Williamson, 2002), yet these long distance dispersal (LDD) events are difficult to quantify accurately due to the challenges of sampling relatively infrequent events (Cain et al., 2000). Instances of LDD are vital to population expansion where even a small proportion of seeds moving long distances can lead to an order of magnitude increase in spread rate (Higgins and Richardson, 1999). However, they are by their very nature rare events that are difficult to quantify (Nathan et al., 2002), in part due to the constraints of time and effort necessary for adequate sampling.

Definitions of both short and long distance dispersal are inconsistent. While Greene and Johnson (1995) suggest that LDD begins at a scale of a few hundred meters from the source, Cain et al. (2000) consider a long distance dispersal event to be anything over 100 meters. Portnoy and Willson (1993) describe LDD events as those occurring in the tail of the seed density distribution, but define the tail as the area under the curve beyond the modal seed density value. Despite this variation in definitions, what remains apparent is that seeds that travel long distances with the help of wind, water, vertebrates, or other vectors have had critical impacts on the spread of plant species (Webb, 1987; Clarke, 1998; Clark et al., 1998) and continue to be important for colonization of islands, plant responses to global change, metapopulation biology and the spread of invasive species (Cain et al., 2000).

One nonnative, invasive plant that may benefit greatly from wind dispersal of its samaras is *Ailanthus altissima* (Mill.) Swingle (tree of heaven). Originally restricted to central China (Feret, 1985), deliberate introduction of *Ailanthus* to the U.S. in the 18th century has since resulted in the establishment of the species throughout a large portion of the contiguous U.S. (Zheng et al., 2004). Although it has served many cultural, economic and even medicinal purposes for centuries in its native range, and was considered a beneficial urban tree species in the eastern U.S. (Hu, 1979), *Ailanthus* has recently been identified as a potentially destructive weed (Knapp and Canham, 2000). Rapid seedling establishment, growth and subsequent vegetative spread via root sprouting aid in the formation of dense, monotypic thickets that inhibit succession of native plants (Mergen, 1959). A female of this dioecious species can produce hundreds of thousands of wind dispersed propagules (Bory and Clair-Maczulajtys, 1980). Seeds

can germinate and grow in a wide range of climatic, soil and topographic conditions (Miller, 1990), producing foci of spread in previously uninhabited areas.

Although *Ailanthus* was previously restricted mainly to urban areas, current rates of landscape disturbance in the mid-Atlantic region, including suburban sprawl and logging, may provide a greater amount of suitable habitat and a decrease in dispersal barriers, possibly resulting in an even higher rate of invasion in the future. Indeed, *Ailanthus* has already been detected in native old growth and second growth forests in New York (Knapp and Canham, 2000) and West Virginia (Kowarik, 1995).

Liriodendron tulipifera L. (tulip poplar) is a native tree often found in the same habitat as *Ailanthus*, likely due to the ecological and reproductive similarities between the species, including a ‘preference’ for mesic temperate environments and high light typical of early succession (Beck, 1990). Both species are wind dispersed, even though their seeds exhibit distinct morphologies, resulting in a classification of *L. tulipifera* seeds as samaras or samaroids (Gleason and Cronquist, 1963; Britton and Brown, 1970). The niche and dispersal similarities shared by these species result in potential interspecific competition, especially in disturbed, high light environments such as old fields and utility, railroad and highway rights-of-way where *Ailanthus* is known to invade (Kowarik, 1995), and *L. tulipifera* could also become established. The outcome of this interaction may largely determine the successional trajectory in these environments.

In this study, the relationship between wing loading and descent velocity in exotic, invasive *Ailanthus* and native *L. tulipifera* samaras were studied to examine whether species differences in these traits could help explain differences in dispersal patterns. We also examined within-species differences in seed properties with distance to

determine whether seed quality might vary away from a forest edge. Primary seed dispersal curves of *Ailanthus* and *L. tulipifera* into an open field were determined and compared in light of samara morphology differences. An analysis of the ratio of *Ailanthus* to *L. tulipifera* seed density with distance from a forest edge was performed to determine whether the exotic gained a numerical advantage with distance from the seed source. Finally, temporal patterns of dispersal were examined.

Materials and Methods

Samara wing loading and descent velocity

Still air descent velocities of samaras of both species were measured using the method of Greene (1989). *Ailanthus* samaras were taken from a local tree in Fall, 2003, and F.W. Schumacher Co. (Sandwich, MA) provided *L. tulipifera* samaras in early February 2004. Samaras of both species were stored in dry conditions until Spring, 2004. Twelve intact samaras of each species were randomly chosen and released from a height of 4 m above the ground and allowed to fall for 2 m before timing began. Ten trials were performed so that a mean velocity per samara could be calculated during analysis, and only trials where samaras were in full rotation at the start of timing were used in the analysis. Time of descent was measured with a digital stopwatch. Samara mass and area was measured to calculate wing loading (mass/area) to investigate species differences in this seed characteristic, and the role it may play in potential dispersal distance. Samaras of each species were photographed with a Canon Powershot G4 digital camera. Since *Ailanthus* samaras twist about their long axis, they were flattened under glass so that the entire wing area was visible in the image. *Liriodendron tulipifera* samaras were placed

on the dorsal surface of the long axis while being photographed. A digital image analysis program (ImageJ, NIH, Bethesda, Md.) was used to determine wing area by producing a binary image, thresholding the image to isolate the samara, and assessing area with the calibration tool.

Still air descent velocity was regressed on wing loading for each species. Seven outlier observations for one *L. tulipifera* samara were excluded when calculating the mean descent velocity in order to meet the assumption of normally distributed residuals of these data. Although an attempt was made to assuage random error associated with timing a seed's descent by performing many drops of each seed using the same timer, it is likely that these outliers were a result of timing error, hence their elimination from the dataset was justified.

Field site

The field site was located at the West Virginia University Agronomy Farm near Morgantown, WV (N 39° 38', W 79° 55'). The farm consisted of a 59 ha hay field, the perimeter of which was surrounded by deciduous forest ca. 100 years old and comprised of oak (*Quercus sp.*), hickory (*Carya sp.*), maple (*Acer sp.*), black cherry (*Prunus serotina*), and tulip poplar (*Liriodendron tulipifera*). The forest acted as a natural buffer of varying width to other adjacent land uses, resulting in a distinct forest/field interface.

An area source of 30 *Ailanthus* ramets, consisting of four reproductive female stems, was located on the western side of the forest/field interface. Mean *Ailanthus* source height was ca. 18 m and mean dbh was 39.6 cm. Along the same edge 50 m southwest of the *Ailanthus* females were one trifurcated and two other reproductively

mature *L. tulipifera* individuals (Fig. 2.1). Mean *L. tulipifera* source height was ca. 30 m and dbh was 44.8 cm. The adjacent individuals of these two species served as the source from which dispersal was measured.

Nearby *Ailanthus* seed sources were removed to ensure that the focus trees were a single area source for seeds. Other nearby, mostly smaller, *L. tulipifera* seed sources were not removed. Wind data obtained from the National Oceanic and Atmospheric Administration (NOAA) weather station at the Morgantown Municipal-Walter Hart Field Airport, approximately 1 km southwest of the source trees indicated that seed dispersal was sampled in the direction of prevailing winds throughout the dispersal season (Fig. 2.1). Therefore, although some of the nearby *L. tulipifera* seed sources located west of the desired source may have contributed to the ‘seed rain’ observed, owing to the prevailing winds, the primary focus trees were considered to be the main seed source for the downwind seed traps. Given the prevailing winds throughout the dispersal season it is highly unlikely that seeds located to the north, east and south of the focus *L. tulipifera* source were sampled.

Sampling of seed dispersal

A total of 482, circular 0.25 m² seed traps were constructed of 13 cm-wide aluminum flashing with nylon mesh screen attached to the bottom. The sample area consisted of two adjacent 50 m × 200 m plots, with a single plot devoted to each species, for a total sample area of 2 ha. Eleven transects were established in each single-hectare plot at 20 m

Figure 2.1. Trap array and prevailing wind direction at the study site. Trap density along transects between 120 and 200 m is indicated by the number below the seed trap symbol (white dots). Wind vector position represents the direction of maximum daily 2-minute sustained wind gusts taken 10 m above the ground at the Morgantown Municipal-Walter Hart Field Airport, approximately 1 km southwest of the source trees. Vector length shows the number of days in that direction.

intervals from 0 m to 200 m into the field directly east of each of the two focus populations, enabling capture of seeds along prevailing westerly winds. Each transect was 50 m wide, with the largest *Ailanthus* and the trifurcated *L. tulipifera* used to determine the midpoint of each transect at 25 m (Fig. 2.1).

Five seed traps were randomly placed along the five transects from 0 m to 80 m in each plot. However, to better characterize long distance dispersal, the number of seed traps per transect was increased between 100 m and 200 m distances. A study of short-distance *Ailanthus* seed dispersal to 100 m in the same field the previous year showed that there was a log-linear decrease in mean seed density per square meter with increasing distance (Landenberger et al., submitted). Using the regression equation from these data, the mean number of expected seeds per square meter was extrapolated for distances between 100 m and 200 m. This allowed a determination of the number of 0.25 m² seed traps necessary to capture 20 seeds at each sampled distance past 80 m (Fig. 2.1).

Seeds of both species were removed from all traps every two weeks between October 24, 2003 and April 23, 2004, for a total of 13 collection dates. All collected seeds were stored in the lab and allowed to dry at room temperature.

Mean seed density was calculated for both species by dividing the total seeds captured at a given distance by the number of traps at that distance. Means from all distances were then divided by the mean at 0 m to produce a relative measure of seed density that controlled for differences in the total amount of source seed (Landenberger et al., submitted). Two-way factorial analysis of covariance (ANCOVA) was used to test whether the effect of distance on relative seed density differed for the two species. This was done for linear versions of an exponential model as well as a power model. The

exponential model was linearized by regressing log of relative density on distance, producing a “semilog plot” (Portnoy and Willson, 1993) while the power model was linearized by regressing log of relative density on log of distance, referred to as a “log-log plot” (Portnoy and Willson, 1993). Because the relative density at the source (0 m) was always one, these data were excluded from the regression models.

A significant interaction term (distance $\times$ species) indicated different slopes of the species’ log-linear functions. Residuals for both ANCOVA models were tested for, and exhibited, normality using a Shapiro-Wilk W test and the assumption of homoscedasticity of variances was examined by Bartlett’s tests.

Temporal patterns of seed dispersal of the two species were examined by histograms showing the monthly proportion of the total number of seeds captured throughout the dispersal season for each species, as well as the proportion of seeds of each species that contributed to each monthly total of captured seeds.

Ratio of invasive to native seed density with increasing distance into the site

The ratio of native to invasive seed density was determined by dividing the relative mean *Ailanthus* density by the relative mean *L. tulipifera* density at each distance. Regression of this ratio on distance provided a measure of the shift in numerical advantage away from the edge of the open field.

Mass, area and wing loading of field-collected samaras

To determine whether the relationship between samara weight, size and wing loading varied between the species with increasing distance from the source, mass and

area of a sub-sample of up to five completely intact samaras of each species was measured from each transect for every collection date.

Mean samara mass, area and wing loading were analyzed by two-way ANCOVA to test whether there were significant main effects of (nominal) species and (continuous) distance, or a dependency of the factors, on variation in the dependent variables. Due to differences in the sample size of samaras used to calculate mean values, the sample size associated with each value was used as a weighting term for the analyses. All statistical models were performed in SAS JMP (v. 5.1; SAS Institute Inc., Cary, NC).

Results

Samara wing loading and descent velocity

There was a significant, positive linear relationship between wing loading and descent velocity for *L. tulipifera* samaras ($b = 0.02$, $p = 0.001$). Descent velocity increased with increasing wing loading (Fig. 2.2). This relationship did not exist for *Ailanthus*, as samaras with greater wing loading did not descend significantly more slowly than samaras with lower values of wing loading ($b = 0.03$, $p = 0.231$; Fig. 2.2). The linear functions of the two species were not directly compared due to the lack of overlapping wing loading data points (Gotelli and Ellison, 2004). However, both wing loading and descent velocity were lower for *Ailanthus* (Fig. 2.2). The range of wing loading values for the tested *Ailanthus* samaras was 8.60 to 11.03 mg cm^{-1} , while *L. tulipifera* values ranged from 15.34 to 30.52 mg cm^{-1} .

Figure 2.2. Regression of still air descent velocity on wing loading for *A. altissima* and *L. tulipifera* samaras.

Timing of seed dissemination and dispersal pattern comparison

A total of 163 *Ailanthus* seeds were removed from all of the traps throughout the sampling period. Of these, 113 were deposited in the trap array devoted specifically to capturing *Ailanthus* seeds and were used to fit the dispersal models. A total of 3018 *L. tulipifera* seeds were trapped throughout the dispersal season, 2370 of which were removed from the array intended to sample *L. tulipifera* dispersal.

Both species dispersed the largest portion of all total collected seeds within the first month of sampling, but the percentage of the total differed between species. The majority of the *L. tulipifera* seeds (82%) were dispersed in the month of November, while only 40% of the total *Ailanthus* seeds were removed from the traps in the same month (Fig. 2.3A). This percentage declined more sharply for *L. tulipifera* in the subsequent months, such that the second highest percentage of total dispersed seeds occurred in December when only 8.6% of the total was captured. Although there was a more gradual decline in *Ailanthus* seed density over the dispersal season, *L. tulipifera* seed density was at least two times greater in every sampled month (Fig. 2.3B). The smallest discrepancy in seed density between the species occurred in February. Timing of dispersal was not included in the model due to an abundance of zero density values near the end of the dispersal season that did not allow for normally distributed residuals or homogeneous variances.

The overall spatial pattern of dispersal was similar for both species in that both the semilog and log-log models showed the expected, significant decrease in seed density with increasing distance (both models, $p < 0.0001$; Fig. 2.4A-B). Qualitative assessment of the coefficient of determination (r^2) of the models revealed that the log-log plot

Figure 2.3. Proportion of total amount of trapped seed of each species by (A) month and (B) proportion of monthly overall seed total by species.

Figure 2.4. (A) Linearized exponential and (B) power function models of relative mean seed density regressed on distance from the source for *A. altissima* and *L. tulipifera*.

($r^2 = 0.94$) obtained a slightly better linear fit than the semilog plot ($r^2 = 0.88$). Whereas the semilog plot underestimated the densities of both species at distances closer to the source (between 20 and 40 m), both models underestimated seed densities at the extreme tail of the distributions.

Statistical comparison of the slopes of the semilog model showed that the effect of distance on seed density did not differ between the species ($F = 1.754$, $p = 0.204$; Fig. 2.4A). However, for the log-log model the effect of distance on relative seed density tended to differ for the two species ($F = 3.986$, $p = 0.063$; Fig. 2.4B). Individual regression of relative density data of each species showed that the *L. tulipifera* linear function descended towards zero at a slightly greater rate than the *Ailanthus* linear function (*L. tulipifera*, $b = -1.722$; *Ailanthus*, $b = -1.328$). Although not indicative of a significant difference in the slope of the species' linear functions, the presence of this statistical trend may be due to the compression of the power function model's log-transformed x-axis, which may have made the model more sensitive to changes in relative density.

Ratio of native to invasive seed density with increasing distance into the site

There was no significant change in the ratio of invasive seeds to native seeds with distance from the seed source ($F = 2.101$, $p = 0.185$; Fig. 2.5).

Samara mass, area and wing loading

In the field, variation in seed mass with increasing distance tended to differ for *Ailanthus* and *L. tulipifera* ($F_{\text{species} \times \text{distance}} = 3.523$, $p = 0.077$). *Post-hoc* regression analyses

Figure 2.5. Ratio of mean *A. altissima* seed density to mean *L. tulipifera* seed density with increasing distance from the forest edge.

showed that while there was a trend towards a significant increase in mean *L. tulipifera* seed mass with increasing distance from the source ($b = 0.00004$, $p = 0.053$), mean *Ailanthus* mass did not change as distance increased ($b = -0.00001$, $p = 0.294$; Fig. 2.6A).

Seed area differed for the two species, and with increasing distance into the site (main effect of species, $F = 1220.081$, $p < 0.0001$; main effect of distance, $F = 6.192$, $p = 0.023$). At all distances, mean *Ailanthus* seed area was approximately two times greater than *L. tulipifera* area (Fig. 2.6B). Regression revealed that mean *Ailanthus* seed area did not change with increasing distance from the source ($b = 0.0004$, $p = 0.515$), but mean *L. tulipifera* area significantly increased with increasing distance ($b = 0.002$, $p = 0.006$; Fig. 2.6B).

Mean *L. tulipifera* wing loading was significantly greater than that of *Ailanthus* at all distances (main effect of species, $F = 123.337$, $p < 0.0001$), but wing loading was not significantly affected by distance for either species ($p > 0.05$; Fig. 2.6C).

Discussion

Previous research suggests that light seeds travel farther than heavy seeds (Augspurger, 1986; Sorensen, 1986; Greene and Johnson, 1993). Although mass is an important determining factor in dispersal, especially in its relation to still air descent (Guries and Nordheim, 1984), the mass to area relationship (i.e. wing loading) of a seed may be more important in determining dispersal potential (Augspurger and Franson, 1987). This is true particularly for winged species such that, for example, Matlack (1987) found that *Acer platanoides* wing loading accounted for the majority of variation in descent rate compared to investigations of diaspore area or mass alone. The resulting

Figure 2.6. Regression of (A) mean samara mass, (B) area, and (C) wing loading on distance. Data was based on a sub-sample of trapped *A. altissima* and *L. tulipifera* samaras.

rate of descent of a winged seed in its full rotational form could impact the potential dispersal distance of that species.

Although invasive *Ailanthus* and native *L. tulipifera* share the same mode of dispersal by wind, the differing characteristics of their samaras affect their specific descent patterns. *Liriodendron tulipifera* seeds reside on the terminus of the samara, while *Ailanthus* seeds are centrally-located. This results in the seed-side of an *L. tulipifera* samara becoming the leading edge during flight, while *Ailanthus* samaras are twisted at their leading edge. Even though samaras of both species descend in a manner similar to seeds in the “roller” category, *Ailanthus* samaras exhibit an added descent property similar to the “autogyro” (Augspurger, 1986), possibly due to the twisted leading end. Rotation occurs about the long axis as well as spiraling in a helical manner about the short axis, much like a Flettner rotor (Vogel, 1981). Together these movements help to increase drag and slow the rate of descent. The combination of the specific descent pattern of a samara and its wing loading value influence the overall descent velocity.

In this study, *L. tulipifera* samaras exhibited greater values of wing loading resulting in overall higher descent velocity of the species. Given that seeds with greater wing loading are often dispersed shorter mean distances for some herbs (Platt and Weis, 1977), tropical trees (Augspurger and Hogan, 1983), and various *Acer* species (Guries and Nordheim, 1984), *L. tulipifera* samara density was expected to decline more rapidly than *Ailanthus* density as distance increased. However, the field measurements of dispersal by these two species did not support this hypothesis.

Both *L. tulipifera* and *Ailanthus* were effective long distance dispersers. Seeds of *Ailanthus* and *L. tulipifera* were collected from the farthest distance of 200 m in 62% and 92% of the collection dates, respectively. Furthermore, the slopes of the linear functions of both models showed no significant inter-specific difference in the rate of decline in relative seed density with increasing distance, indicating similar mean dispersal distance of the samaras of these species. These results suggest that factors other than the evident differences in wingloading and descent velocity must explain why the two dispersal curves are equivalent.

Other important external factors that may greatly affect dispersal distance are summarized by a simple ballistic equation that has been employed by previous investigators of seed dispersal (Cremer, 1977; Augspurger, 1986; Matlack, 1987). This equation incorporates the effect of release height (H) and the horizontal wind speed at the time of release (W), as well as descent velocity of a seed (V) in determining dispersal distance (D).

$$D \propto \frac{H \times W}{V}$$

Given the mean descent velocities calculated for the two species in this study (*Ailanthus* $\approx 0.71 \text{ m s}^{-1}$, *L. tulipifera* $\approx 1.15 \text{ m s}^{-1}$), if samaras of both species were released from the same height of 20 m during a 6.71 m s^{-1} (ca. 15 mph) wind gust, *Ailanthus* samaras would travel ca. 188.9 m, compared to ca. 116.6 m for *L. tulipifera*. Under identical horizontal wind conditions an *L. tulipifera* samara would have to be released at a 62% greater height than an *Ailanthus* samara to be dispersed at approximately the same distance. The likelihood of encountering this situation in a natural setting is high considering that *L. tulipifera* is one of the tallest eastern deciduous

trees, reaching heights at maturity between 30.5 and 45.7 m (100 to 150 ft) (Beck, 1990), while *Ailanthus* maximum height vary from 17 to 27 m (56 to 90 ft) (Miller, 1990). Height differences of the sampled trees in this study (*Ailanthus*, ca. 18 m; *L. tulipifera*, ca. 30 m) were sufficient to explain the similarity in dispersal distance between *L. tulipifera* and *Ailanthus* despite a theoretical advantage of *Ailanthus*, based on wing loading and descent velocity values.

Release height influences dispersal distance indirectly (as well as directly) by affecting the wind speed encountered during, and after, release. Winds are higher at greater canopy heights (Grace, 1977) and canopies may also provide friction necessary to create turbulence (Finnigan, 1985), especially at a forest edge (DeWalle, 1983). This turbulence is often adequate and may even be necessary for dispersal, particularly at long distances (Nathan et al., 2002).

Another factor that could influence dispersal distance is the strength with which samaras are connected to the infructescence. Each *Ailanthus* samara in a cluster is individually attached to the gynophore, with fibrovascular bundles extending down one edge of the wing that tear away from the wing given sufficient mechanical force (Landenberger et al., submitted). In contrast, *L. tulipifera* samaras are tightly packed in a conical-shaped cluster, where the finiculus of each carpel detaches from an elongated receptacle during development. Only the outermost layer of samaras closest to the peduncle of the cluster remains attached after ripening. Therefore, whereas each *Ailanthus* samara in a cluster is attached independently of the others, *L. tulipifera* samaras are neatly stacked yet unconnected within the infructescence. These morphological

differences between the seed clusters also influence the mechanism and form of samara release for the two species.

A wind event that releases any amount of seed from an *L. tulipifera* cluster may disrupt and weaken the resistance of the remaining unconnected, previously stacked samaras to being dislodged. Thus, if one seed is released it is likely that others will follow soon thereafter. Close synchronization of seed release would be expected to lead to a shorter temporal range of complete samara dispersal of *L. tulipifera*. Indeed, previous research suggests that the majority of *L. tulipifera* seed is disseminated in October and November (Carvell, 1955; Bonner and Russell, 1974; Kavanagh, 1990). This study is consistent with those data in that the largest portion of the total *L. tulipifera* seeds distributed into the traps were removed in the first month of sampling. In contrast, the individually held *Ailanthus* samaras are frequently dispersed well into the following spring (Miller, 1990).

Temporal differentiation of seed dispersal may have varying consequences in natural systems. Early dispersal could be beneficial by allowing the seed a longer time to infiltrate a leaf or vegetation layer (Kavanagh, 1990), increasing seed contact with a moist surface and subsequently increasing the probability of germination (Schopmeyer, 1974). Differences in stratification requirements may also drive this phenomenon, as *Ailanthus* requires none (Graves, 1990), but *L. tulipifera* must over-winter in natural conditions (Beck, 1990). Alternatively, a seed that is lying on the ground for an extended amount of time could be more vulnerable to predation by rodents or pathogens that can lower seed survival rates (Chambers and MacMahon, 1994; Ostfeld et al., 1997).

Regardless of these possible outcomes, differences in samara release due to differential seed cluster morphology may also explain the tendency of larger *L. tulipifera* seeds to be transported at greater distances. If *L. tulipifera* samaras are released in greater synchrony during greater wind speed and turbulence events, then this could have aided the transport of seemingly heavier, yet larger-winged *L. tulipifera* samaras longer distances, as more wing surface area allowed greater exposure to wind.

Since seed weight is often assumed to be related to fitness (Harper, 1977), then the combination of the seed cluster and whole tree traits that allow for farther dispersal of these *L. tulipifera* seeds may be interpreted as evolutionary mechanisms to increase the probability of robust seed reaching optimal sites. What becomes important to know is whether these *L. tulipifera* seeds exhibit greater viability and vigor than their own counterparts at shorter distances and *Ailanthus* seeds at the same distances.

In terms of seed viability, *Ailanthus* seems to have an advantage in that its germination capacity is high (75 to 96% per seedlot; Al'benskii and Nikitin, 1956; Little, 1974; Graves, 1990) whereas *L. tulipifera* seed viability is much lower (5 to 20% throughout the dispersal season; Beck, 1990), possibly due to inefficient pollination (Boyce, 1961). Moreover, *L. tulipifera* samaras are 1-2-seeded (Britton and Brown, 1970) but may be completely devoid of an embryo, or may have one or two intact embryos. Whether or not seed size of these two species is correlated with embryo existence or germinability has yet to be tested.

Due to the immotility of the adult life history stage of most plants, seed dispersal is the initial, and perhaps most important, process determining species spread. The present study describes the likely dispersal scenario of an uncommon invasive into an

open environment surrounded by a common native. Because species migration on a landscape scale is severely dispersal-limited (Takahashi and Kamitani, 2004), the implications of these results are important to consider given increasing rates of forest disturbance by humans that can eliminate dispersal barriers, particularly in the eastern U.S. where both species are widespread. The fact that they both effectively exhibit long distance dispersal at circum-equal proportions regardless of distance suggests that the template for subsequent succession in an environment such as this is equally laid which, combined with factors such as seed quality and environmental conditions in the final resting place of the seed, will greatly affect seedling establishment and influence the outcome of succession.

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CHAPTER 3

Germination and early growth response of invasive *Ailanthus altissima* and native *Liriodendron tulipifera* in three levels of forest disturbance

Abstract

Increasing rates of forest disturbance may provide greater opportunity for invasion of nonnative species, perhaps altering the successional trajectory of native plant communities. Invasive *Ailanthus altissima* and native *Liriodendron tulipifera* have similar life histories and niches, and therefore often co-occur. To examine how disturbance affects the establishment of these species, I performed a field experiment to evaluate the response of seeds and transplanted seedlings to three types of recent disturbance on north and south-facing aspects. *Liriodendron tulipifera* germination was severely limited by inviability, and significantly lower than *Ailanthus* germination in all sites. The effect of disturbance type on *Ailanthus* germination depended on aspect only in the second growing season. A growth chamber experiment indicated that differences in light exposure indirectly affected *Ailanthus* germination, suggesting that other factors were more important. In contrast, mean seedling survival, biomass, leaf area and leaf area ratio was greater for *L. tulipifera* in all field sites. Overall, the north-facing selective cut provided a disproportionately large number of ideal microsites for *L. tulipifera* establishment. Collectively, this study demonstrated that different timber harvest practices produce heterogeneous mosaics of suitable microsites for germination and establishment not described by mean light levels. Limited *L. tulipifera* germination may be a serious constraint to population establishment if seeds are deposited for the first time immediately after a disturbance event. However, if viable seeds of both species exist, native individuals are more likely to out-perform the invasives. This does not preclude the possibility that a small number of *Ailanthus* may establish a foothold in newly-created habitat.

Introduction

Forest disturbance is typically characterized by biomass removal (Grime 1979) that creates new growing space (White and Pickett, 1985), the amount of which is determined by the type and extent of disturbance. Natural disturbances resulting from stochastic events such as fire (Thonicke et al., 2001) and strong winds (Runkle, 1982; Rebertus and Meier, 2001) are important components of botanical communities and may even be necessary for maintenance of historical plant associations (e.g. Cowling et al., 1986; During and Willems, 1986) and distributions, due to plant adaptation to a particular disturbance regime (Keeley and Keeley, 1981; MacDonald, 2003). Mechanisms affecting post disturbance succession are complex, but an important factor in the process is species performance after arrival in the site (Pickett et al., 1987). Those that regenerate early and quickly in new openings may dominate for long periods of time and have momentous effects on the trajectory of stand initiation (Oliver and Larson, 1996). Exotic, invasive species frequently exploit this 'regeneration niche' (Grubb 1977), especially when disturbance regimes are altered or interacting (Rejmanek, 1989; Hobbs, 1989; Hobbs and Huenneke, 1991).

Anthropogenic causes often result in different frequency and type of disturbance than natural ones (Oliver and Larson, 1996) and may promote invasion of nonnative species (McNab and Meeker, 1987; Parker et al., 1993; Stylinski and Allen, 1999; Silveri et al., 2001) that may expand their range and numbers in direct proportion to disturbance. Invasion probability also depends on species' propagule pressure on a disturbed area as a result of proximity and dispersal capacity (Hobbs and Huenneke, 1991), as well as the response of species to the disturbance (Moore and Noble, 1990).

Timber harvest is an increasingly common anthropogenic disturbance, and many types of harvest exist. The frequency of timber harvest in the U.S. has continually increased since the 1970's, predominantly in the hardwood regions (Adams et al., 2000), reflecting both the rising demand for forest products (Fajvan et al., 1998; Adams et al., 2000) and maturation of second growth forest (Fajvan et al., 1998).

Effects of harvest include increased understory light availability and soil disturbance (Mou et al., 1993), as well as indirect effects of soil and tree nutrient and carbon removal (Adams et al., 2000). These effects are expected to be greater in areas of whole-stand removal (i.e. clearcuts) than in forests subject to partial harvest methods such as selective cutting or diameter limit cuts, where trees of the highest economic value, often of a specific size, are removed (Oliver and Larson, 1996; Adams et al., 2000). Although clearcutting does occur, partial cutting methods currently represent the most frequent type of harvest of eastern hardwoods (Miller and Kochenderfer, 1998; Stoyenoff et al., 1998). At this time, harvest occurs primarily on private lands (Adams et al., 2000).

Several 'shade-intolerant' native species are expected to invade large gaps and clearings created by timber harvesting. For example, in the mesic areas of the mid-Atlantic region, native *Liriodendron tulipifera* (i.e. yellow poplar or tulip poplar) frequently colonizes these areas since regeneration requires significant openings (Busing, 1995). However, it is also an important timber species (Fajvan et al., 1998) due to its economic value (Beck, 1990). Rapid early establishment and growth and stump sprouting (Beck, 1990), make this species a principal pioneer species that may even form

nearly pure stands, depending on resource availability, interference and competition from other species (Della-Bianca, 1983).

Although numerous invasive herbaceous plants and vines are found in the eastern deciduous forest, fewer exotic trees have successfully invaded. However, *Ailanthus altissima* (henceforth referred to as *Ailanthus*) has expanded its range dramatically since the previous extensive timber cutting in the eastern U.S. and has recently been found in old and second growth forest (Kowarik, 1995; Knapp and Canham, 2000). In its native range of China, *Ailanthus* is used for ornamental planting and timber, and acts as forage for the silk-producing caterpillar *Samia cynthia* (Zheng et al., 2004). However, since its introduction to the U.S. as an urban horticultural species (Hu, 1979), *Ailanthus* has since become an aggressive invader in more natural habitats. Rapid establishment and growth, and vegetative reproduction in high light environments make disturbed areas such as timber harvests particularly prone to invasion by *Ailanthus* (Call and Nilsen, 2003). An allelopathic compound found in leaves, wood and roots (Heisey 1990, Heisey 1996) may exacerbate competitive exclusion of native plants, aiding in the formation of dense, monotypic stands (Mergen, 1959).

Given the life history, ecological, and reproductive similarities between *Ailanthus* and *L. tulipifera*, as well as escalating levels of human disturbance of natural habitats, these species may increasingly encounter one another during early forest succession. Moreover, despite differences in seed morphology these two wind-dispersed species had very similar dispersal curves into an open field (Kota, 2005) suggesting that the template for succession can be evenly laid, given equivalent numerical representation of reproductive females. Therefore, early species differences in germination and

establishment can be critical in determining the trajectory of succession (Grubb, 1977; Connell and Slatyer, 1977; Picket et al., 1987; Oliver and Larson, 1996).

The purpose of this study was to compare germination and growth of invasive *Ailanthus* and native *L. tulipifera* in three levels of forest disturbance; clearcut forest, selective cut forest, and intact forest over two growing seasons. Since both species are reported to be shade-intolerant, we hypothesized that germination and growth would increase with increasing levels of harvest, regardless of species. We tested whether different *Ailanthus* maternal seed sources differed in their germination potential. We predicted that the species that allocated relatively more energy towards aboveground resources might become established more rapidly. By systematically locating our sampling sites (within disturbance type), we determined whether aspect and the distance from forest edges influenced seedling germination and growth. A growth chamber study was employed as an attempt to confirm the direct role of light variability in germination.

Materials and Methods

Study sites

Each of the three disturbance types had a north-facing and a south-facing site, for a total of six study sites. All sites were located within 11 km of Morgantown, WV (N 39° 38', W 79° 55') and were comprised of ca. 100 year-old, second-growth forest consisting of the yellow poplar- white oak- northern red oak dominant cover type (Carvell, 1980).

The two sites within each disturbance level (one south and one north aspect) were closely associated spatially such that they had similar disturbance histories. The high-

level disturbance sites were clearcut in spring 2003, and the intermediate sites were selectively cut by the 14 in diameter limit method in late Fall 2002. While no residual stems remained in the clearcut sites, remnant trees (primarily *Prunus serotina* and *Acer rubrum*) were scattered throughout the selective cut sites.

All sites were adjacent to open fields, creating a distinct edge along the site/field interface. *Ailanthus* was not a component species in either of the intact sites or the south-facing selective cut; however, two females were within 200 m west of the north-facing selective cut. Seven and five females existed along the edge of the north-facing and south-facing clearcuts, respectively.

A single 0.5 ha experimental plot was established in each site. Each plot was centrally located within the overall disturbed (and intact forest) area, and consisted of seven, 50 m long transects laid parallel to the edge from 0 to 100 m in the site (Fig. 3.1). Six 0.25 m², circular germination “arenas” made of 13 cm high aluminum flashing were randomly placed along each transect (Fig. 3.1).

Field study of germination

On May 30, 2003 fifty *Ailanthus* seeds were sown in every arena in all sites for a total of 12,600 seeds. The seeds had been previously stratified in cold, wet sand for approximately 1 year and originated from six different source trees. All seeds placed within an arena were from the same randomly chosen source. The number of arenas containing seeds from a single source differed among sites due to unequal amounts of source seed. Any naturally occurring *Ailanthus* seedlings were removed from an arena before sowing experimental seeds. All arenas were visited every two weeks for the

Figure 3.1. Experimental layout of plots in each site. Seed arenas were placed at six random locations along each transect. An experimental seedling phytometer of each species was planted at five of the arena locations.

subsequent eight weeks and the number of germinated seeds was recorded. Germinated seeds were removed from arenas at each census.

Since stratified *L. tulipifera* seeds were not available to provide a comparison of germination in 2003, the experiment was repeated in 2004 with some modifications. Seeds of both species were stratified in cold, wet sand for ca. three months prior to being sown on May 10, 2004. *Ailanthus* seeds were removed from a single tree in December 2003 and *L. tulipifera* seeds were provided by the F.W. Schumacher Co. (Sandwich, MA) in early February 2004.

The same arena locations from the previous year were reused for this comparative germination study, except that two arenas from each transect were randomly chosen as controls and received no seeds. Fifty seeds of both species were sown in each of the four experimental arenas along all transects in the six sites, for a total of 8,400 experimental seeds per species. The interior biotic and abiotic composition of each arena was left undisturbed except for the removal of any visible seedlings of either species prior to sowing experimental seeds. The number of germinated seeds of each species was recorded at two week intervals over the following eight weeks, and germinated seeds were removed from the arenas.

Loglikelihood was first used to test whether the probability of *Ailanthus* germination in 2003 varied among seed sources. Effects in the model included site, seed source (i.e. tree), site $\times$ source, and arena nested within the site $\times$ source interaction. A significant source or site $\times$ source effect would indicate differential germination among sources.

To characterize the germination environment in broad terms, we examined the frequency of 'safe microsites', defined here as arenas in which at least one seed germinated. Loglikelihood was used to determine how the probability that an arena was a safe microsite for germination varied with disturbance type (nominal), distance from the forest edge (continuous), aspect (nominal) and all combinations of these factors. The nominal main effect of year was added to this model to test for a difference in the probability of safe microsites for *Ailanthus* germination between 2003 and 2004. Similarly, for 2004 only, the nominal main effect of species was added to the original model to determine whether the abundance of safe microsites differed for *Ailanthus* and *L. tulipifera*. Since there were so few safe *Ailanthus* germination microsites in the intact forest in both years, these data were excluded from the 2004 *Ailanthus* analysis.

Analysis of covariance was used in the same models as above to determine how the continuous independent variable of rate of germination in the safe microsites (arenas with germination > 0) varied between years for *Ailanthus* and between species in 2004. Data from the intact forest sites were excluded from analyses exclusively examining *Ailanthus* due to the occurrence of so few safe germination microsites. The same ANCOVA model was applied to the number of germinated seeds in each safe microsite to provide interspecific comparison of germination.

To test for potential movement of seeds either into or out of arenas, additional seeds were demarcated and placed inside and outside of arenas at one representative site of each disturbance level. In 2003, ten *Ailanthus* seeds were painted green and placed within two randomly chosen arenas and another ten seeds were painted red and placed just outside of the same arenas. The number of green and red colored seeds within an

arena was counted at each germination sampling date. This method was repeated with both species in 2004. Only one seed was found to have emigrated out of an arena located on a steep slope in the intact forest in 2003. Therefore, movement of experimental seeds of both species was considered negligible, and the count of germinated experimental seeds was therefore considered reliable.

Light Measurements

One of the most important environmental factors thought to affect establishment of shade-intolerant species is light. To test how daily light exposure varied among and within sites with increasing disturbance, total integrated light was measured in all sites by the diazo method (Friend, 1961; Sullivan and Mix, 1983; Landenberger and Ostergren, 2002). One sensor was placed within each germination arena in all plots ($n = 35$ samples per plot) to measure light on a cloudless day in July 2003. Each sensor was mounted on a 13 cm nail and exposed from sunrise until after sunset. The sensors were later calibrated using a LI-COR quantum sensor (LI 1000; LI-COR Biosciences, Lincoln, NE) on a second cloudless day by placing them in the open for varying lengths of time to determine the relationship between light exposure and diazo bleaching ($n = 18$ sensors, $r^2 = 0.94$; $y = 0.401x + 3.45$). All sensors were developed in ammonium hydroxide vapor for 20 minutes then scored by counting the number of bleached diazo sheets. Light measurements provided an estimate of integrated photosynthetic active radiation (PAR) ($\mu\text{mol m}^{-2} \text{d}^{-1}$) for all sites.

Mean integrated PAR (± 1 standard error) was plotted for each disturbance type. For germination arena locations at which light measurements were taken, logistic

regression was used to determine how the probability of a safe *Ailanthus* germination microsite changed with increasing light, followed by linear regression of germination rate within safe microsites on cumulative PAR.

Instantaneous PAR measurements were taken in all sites with a LI-COR quantum sensor between noon and 1:30 p.m. on two consecutive cloudless days in July 2004. No less than five measurements were taken along each transect. Observations from the 0 m and 10 m transects were excluded from analyses to avoid including measurements of possible edge-affected light. Mean PAR ($\pm$ 1 standard error) was plotted to show how overall light measurements differed among the interior of the disturbance types in 2004. The coefficient of variation was calculated as a measure of relative variation in light for each disturbance type (Sokal and Rohlf, 1995; Gotelli and Ellison, 2004).

Growth chamber germination study

A growth chamber experiment was performed in Fall of 2004 to investigate whether light alone is a significant influential factor for germination. Fifteen replicate 15 cm 'azalea' pots containing homogenized field soil and 15 seeds of both species were exposed to two levels of light that closely mimicked mean instantaneous values of the selective cut ($715.9 \mu\text{mol m}^{-2} \text{s}^{-1}$, ± 56.8) and the intact forest ($14.7 \mu\text{mol m}^{-2} \text{s}^{-1}$, ± 0.95). These levels were chosen based on observations of large differences in germination in the field between those two sites. Shade cloth was placed over frames to allow for light treatments of ca. 675 and $14 \mu\text{mol m}^{-2} \text{s}^{-1}$, respectively, which are within the confidence interval range for field measurements. All pots were placed in a growth chamber set at 20°C , which is an optimal temperature for *Ailanthus* germination and

close to the optimal germination temperature of 21° C for *L. tulipifera* (Baskin and Baskin, 1998). May 2004 mean daytime relative humidity of 70% was calculated from data collected by the National Climatic Data Center (NCDC) at Morgantown Municipal-Walter Hart Field Airport, and a photoperiod cycle provided 14.5 hrs light and 9.5 hrs dark. Carbon dioxide concentrations were set at the approximate current ambient atmospheric level of 375 ppm. To eliminate positional effects within the growth chamber, pots and associated shade treatments were randomly rotated within the growth chamber every other day throughout the experiment. Seeds were watered every other day and scored for germination once per week for six weeks.

Every seed was scored as germinated or not germinated and loglikelihood was used to determine whether the probability of germination differed between species. Data were then separated by species and loglikelihood was used to test for a differential effect of light on the probability of germination of each species.

Seedling survival and growth

To compare the growth response of the two species in varying levels of forest disturbance on north- and south-facing aspects, the experimental 'phytometer' method was used (Antonovics and Primack, 1982; McGraw and Antonovics, 1983). Two holes were bored immediately adjacent to five randomly chosen germination arenas along all transects in every site by removing a soil plug. Naturally germinated first year seedlings of both species were removed from the north-facing, selective harvest site in early May 2003. Seedlings were grown separately in peat containing no additional nutrients in greenhouse flats for one month under light conditions similar to the selective cut site

from where they were extracted, then randomly planted into the holes that resulted from soil extraction. One individual of each species was planted at each of five locations along all transects in every site. After planting, initial stem height was measured on all phytometers. Height measurements and leaf damage were recorded for surviving plants in late September 2003, and stem height was measured again in July 2004. All surviving plants were harvested in early September 2004. Leaf area was measured with a LI-COR area meter (model LI 3000 A; LI-COR Biosciences, Lincoln, NE). Plants were dried at 65° C for 72 hours and then leaf, stem and root mass were measured.

To first determine whether survival differed between the species at the end of two growing seasons, the main effect of species was examined in the context of a loglikelihood model also containing the effects of disturbance, aspect, distance, and all possible interactions. In the event of a significant effect of species, data for each species were separated and the three-way model repeated.

Low survival on many transects within the sites prompted the pooling of data across distance to eliminate possible spurious results due to small sample size when analyzing phytometer growth variables. Removal of distance from the model is further justified since the remaining effects, disturbance, aspect and species, still permitted us to determine whether the two species were differentially responding to varying levels of forest disturbance. Three-way factorial ANOVA with the above-mentioned model effects was performed on total biomass, leaf area, leaf mass ratio, height growth and the ratio of root to shoot mass.

Results

Field study of germination

The source from which experimental *A. altissima* seeds originated in 2003 did not significantly affect the probability of germination (source; loglikelihood = 0.92, $p = 0.97$), nor did the effect of a site depend on the source (source; loglikelihood = 0.01, $p = 1.0$). These results indicated that seeds from all six sources used for the 2003 germination study did not differ in their probability of germination, and justify the use of seeds from a single source in the 2004 experiment. This suggests that seeds sampled from one source would likely represent the response of *A. altissima* in general.

In 2003, the abundance of safe sites for *Ailanthus* germination varied with disturbance type (disturbance; loglikelihood = 23.27, $p < 0.0001$). This difference was due to a minimal number of safe microsites in the intact forest; less than 20% of these arenas contained germinated seeds. There was no difference in safe site abundance between the clearcut and selective cut sites (disturbance; loglikelihood = 0.017, $p = 0.89$; Fig. 3.2).

Within the safe germination microsites of the clearcut and selective harvest, the effect of disturbance on *Ailanthus* germination rate depended on aspect (disturbance $\times$ aspect; $F = 13.67$, $p = 0.0003$). In 2003, a greater number of *Ailanthus* seeds germinated on the south-facing aspect in the clearcut sites, whereas seed germination in the selective-cut forest was greater on the north-facing aspect (Fig. 3.3).

In 2004, the effect of disturbance on the abundance of safe microsites for *Ailanthus* germination depended on aspect (disturbance $\times$ aspect; loglikelihood = 6.62,

Figure 3.2. Frequency of safe germination microsites in each field site. Safe microsites were defined as experimental arenas containing at least one germinated seed. Experimental *Ailanthus* seeds were sown in two consecutive years, and *L. tulipifera* seeds were sown only in the second year.

Figure 3.3. Mean *Ailanthus* germination rate in safe germination sites in the first and second growing seasons after timber harvest. Intact forest data was not included due to low overall germination in those sites.

$p = 0.01$). The north-facing clearcut had the highest frequency of safe microsites, while the south-facing clearcut and the two selective harvests had similar frequencies of safe *Ailanthus* germination microsites (Fig. 3.2). Within these safe microsites, the effect of disturbance on *Ailanthus* germination rate depended on aspect (disturbance $\times$ aspect; $F = 9.82$, $p = 0.003$). Contrary to 2003 results, in 2004 *Ailanthus* germination rate was greatest in the north-facing clearcut, while germination was similar for the south-facing clearcut and the selective harvest sites (Fig. 3.3). An unexpected observation in this study was that 3.5% of *A. altissima* seeds sown in the intact forest sites in 2003 germinated in 2004.

There were significantly more safe *Ailanthus* germination microsites in 2003 than in 2004 (year; loglikelihood = 11.57, $p = 0.0007$). Within those safe microsites, there was also a lower overall germination rate in 2004 than in 2003 (year; $F = 22.16$, $p < 0.001$).

The control arenas in 2004 allowed for observation of natural germination. When compared on a per trap basis across all sites, a mean of 0.057 *Ailanthus* seedlings germinated within each control arena, while 2.62 experimental seeds germinated per experimental arena. Therefore, I was confident that ca. 99% of the germinated seeds in experimental arenas were from seeds we placed there. Only ca. 82% of *L. tulipifera* counted were our experimental seeds since a mean of 0.071 natural seedlings germinated per control arena, and 0.429 in each experimental arena. Despite this discrepancy, a uniform method of adjusting for the possibility of counting non-experimental *L. tulipifera* seedlings was not apparent. The initial number of natural seeds within the control and experimental arenas was unknown, despite the removal of any obvious natural seeds

when sowing the experimental seeds. Therefore, no adjustments were made to the experimental observations.

The abundance of safe germination microsites differed for the two species in 2004 (species; loglikelihood = 20.32, $p < 0.0001$). There were approximately twice as many safe sites for *Ailanthus* germination (47% of arenas) than for *L. tulipifera* (25% of arenas). Germination rate within those safe sites was significantly greater for *A. altissima* (6.8%) than for *L. tulipifera* (2.9%) (species; $F = 26.39$, $p < 0.001$). Germination within the *L. tulipifera* safe microsites did not differ by disturbance, aspect, distance, or any combination of those model effects (all effects, $p > 0.05$).

Light measurements

Cumulative light was highest in the clearcuts, followed by the selective-harvest sites, and lowest in the intact forest sites (Fig. 3.4A), indicating that the overall light environments of the disturbances were consistent with the expected pattern of increasing light as the amount of disturbance increased. The probability that an arena was a safe microsite for *Ailanthus* germination in 2003 increased significantly with increasing PAR (loglikelihood = 46.97, $p < 0.0001$; Fig. 3.5A). Among those safe sites, germination rates also increased with increasing light ($p < 0.001$; Fig. 3.5B).

The same difference among disturbance types was observed for instantaneous light measurements in 2004 (Fig. 3.4B), suggesting that the expected difference in mean light remained consistent at least into the second growing season after disturbance. Furthermore, the coefficient of variation of mean instantaneous PAR was greatest in the selective harvest sites (Fig. 3.4B). This suggests that the light environment in the forest

Figure 3.4. Mean *Ailanthus* germination rate under mimicked relative light levels of the selective cut and intact forest sites, and actual germination rate in the interior of those sites.

Figure 3.5. (A) Cumulative photosynthetically active radiation (PAR) measured over one full day in the first growing season after disturbance for each site category and (B) relative measures of PAR, and associated coefficient of variation, for each disturbance type in the second growing season. Residuals of these data were not normally distributed and thus could not be tested for differences using parametric statistics.

subject to selective harvest became more variable, with shady areas remaining under residual individuals while tree removal results in areas exposed to more light.

Growth chamber germination study

The probability of seed germination differed between the two species (species; loglikelihood = 71.18, $p < 0.0001$) in that the overall germination rate of *Ailanthus* was 35.3% compared to 1.1% for *L. tulipifera*. Possibly due to this low germination rate for *L. tulipifera*, the probability of germination was not significantly different between the light levels (light; loglikelihood = 0.007, $p = 0.93$). However, the probability of *Ailanthus* germination depended on the light level (light; loglikelihood = 16.06, $p = 0.0001$). *Ailanthus* germination rate was significantly greater under the low light conditions (44.4%) than under high light (26.2%; Fig. 3.6). This was inconsistent with *Ailanthus* germination in the field. Excluding the 0 and 10 m transects to remain consistent with the instantaneous light measurements from the field, overall *Ailanthus* germination rate was greater in the higher light environment of the selective cut (14.7%) compared to the low light of the intact forest (0.26%; Fig. 3.6).

Seedling survival and growth

Overall experimental phytometer survival was significantly greater for *L. tulipifera* (42.4%) than *Ailanthus* (15.7%) after two growing seasons (species; loglikelihood = 34.02, $p < 0.01$). Among *L. tulipifera* seedlings, survival differed among the types of disturbance (loglikelihood = 22.59, $p < 0.01$), such that seedling survival was greatest in the selective cut, followed by the clearcut, and then intact forest sites (Fig. 3.7A). The

Figure 3.6. (A) Increase in the probability that a safe germination microsite was encountered and (B) increase in germination rate within those safe sites with increasing levels of cumulative PAR. Data is for *Ailanthus* from the clearcut and selective cut sites in the first growing season after disturbance.

Figure 3.7. Survival rate of (A) *L. tulipifera* and (B) *Ailanthus* experimental phytometer seedlings after two growing seasons.

effect of disturbance on *Ailanthus* seedling survival depended on aspect (disturbance $\times$ aspect; loglikelihood = 8.23, $p = 0.02$). Survival was greatest in the south-facing clearcut, did not differ between the selective harvest sites, and was greater in the north-facing intact forest (Fig. 3.7B). Regardless of species, the probability of second-year survival was significantly lower for plants whose leaves were damaged or missing at the end of the first growing season (loglikelihood = 34.41, $p < 0.001$).

There was a large significant main effect of species on total plant biomass, leaf area and leaf mass ratio (Tab. 3.1). After two growing seasons mean *L. tulipifera* total biomass (4.47 g) was more than three times greater than *Ailanthus* biomass (1.35 g), regardless of disturbance or aspect (Fig. 3.8A). Furthermore, mean *L. tulipifera* leaf area was ca. nine-fold greater (Fig. 3.8B) and *L. tulipifera* leaf mass ratio was two times greater (Fig. 3.8C) than those values for *Ailanthus*.

The effect of aspect on total biomass also differed for the two species (aspect $\times$ species; $F = 5.77$, $p = 0.02$). When separated by species, one-way ANOVA showed that mean biomass was significantly greater for *L. tulipifera* growing in the north-facing selective cut (main effect of disturbance; $F = 7.09$, $p = 0.01$; Fig. 3. 9).

Although there was only a statistical trend towards a differential effect of aspect on seedling height growth between the two species ($F = 3.49$, $p = 0.07$), there was a significant effect of disturbance that depended on site aspect ($F = 5.37$, $p = 0.02$). Regardless of species, seedlings grew taller in the south-facing clearcut, but plant height was greatest in the north-facing selective cut site. Overall, after two growing seasons mean seedling height was significantly greater in the selective cut sites compared to the clearcut sites (main effect of disturbance: $F = 8.89$, $p < 0.01$).

Table 3.1. F-ratio and p-value for ANOVA model effects on measured and calculated phytometer growth and allocation variables. Significant p-values ($p < 0.05$, denoted by (*)) and trends ($0.05 < p < 0.1$, denoted by (†)) are in bold print.

Model Effect	<i>df</i>	Total Biomass	Height Growth	Leaf Area	LMR	Root: Shoot
Disturbance (D)	1	F = 1.01 (p = 0.32)	F = 8.89* (p = 0.00)	F = 2.06 (p = 0.16)	F = 0.06 (p = 0.81)	F = 3.09† (p = 0.08)
Aspect (A)	1	F = 0.48 (p = 0.49)	F = 1.47 (p = 0.23)	F = 1.08 (p = 0.30)	F = 2.28 (p = 0.14)	F = 0.29 (p = 0.59)
Species (S)	1	F = 18.1* (p < 0.01)	F = 2.29 (p = 0.13)	F = 48.8* (p < 0.01)	F = 38.6* (p < 0.01)	F = 1.35 (p = 0.25)
D × A	1	F = 3.98† (p = 0.05)	F = 5.37* (p = 0.02)	F = 0.79 (p = 0.38)	F = 0.79 (p = 0.38)	F = 4.02† (p = 0.05)
D × S	1	F = 0.73 p = (0.39)	F = 0.08 (p = 0.78)	F = 0.06 (p = 0.81)	F = 0.64 (p = 0.43)	F = 0.00 (p = 0.96)
A × S	1	F = 5.77* (p = 0.02)	F = 3.49† (p = 0.07)	F = 0.55 (p = 0.46)	F = 0.11 (p = 0.74)	F = 0.45 (p = 0.50)
D × A × S	1	F = 0.00 (p = 0.96)	F = 0.64 (p = 0.42)	F = 0.59 (p = 0.45)	F = 1.24 (p = 0.27)	F = 0.02 (p = 0.89)

Figure 3.8. Species differences in phytometer biomass, leaf area and leaf mass ratio after two growing seasons.

Figure 3.9. Differential effect of aspect on phytometer root mass of each species.

The effect of disturbance on root to shoot ratio tended to differ by aspect ($F = 4.02$, $p = 0.05$). Separate analyses by species showed a similar trend towards a dependency of disturbance on aspect only for *L. tulipifera* ($F = 4.04$, $p = 0.05$) where root to shoot ratio tended to be higher in the north-facing selective cut. Regardless of species, the ratio of root to shoot mass tended to be greater in the selective cut sites ($F = 3.09$, $p = 0.08$).

Discussion

Distinctions among photosynthetic and growth response of tree species to varying light levels have led to classifications of their light tolerance (Spurr and Barnes, 1973; Daniel et al., 1979). For seeds of ‘shade intolerant’ species light sensitivity would seem to be an adaptive quality, as it could indicate whether the seed is in an area that may provide a reasonable probability of a seedling reaching reproductive maturity (Vidaver, 1977). Results of this study suggest that the germination response to light of species in particular tolerance categories varies greatly, and may not be the same as their expected growth response to light. In 2003, *Ailanthus* germination increased with increasing light, but germination was greatest in the lowest light conditions of the growth chamber. Although light measurements were only taken once during the germination trials, and therefore may not accurately represent overall diurnal light conditions throughout the season, the light-germination relationship was clear. The contrasting patterns between the field and growth chamber studies indicate that light quantity itself was not the direct factor influencing *Ailanthus* germination.

Germination response of some temperate trees is positively associated with increasing light (McDermott, 1953), but many tree seeds germinate equally well in light or dark conditions (Daniel et al., 1979). There are a multitude of effects that interact in complex ways to induce the breaking of seed dormancy and promote germination (Vidaver, 1977; Fenner, 1985; Baskin and Baskin, 1998). These factors are often species-specific and include endogenous effects such as genetic controls, maternal effects and seed quality as well as exogenous effects of light, temperature, water, soil microtopography and soil chemistry (Maguire, 1977; Vidaver, 1977; Grime et al., 1981; Fenner, 1985). Results of this study suggest that interaction among many factors may control water availability and thus *Ailanthus* germination.

High levels of light may increase soil temperature and soil moisture evaporation that can interfere with water imbibition, which is necessary for germination (Fenner, 1985). Soil dried more quickly in the pots exposed to higher light in the growth chamber which may have interfered with imbibition, resulting in lower germination compared to the low light treatment. Alternatively, in the shaded environment of the clearcut, seed contact with leaf litter may have resulted in decreased germination due to inadequate moisture availability.

For some plant species germination in the presence of leaf litter is often similar to (Williams et al., 1990), or even increased (Walk et al., 1999), when compared to bare soil conditions. This is most likely due to greater retention of soil moisture under a litter layer (Williams et al., 1990). However, Facelli (1994) found that litter reduced overall emergence specifically of *Ailanthus* seedlings, but this was attributed to arthropod predation rather than moisture content of the germination substrate. Most studies

examining the effect of leaf litter on germination exclusively place seeds under the substrate whereas, in both years of this study, seeds sown in the clearcut sites were placed directly on top of an existing litter layer. Positional difference is important since a seed resting on top of the litter layer may dry more quickly while being inhibited from reaching the moist soil surface underneath. Further evidence of ‘litter inhibition’ comes from the observation of successful germination of *Ailanthus* seeds in 2004, after penetrating the leaf litter surface.

In addition to moisture limitation, germination in the intact forest may have been inhibited further by light quality. Sunlight filtered through green leaves often reduces the red:far-red ratio, resulting in increased absorption of red light that inhibits germination (Baskin and Baskin, 1998). Sensitivity of a seed to other factors such as moisture and temperature may also increase with exposure to leaf-filtered light due to changed levels of phytochrome within the seed (Baskin and Baskin, 1998). Therefore, phytochrome-mediated light quality, rather than light quantity, may have interacted with other environmental conditions in the intact forest to affect germination.

The fact that even a small percentage of *Ailanthus* seeds remained viable long enough to germinate the following growing season in the intact forest has implications beyond the effects of light quality, quantity and the germination substrate. This observation demonstrates that *Ailanthus* exhibits a seed bank of at least one year. Viability may exceed one year, so quantification of the actual longevity of viable *Ailanthus* seed is an important question to be resolved.

Combination of a species’ germination requirements (Barik et al., 1996), spatial availability of ‘safe sites’ (Harper, 1977) over a temporal range, and timing of dispersal

all influence germination and establishment success. In this study a significant decrease in the abundance of safe *Ailanthus* germination microsites, and germination rate within those microsites, demonstrated a temporal limitation between the first and second growing seasons after disturbance. The inter-site pattern of available microsites and associated *Ailanthus* germination rate also changed between years. Although these measures remained high in the north-facing clearcut, suitable microsites and germination rate declined in all other sites (Fig. 3.2, 3). Moreover, the pattern of *Ailanthus* germination rate in 2003 was similar to the seedling survival rate in 2004 (Fig. 3.2, 7). These results first suggest that prompt post-disturbance germination may be ideal to secure a space in a newly-opened habitat. They also indicate that the mosaic of suitable microsites favorable for germination and establishment become more heterogeneous and limited since patches devoid of vegetation often exist only for a short time after disturbance such as timber harvest (Pykala, 2004).

Despite classification of *Ailanthus* seed dormancy as physiological and *L. tulipifera* as complex morphophysiological, seeds of both types usually require cold stratification (Baskin and Baskin, 1998), although *Ailanthus* may germinate without stratification (Graves, 1990). Given that ample stratification time was supplied for both species in this study it is unlikely that this was a cause of the negligible *L. tulipifera* germination under all field and growth chamber conditions.

It is also unlikely that the disturbed sites of the field study were unsuitable for *L. tulipifera* germination, as harvested areas usually provide scarified soil and other environmental conditions ideal for germination and establishment (Beck, 1990). Considerable soil disturbance was characteristic of all logged field sites, and pots in the

growth chambers, and rainfall events were ample throughout both growing seasons. Therefore, natural germination conditions seemed sufficient in this study. Many seeds in the field and the growth chambers also became at least partially buried naturally throughout the germination trials, which can positively affect germination (Bonner and Russell, 1974). Therefore, attributes other than site-specific environmental conditions may be responsible for the lack of *L. tulipifera* germination.

Evidence in this study suggested that low seed quality was the primary cause of reduced *L. tulipifera* germination. Seed quality is most often considered viability and is influenced by interacting genetic, physiological, pathological and mechanical factors (Maguire, 1977). Although viability of experimental seeds was not investigated prior to seed placement in the field or growth chambers, a sub-sample of 100 *L. tulipifera* seeds bathed in tetrazolium chloride for 24 h (Baskin and Baskin, 1998) indicated 9% viability of the experimental source. This value is within the range of 5-25% estimated by Boyce and Kaeiser (1961) for natural populations. DeSteven (1991) also found that viability limited *L. tulipifera* germination in old field succession.

Regardless of negligible *L. tulipifera* germination in this study, experimental seedling survival and growth were much greater compared to *Ailanthus*. Even though canopy removal initially increases light and decreases competition with trees, plant species richness is positively affected (Grubb, 1994) as new growing space is immediately infiltrated by many species (Pykala, 2004). Therefore, a competitive environment quickly develops in logged sites and a species' competitive ability may become the limiting factor of establishment. Facelli (1994) found that competition with herbs had the most important negative influence on *Ailanthus* biomass in invasion of old

fields. Given the close spatial proximity of experimental phytometer species pairs, results of this study suggest that *L. tulipifera* has superior competitive ability compared to *A. altissima* since they were present in many of the same microsites. Further studies should focus on competition of *Ailanthus* and *L. tulipifera* together, and in combination with other species, to confirm this suggestion and reconcile the large differences in survival and growth between the species in the first two years following disturbance.

The ability of native *L. tulipifera* to accumulate more biomass and leaf area than invasive *Ailanthus* in the early stages of forest succession confers an advantage of the native to become established after significant disturbance. Greater leaf mass ratio also indicates that *L. tulipifera* is incorporating more mass into production of photosynthetic machinery, which may increase its ability to intercept sunlight, enhancing photosynthesis. Even though mean light availability was highest in the clearcut sites in both years (Fig. 3.4) plant growth response of ‘shade-intolerant’ *Ailanthus* and *L. tulipifera* (Daniel et. al., 1979; Miller, 1990) were greater in the selective cut forest (Tab. 3.2). This suggests that other influences such as competition for nutrients and water, or summer drought stress may be greater in the seemingly more suitable high light environment of the clearcut site.

No *Ailanthus* seedlings approached the reported potential first year height growth of ca. 1 m (Adamik and Brauns, 1957; Hu, 1979), but mean *L. tulipifera* height growth after two growing seasons was within the lower expected level of at least 0.3 m (Beck, 1990). However, the two species seemed to be putting equal energy into height growth, and the greatest mean response in terms of this measure occurred in the north-facing selective cut. Overall, the north-facing selective cut site seemed to be highly favorable as

Table 3.2. Mean value and upper and lower 95% confidence limits for each measured and calculated phytometer growth and allocation variable in the north and south facing disturbed sites. (LMR represents leaf mass ratio).

Variable	Units	<i>Ailanthus altissima</i>				<i>Liriodendron tulipifera</i>			
		South		North		South		North	
		Clearcut	Selective Cut	Clearcut	Selective Cut	Clearcut	Selective Cut	Clearcut	Selective Cut
Total Biomass	g	2.47 (0.87, 7.02)	1.44 (0.38, 5.47)	0.57 (0.05, 7.27)	1.07 (0.49, 2.29)	3.23 (1.97, 5.29)	3.15 (2.13, 4.66)	3.01 (1.59, 5.72)	8.88 (5.84, 13.5)
Height Growth	cm	17.95 (10.5, 30.7)	21.79 (14.4, 32.9)	8.40 (2.33, 30.2)	16.83 (11.3, 24.9)	18.43 (13.4, 25.3)	18.89 (14.1, 25.3)	12.26 (8.08, 18.6)	35.24 (27.8, 44.7)
Leaf Area	cm ²	24.4 (50.4, 16.4)	34.5 (68.6, 22.9)	25.8 (71.1, 18.9)	39.7 (24.7, 15.2)	223.5 (133, 374)	224.9 (149, 339)	233.2 (141, 383)	693.9 (491, 980)
LMR	g g ⁻¹	0.05 (-0.22, 0.13)	0.14 (-0.44, 0.25)	0.16 (-0.43, 0.23)	0.12 (-0.33, 0.18)	0.24 (-0.54, 0.28)	0.23 (-0.49, 0.25)	0.26 (-0.58, 0.29)	0.25 (-0.54, 0.27)
Root: Shoot	mg mg ⁻¹	1.70 (1.25, 2.32)	1.63 (1.07, 2.49)	1.24 (0.81, 1.89)	1.78 (1.41, 2.27)	1.75 (1.46, 2.10)	1.74 (1.48, 2.05)	1.49 (1.16, 1.89)	2.11 (1.85, 2.40)

L. tulipifera biomass and leaf area accumulation was greatest there (Tab. 3.2), and most surviving seedlings were in that site (31.4% of survivors).

Regardless of the exact mechanisms leading to the differential species responses to the disturbed environments, superior performance of natives over invaders is well reported in the literature. Daehler (2003) provides a review in which the majority of the documented articles show that native plant response was either equivalent to or better than competitors under at least some growing conditions, excluding any indication of a 'super invader'. There were also many cases where invaders had an advantage during one life history stage, but the co-occurring native was better suited for another (Daehler, 2003), as in this study.

Investigations of initial plant responses to disturbance are important, especially since species that regenerate early and quickly in forest openings may profoundly influence successional trajectory (Connell and Slatyer, 1977; Oliver and Larson, 1996). Comparison of germination and early growth response of native and exotic, invasive plants that are likely to co-occur due to similar environmental requirements and life histories are particularly meaningful. The outcome of plant recruitment and succession in a disturbed forest could determine not only the future timber value of that property, but also the aesthetic value.

While it may be argued that regeneration success is estimable after a longer time than allotted in this study, Landis and Peart (2005) suggest that early growth rates strongly determine a species' success in reaching the canopy. This is especially applicable to opportunistic, 'gap obligate' pioneer species such as *Ailanthus* and *L.*

tulipifera (Knapp and Canham, 2000; Orwig and Abrams, 1994) that must instantly take advantage of available light and resources.

The general dissimilarity among species responses to sites demonstrates that categorical definitions of disturbances (i.e. clearcut vs. selective cut) are not necessarily accurate indicators of expected differences among disturbance levels as environmental factors at work on the microsite scale may override expected effects of aspect and disturbance type on germination and seedling growth. However, a constraint of this study was the lack of site replication within aspect $\times$ treatment combinations, thus site differences other than aspect and treatment are confounded within this interaction.

Although *L. tulipifera* may retain a seed bank for up to 7 years (Clark and Boyce, 1964), lack of germination may be a serious constraint in areas where seeds are dispersed for the first time after a disturbance; however, if given a chance, this highly-regarded native tree may thrive even in the presence of a noxious invader. Conversely, poor establishment rate may explain why *Ailanthus* was described as ‘becoming a great nuisance’ by Millspaugh in 1892 (Strausbaugh and Core, 1977) in many areas of West Virginia and today, while it has likely spread, is still ‘becoming a nuisance’ more than a century later.

Management implications of the existence of at least a one year *Ailanthus* seed bank are that invasion would not be completely precluded by simply cutting out female trees prior to timber harvest because viable seeds may be present in the soil. Therefore, good harvest techniques such as removal of *Ailanthus* must be practiced with consideration of the seed bank. Although this may help to reduce the risk of invasion, Clark and Clark (2001) and Landis and Peart (2005) warn against the use of mean growth

(as in this study) compared to maximum growth in determining transit time to the canopy. *Liriodendron tulipifera* is likely able to remain a dominant species in the landscape given current large-scale, human-induced forest disturbance; however, 75% of the germination arenas in this study were not safe microsites for *L. tulipifera* germination. Therefore, there is ample space for *Ailanthus* establishment in harvested forests unless steps are taken to ensure an abundance of native seed to increase competition with nonnative invaders such as *Ailanthus altissima*.

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CHAPTER 4

General Conclusions

Comparative studies involving co-occurring exotic and native plants sometimes result in differing performance advantages depending on the life history stage under investigation (Daehler, 2003). Seed dispersal, germination, and growth responses of target species may also be differentially influenced by environmental disturbance. The results from this thesis work show evidence of a differential advantage at different life history stages for exotic *Ailanthus altissima* and native *Liriodendron tulipifera* after forest disturbance. Whereas dispersal potential was virtually equal for the two species, *Ailanthus* had a germination advantage, while *L. tulipifera* seedlings outperformed *Ailanthus* in terms of establishment and growth.

Under identical environmental conditions, seeds with lower wing loading and slower still air descent velocity are expected to be deposited farther from the parent plant than heavier, more quickly descending seeds (Platt and Weis, 1977; Green, 1980; Augspurger and Hogan, 1983; Guries and Nordheim, 1984; Augspurger, 1986). Despite a theoretical dispersal advantage for *Ailanthus* based on lower mean wing loading and descent velocity, I found that field conditions negated the effect of seed characteristics on dispersal distance (Chapter 2). In general, the height growth advantage and seed cluster architecture of *L. tulipifera* may allow exposure to greater canopy wind speeds, and result in the simultaneous dispersal of more seeds during high wind events, thus compensating for higher wing loading. Therefore, if *Ailanthus* and *L. tulipifera* seeds are present in equal quantities, seed deposition will occur in circum-equal proportions at all distances into a forest opening.

Forest disturbance not only diminishes dispersal barriers (Heywood, 1989), but also provides new habitat for invasion by both native and exotic species (Oliver and

Larson, 1996), but establishment depends on the response of species to the new environment (Moore and Noble, 1990). I found that availability of suitable microsites for germination and establishment after logging varied greatly within and among different types of harvest. More microsites contained suitable conditions for *Ailanthus* seed germination, but *L. tulipifera* germination was constrained by unviable seed (Chapter 2). Low seed viability is common for *L. tulipifera* (Boyce and Kaeiser, 1961; Kavanagh, 1990) and has been previously reported as a limiting factor in germination during succession (DeSteven, 1991). However, I found that mean *L. tulipifera* seedling survival and growth was greater than *Ailanthus* after timber harvest, even though both are 'intolerant', pioneer species (Spurr and Barnes, 1973; Beck, 1990; Miller, 1990; Knapp and Canham, 2000).

Although exotic *Ailanthus* and native *L. tulipifera* maintain equal dispersal capability into open habitats, *Ailanthus* recruitment will be likely in microsites that do not contain viable *L. tulipifera* seed, assuming the presence of only these two species. The germination limitation exhibited by *L. tulipifera* in this study suggests that *Ailanthus* recruitment may be greater in a recently disturbed area into which both species are dispersing seed for the first time. However, a greater abundance of seed-bearing *L. tulipifera* than *Ailanthus* is more common in rural areas where logging is likely to occur. Given a greater quantity of seed, the probability of *L. tulipifera* germination should increase, thereby further decreasing the likelihood of *Ailanthus* establishment. Nevertheless, even if only a few *Ailanthus* individuals establish a foothold after disturbance, they may become the foci of subsequent spread into any opening (Kowarik, 1995; Knapp and Canham, 2000). Another factor that could shift the balance in favor of

Ailanthus is allelopathy, which may aid the formation of dense thickets and exclude native species (Mergen, 1959).

Active management of *Ailanthus* along with human-induced disturbance can help to assuage the threat of invasion. I found that *Ailanthus* exhibits at least a one year seed bank under natural conditions (Chapter 2), and it is possible that viability may exceed that time. Therefore, complete removal of female individuals within no less than 200 m of a harvest site is recommended at least one year prior to forest disturbance. Treatment of the aggressive invader must often continue past initial removal (Swearingen, 1999) since *Ailanthus* also reproduces clonally, but the effort and cost to preventing spread will pale in comparison to the long-term value of a stand of native species regeneration.

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