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Germination and early growth of *Ailanthus* and tulip poplar in three levels of forest disturbance

Nathan L. Kota · Rick E. Landenberger · James B. McGraw

Abstract Increasing rates of forest disturbance may provide greater opportunity for invasion of nonnative species, thereby altering the successional trajectory of native plant communities. In the eastern U.S., invasive *Ailanthus altissima* and native *Liriodendron tulipifera* have similar life histories and niches and often co-occur. To examine how disturbance affects the establishment of these species, we performed field experiments to evaluate the response of sown seeds and transplanted seedlings to three levels of disturbance on north- and south-facing aspects. *L. tulipifera* germination was severely limited by low seed viability and had significantly lower germination than *A. altissima* in all sites. The effect of disturbance regime on *A. altissima* germination depended on aspect in the second growing season. In contrast, mean seedling survival, biomass, leaf area and leaf area ratio were greater for *L. tulipifera* in all field sites. Overall, the north-facing selective cut forest provided a disproportionately large number of suitable microsites

for *L. tulipifera* establishment. Collectively, this study demonstrated that different timber harvest practices produce heterogeneous mosaics of suitable microsites for germination and establishment. 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 sufficient viable seeds of both species exist, *L. tulipifera* out-performs the invasive in the first two years following disturbance. This may explain why *A. altissima* has shown explosive population growth in a limited number of sites in the past century.

Keywords *Ailanthus altissima* · Forest disturbance · Germination · Invasive species · *Liriodendron tulipifera* · Seedling establishment

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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 is species performance after arrival in the site (Pickett et al. 1987). Those that regenerate early and quickly 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 window of opportunity in the 'regeneration niche' (Grubb 1977), most notably when disturbance regimes are altered (Rejmanek 1989; Hobbs 1989; Hobbs and Huenneke 1991).

Anthropogenic effects 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). Invasion probability further depends on 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), and 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 forest 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 are most often used in eastern hardwood forest (Miller and Kochenderfer

1998; Stoyenoff et al. 1998) where timbering 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* (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 that may 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, few exotic trees have successfully invaded. However, nonnative *Ailanthus altissima* 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). Since its introduction to the U.S. as an urban horticultural species (Hu 1979) *A. altissima* has become an aggressive invader in 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 *A. altissima* (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 ecological, and reproductive similarities between *A. altissima* and *L. tulipifera*, coupled with 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 and tree stature 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 equal seed production. Therefore, early

species differences in germination and establishment may 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 *A. altissima* and native *L. tulipifera* over two growing seasons in three levels of forest disturbance; clearcut forest, selective cut forest, and intact forest. 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 *A. altissima* 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. And a growth chamber study was employed as an attempt to confirm the direct role of light quantity on germination.

Materials and methods

Study sites

Six study sites were located within 11 km of Morgantown, West Virginia (N 39°38′, W 79°55′). Prior to disturbance, all 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 high level disturbance sites (one north and one south aspect) were completely clearcut (leaving no residual boles) in Spring, 2003. The two intermediate disturbance sites (also north and south aspects) were selectively cut using a 14 in diameter limit method in late Fall, 2002, leaving a thinned forest dominated by *Prunus serotina* and *Acer rubrum*. The two remaining sites (north- and south-facing) were undisturbed during the period of the study.

All sites were adjacent to open fields, creating a distinct edge along each site/field interface. *Ailanthus altissima* 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. 1). Six 0.25 m², circular germination 'arenas' constructed of 13 cm high aluminum flashing were randomly placed along each transect (Fig. 1).

Field study of germination

On May 30, 2003 fifty *A. altissima* seeds were sown in every arena in all sites for a total of 12,600 seeds. The seeds were stratified in cold, wet sand for approximately one 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 *A. altissima* seedlings were removed from an arena before sowing experimental seeds. All arenas were visited every two weeks for the subsequent eight weeks and the number of germinated seeds was recorded. Germinated seeds were removed from arenas at each census.
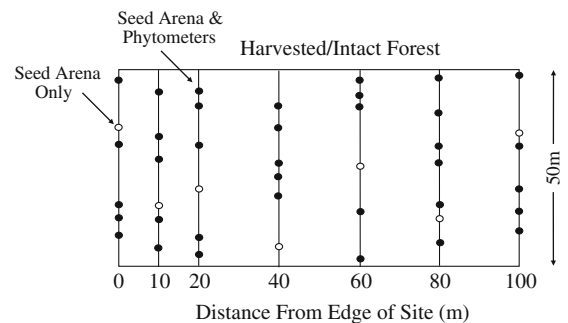
Fig. 1 Experimental layout of plots in each site. Seed arenas were placed at six random locations along each transect. An experimental seedling phytometer of each species was planted at five of the arena locations

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 altissima* seeds were removed from a single tree in December 2003 and *L. tulipifera* seeds were provided in bulk by the F.W. Schumacher Co. (Sandwich, MA) in early February 2004. The number of *L. tulipifera* source trees was unknown. 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 each 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 every two weeks over the following eight weeks, and seedlings were removed from the arenas. In cases where residuals of germination data were not normally distributed and no transformation could solve this problem, dependent variables were changed to a nominal type and loglikelihood was carried out.

A loglikelihood test was first used to determine whether the probability of *A. altissima* germination in 2003 varied among seed sources. Effects in the model included site, seed source (tree), site × source, and arena nested within the site × source interaction. A significant source or site × 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 *A. altissima* germination between 2003 and 2004. For 2004 data the nominal main effect of species was added to the model to determine whether the abundance of safe microsites differed for *A. altissima* and *L. tulipifera*. Since there were so few safe *A. altissima* germination microsites in the intact forest in both years, these data were excluded from the 2004 *A. altissima* analysis.

Analysis of covariance was used in the same models as above to determine how the continuous independent variable germination proportion within safe microsites varied between years for *A. altissima* and between species in 2004. Data from the intact forest sites were excluded from analyses exclusively examining *A. altissima* 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 marked seeds were placed inside and outside of arenas at one site within each disturbance type. In 2003, ten *A. altissima* 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 census date. This method was repeated for 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. None migrated into the other arenas. Therefore, movement of experimental seeds of both species was considered negligible.

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. They were calibrated using a LI-COR quantum sensor (LI 1000; LI-COR Biosciences, Lincoln, NE) on another cloudless day by exposing sensors 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 min then scored by counting the number of bleached diazo sheets. Light measurements provided an estimate of integrated photosynthetic active radiation (PAR) (mol m^{-2} d^{-1}) for all sites.

Mean integrated PAR (± 1 standard error) was plotted for each disturbance type. Logistic regression was used to determine how the probability that an arena was a safe *A. altissima* germination microsite changed with light quantity. This was followed by linear regression of germination proportion within safe microsites on integrated 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 (± 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 autumn 2004 to investigate whether light quantity alone could explain germination variation observed in the field. Fifteen replicate 15 cm diameter pots containing homogenized field soil and 15 seeds of both species were exposed to two levels of light that closely mimicked mean PAR levels in the selective cut (715.9 μmol m^{-2} s^{-1}, ± 56.8) and

the intact forest (14.7 μmol m^{-2} 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 μmol m^{-2} s^{-1}, respectively, which are well 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 *A. altissima* 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 h light and 9.5 h dark. To eliminate positional effects within the growth chamber, pots and associated shade treatments were randomly rotated within the growth chamber every two days throughout the experiment. Seeds were watered every two days and scored for germination weekly for six weeks.

Residuals of germination data were not normally distributed so every seed was scored as germinated or not germinated and loglikelihood was used to determine the effects of light availability, species, and their interaction on the probability of germination. However, low *L. tulipifera* germination prompted the separation of data by species and loglikelihood was used to test for an effect of light on the probability of *A. altissima* germination.

Seedling survival and growth

Experimental 'phytometers' were used to compare the growth response of the two species in varying levels of forest disturbance on north- and south-facing aspects. This method requires that target species are planted in environments in which the effects of particular factors on plant growth may be examined (Antonovics and Primack 1982; McGraw and Antonovics 1983). Naturally germinated first year seedlings of both species were removed from the north-facing, selective harvest site in early May 2003. Seedlings were grown for one month in greenhouse flats containing peat with no additional nutrients under
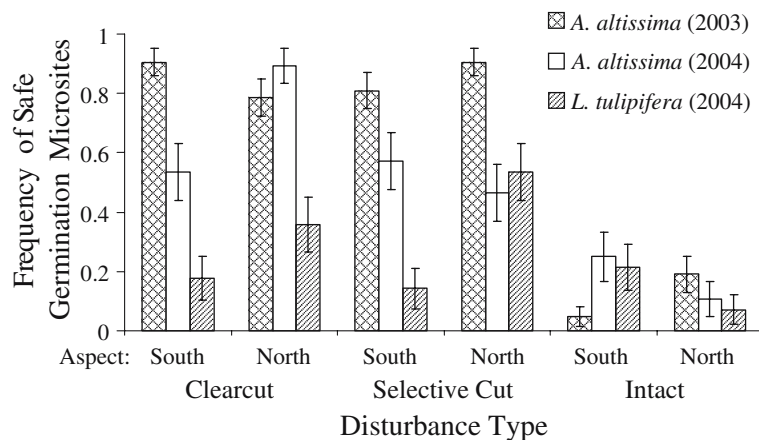
light conditions similar to the selective cut site from where they were extracted. One individual of each species was planted adjacent to five randomly chosen germination arenas along all transects in every site (Fig. 1). Stem height was measured during transplantation, in late September 2003, and in July 2004. Leaf damage was also recorded. 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) and leaf, stem and root mass were measured after drying at 65°C for 72 h.

To first determine whether survival differed between the species at the end of two growing seasons, the main effect of species was examined by loglikelihood in a 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 proportion of germinated seeds did not differ among maternal source trees (loglikelihood = 0.92, P = 0.97), nor did the effect of site on germination depend on the source (loglikelihood = 0.01, P = 1.0). These results justified the use of *A. altissima* seeds from a single source in the 2004 experiment.

In 2003, the abundance of safe sites for *A. altissima* germination varied with disturbance type (disturbance; loglikelihood = 23.27, P < 0.0001). This difference was due to a low number of safe sites in the intact forest; less than 20% of these arenas contained germinated seeds. There was no significant difference in safe site abundance between the clearcut and selective cut sites (loglikelihood = 0.017, P = 0.89; Fig. 2). Approximately 80% (±10%) of arenas had successful germination in these two disturbance types.

Within the safe germination sites of the clearcut and selective harvest, the effect of disturbance on *A. altissima* germination proportion depended on aspect (disturbance × aspect; F = 13.67, P = 0.0003). In 2003, a greater number of *A. altissima* 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).

In 2004, the effect of disturbance on the abundance of safe sites for *A. altissima* germina-

Fig. 2 Frequency of safe germination microsites in each field site. Safe microsites were defined as experimental arenas containing at least one germinated seed. Experimental *A. altissima* seeds were sown in two consecutive years, and *L. tulipifera* seeds were sown only in the second year

tion depended on aspect (disturbance × aspect; loglikelihood = 6.62, $P = 0.01$). The north-facing clearcut had the highest frequency of safe sites, while the south-facing clearcut and the two selective harvests had similar frequencies of safe germination sites (Fig. 2). Within these safe sites, the effect of disturbance on germination proportion depended on aspect (disturbance × aspect; $F = 9.82$, $P = 0.003$). Contrary to 2003 results, in 2004 *A. altissima* germination proportion was greatest in the north-facing clearcut, and similar for the south-facing clearcut and the selective harvest sites (Fig. 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. Half of the total seedlings were in control arenas, and 90% were found during the first census. The partially desiccated, yet germinable, seeds found in germination arenas were easily distinguishable as those from the previous year due to their position under the leaf litter layer and their contrasting appearance to the fresh 2004 seeds.

There were significantly more safe *A. altissima* germination sites in 2003 than in 2004 (year; loglikelihood = 11.57, $P = 0.0007$). Within those safe sites, there was also a greater overall germination proportion in 2003 than in 2004 (year; $F = 22.16$, $P < 0.001$).

The control arenas in 2004 allowed for observation of natural germination. Residuals were not normally distributed, and loglikelihood showed no significant effects on germination, so data were

compared on a per trap basis across all sites. A mean of 0.057 *A. altissima* seedlings germinated within each control arena, while 2.62 experimental seeds germinated per experimental arena. Therefore, we were confident that >97% of the germinated seeds in experimental arenas were from seeds we placed there. The controls indicated that ca. 83% of *L. tulipifera* seedlings counted were from our experimentally-sown seeds. Whereas a mean of 0.071 natural seedlings germinated per control arena, 0.429 seedlings germinated in each experimental arena. However, a uniform method of adjusting for the possibility of counting non-experimental *L. tulipifera* seedlings was not apparent, largely because the initial number of natural seeds within the control and experimental arenas was unknown.

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 *A. altissima* germination (47% of all arenas) than for *L. tulipifera* (25% of arenas). Germination proportion 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

Integrated light was highest in the clearcuts, followed by the selective cut sites, and lowest in the intact forest sites (Table 1), 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 *A. altissima* germination in 2003 increased significantly with increasing PAR (loglikelihood = 46.97, $P < 0.0001$; Fig. 4a). Among those safe sites, germination proportions also increased with increasing light ($P < 0.001$; Fig. 4b).

The same light difference among disturbance types was observed for instantaneous PAR measurements made in 2004 (Table 1), suggesting that the expected difference in mean light
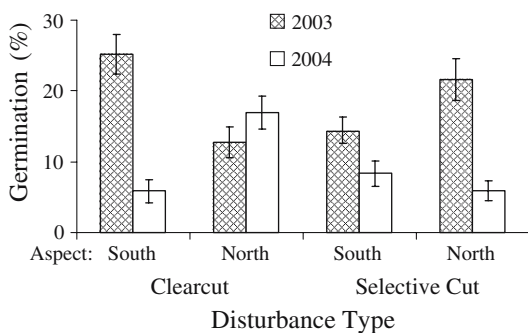
Fig. 3 Mean *A. altissima* germination in safe germination sites in the first and second growing seasons after timber harvest. Intact forest data was not included due to low overall germination in those sites

Table 1 Mean photosynthetically active radiation (PAR) measured over one full day in the first growing season after timber harvest (2003) and relative measures of PAR and associated coefficient of variation in the second growing season (2004). Standard error in parentheses

Year	Units	Clearcut	Selective cut	Intact
2003	mol m^{-2} d^{-1}	0.27 (0.02)	0.21 (0.01)	0.05 (0.004)
2004	μmol m^{-2} s^{-1}	1292.91 (42.05)	715.91 (56.77)	14.70 (0.95)
		CV = 27.98	CV = 76.06	CV = 60.84

remained consistent at least into the second growing season after disturbance. The coefficient of variation of mean instantaneous PAR was greatest in the selective harvest sites (Table 1). This suggests that the light environment in the intermediate disturbance type became more spatially variable, with localized shady areas remaining under residual trees.

Growth chamber germination study

The probability of seed germination differed for the two species (species; loglikelihood = 71.18, $P < 0.0001$) in that the overall germination proportion of *A. altissima* was 35.3% compared to 1.1% for *L. tulipifera*. Possibly due to this low value for *L. tulipifera*, the probability of germination was not significantly different between the light levels (loglikelihood = 0.007, $P = 0.93$). However, the probability of *A. altissima* germination depended on the light level (light; loglikelihood = 16.06, $P = 0.0001$). Germination in the growth chamber was significantly greater under the low light conditions (44.4%) than under high light (26.2%; Fig. 5). This was inconsistent with *A. altissima* germination in the field. Excluding the 0 and 10 m transects to remain consistent with the instantaneous light measurements from the field, overall *A. altissima* germination proportion 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. 5).

Seedling survival and growth

Overall experimental phytometer survival was significantly greater for *L. tulipifera* (42.4%) than *A. altissima* (15.7%) after two growing seasons (species; loglikelihood = 34.02, $P < 0.01$). Among *L. tulipifera* seedlings, survival differed among the types of disturbance (disturbance; loglikelihood = 22.59, $P < 0.01$) and was greatest in the selective cut, followed by the clearcut, and then
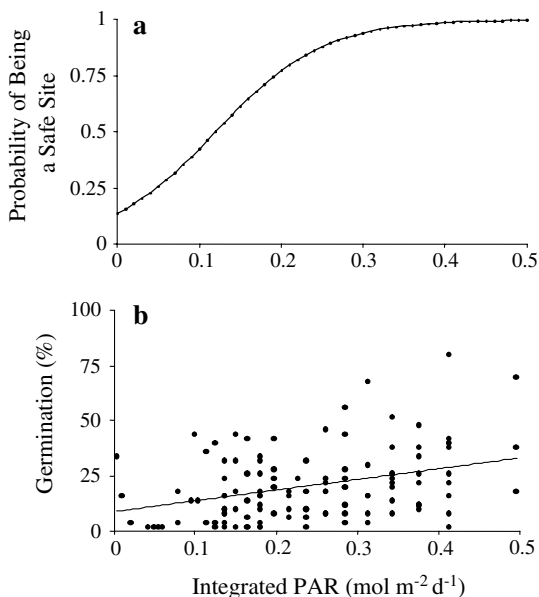

Fig. 4 (a) Increase in the probability of safe germination microsites (b) increase in germination within those safe sites with increasing levels of PAR. Data is for *A. altissima* from the clearcut and selective cut sites in the first growing season after disturbance
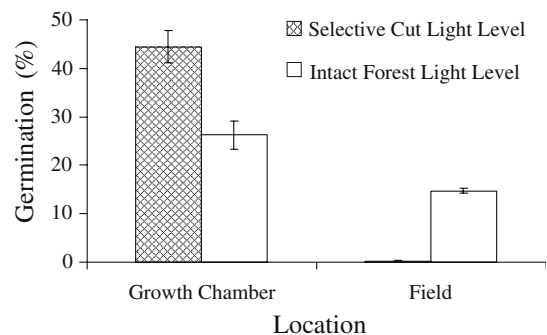
Fig. 5 Mean *A. altissima* germination under mimicked relative light levels of the selective cut and intact forest sites, and actual germination in the interior of those sites
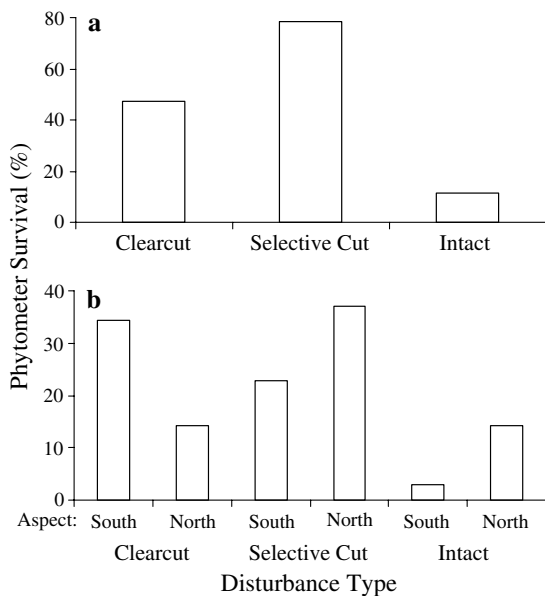
Fig. 6 Survival of (a) *L. tulipifera* and (b) *A. altissima* experimental phytometers seedlings after two growing seasons

intact forest sites (Fig. 6a). The effect of disturbance on *A. altissima* seedling survival depended on aspect (disturbance × aspect; loglikelihood = 8.23, $P = 0.02$). Survival was greater in the south-facing clearcut, did not differ between the selective cut sites, and was greater in the north-facing intact forest (Fig. 6b). 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 difference between species in total plant biomass, leaf area and leaf mass ratio (Table 2). After two growing seasons mean *L. tulipifera* biomass (4.57 g) was more than three times greater than *A. altissima* biomass (1.39 g), regardless of disturbance or aspect. Furthermore, mean *L. tulipifera* leaf area was ca. 11-fold greater (343.9 cm^2 vs. 31.1 cm^2) and leaf mass ratio was two times greater (0.25 g g^{-1} vs. 0.12 g g^{-1}) than *A. altissima*.

The effect of aspect on total biomass also differed for the two 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 ($F = 7.09$, $P = 0.01$; Table 3) whereas *A. altissima* showed no significant difference between aspects.

Although there was only a statistical trend towards a differential effect of aspect on seedling height growth for the two species (aspect × species; $F = 3.49$, $P = 0.07$), the effect of disturbance did depend on 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 (disturbance; $F = 8.89$, $P < 0.01$).

The effect of disturbance on root to shoot ratio tended to depend on aspect ($F = 4.02$, $P = 0.05$). Separate analyses by species showed that this interaction was due primarily to the response of *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

Table 2 *F*-ratio and *P*-value for ANOVA model effects on measured and calculated phytometer growth and allocation variables for *Ailanthus altissima* and *Liriodendron tulipifera*. Only two disturbance categories were considered, hence the degrees of freedom values

Model Effect	df	Biomass	Height growth	Leaf area	LMR	root:shoot
(D)isturbance	1	$F = 1.01$ ($P = 0.32$)	$F = 8.89^*$ ($P = 0.00$)	$F = 2.06$ ($P = 0.16$)	$F = 0.06$ ($P = 0.81$)	$F = 3.09$ ($P = 0.08$)
(A)spect	1	$F = 0.48$ ($P = 0.49$)	$F = 1.47$ ($P = 0.23$)	$F = 1.08$ ($P = 0.30$)	$F = 2.28$ ($P = 0.14$)	$F = 0.29$ ($P = 0.59$)
(S)pecies	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	$F = 0.00$ ($P = 0.96$)	$F = 0.64$ ($P = 0.42$)	$F = 0.59$ ($P = 0.45$)	$F = 1.24$ ($P = 0.27$)	$F = 0.02$ ($P = 0.89$)

$^*P < 0.05$, indicates statistically significant model effect

LMR = leaf mass ratio

Table 3 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

| Variable | Units | Ailanthus altissima | | | | Liriodendron tulipifera | | | |
| | | South | | North | | South | | North | |
		Clearcut	Selective cut	Clearcut	Selective cut	Clearcut	Selective cut	Clearcut	Selective cut
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)
Ht. 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)

LMR = Leaf mass ratio

root to shoot mass tended to be greater in the selective cut sites ($F = 3.09$, $P = 0.08$).

Discussion

Differences in 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 be an adaptive trait, as it could serve to predict the likelihood that a seedling will reach 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 the field study of 2003, *A. altissima* germination increased with increasing light, but germination was greatest in the lowest light conditions of the growth chamber. These contrasting patterns indicate that light quantity is not the primary inhibitory factor of *A. altissima* germination under the shade of an intact canopy.

Two factors provide likely explanations of reduced germination under the intact canopy of the undisturbed forest. First, the deep litter layer there may have prevented seeds from imbibing water. 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 likely due to greater retention of soil moisture under a litter layer when seeds work their way through the litter (Williams et al. 1990). Although Facelli (1994) found that litter reduced overall emergence of *A. altissima* seedlings, he attributed this 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 sites were placed directly on top of an existing litter layer, simulating natural dispersal. Further evidence of 'litter inhibition' in the intact forest comes from the observation of successful germination of *A. altissima* seeds 1 year after they had

been sown, by which time seeds had penetrated the leaf litter surface.

In addition to moisture limitation caused by the leaf litter barrier, germination in the intact forest could have been inhibited 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. Since it was not done in this study, further research measuring germination under controlled red:far-red conditions and various levels of leaf litter would help to accurately determine the true sources of variation.

The fact that even a small percentage of *A. altissima* 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 *A. altissima* exhibits at least a short term seed bank of one year in closed canopy forest. Viability may exceed one year, so quantification of the actual longevity of viable *A. altissima* seed is an important question to be resolved. Removal of female *A. altissima* trees prior to timbering would likely be an important step in lowering rates of spread into the disturbance, however, the presence of a seed bank means that ideally this pre-emptive measure should occur more than one year in advance of timbering.

The combination of germination requirements (Barik et al. 1996), spatial availability of 'safe sites' (Harper 1977), and timing of dispersal all influence germination and establishment success. In this study a significant decrease in the abundance of safe *A. altissima* germination microsites, and germination proportion within those microsites, demonstrated that the window of opportunity for invasion began to close between the first and second growing seasons after disturbance.

The pattern of available microsites and associated *A. altissima* germination proportion also changed between the first and second year. Although site quality as defined by germination proportion remained high in the north-facing clearcut, suitable microsites and germination proportion declined in all other sites. Moreover, the pattern of *A. altissima* germination proportion in 2003 was similar to seedling survival in 2004. These results first suggest that rapid first year germination observed in disturbed sites is an important trait for establishment success of *A. altissima*. The mosaic of suitable microsites favorable for germination and establishment becomes more heterogeneous and limited since patches devoid of vegetation often exist only for a short time after disturbance such as timber harvest (Gilliam et al. 1995). A reduction in available microsites was observed in all four harvested stands, particularly in year two. During the year two growing season (May–Sept.), both herbaceous and woody vegetation became extremely dense, including in the north–facing clearcut where second year germination was highest. Research on Appalachian hardwood regeneration has shown that herbaceous and woody vegetation grows rapidly in the first several years following harvesting, occupying much of the available soil substrate (Trimble and Hart 1961; Smith and Miller 1987; Miller and Smith 1991; Gilliam et al. 1995).

This study suggested that low seed quality was the primary cause of low *L. tulipifera* germination. Seed viability 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 subsample of 100 *L. tulipifera* seeds were subjected to the tetrazolium chloride viability test (Baskin and Baskin 1998), indicating only 9% viability. 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.

Although canopy removal initially increases light availability and decreases competition with trees, plant species richness is positively affected

(Grubb 1977) as new growing space is immediately infiltrated by many species (Gilliam et al. 1995). Therefore, a competitive environment quickly develops in logged sites and species' competitive abilities may become the limiting factor of establishment. While *L. tulipifera* germination was low in this study, experimental seedling survival and growth were much greater than *A. altissima*. Facelli (1994) found that competition with herbs had the most important negative influence on *A. altissima* biomass in invasion of old fields. Given the close spatial proximity of experimental phytometer species pairs, results of this study suggest that *L. tulipifera* may have superior competitive ability to *A. altissima* since they were present in many of the same microsites. Greater leaf mass ratio indicates that *L. tulipifera* was incorporating more mass into production of photosynthetic machinery which may increase its ability to intercept sunlight and enhance photosynthesis. Further studies should focus on competition of *A. altissima* 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.

No *A. altissima* seedlings in this study 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 *L. tulipifera* biomass and leaf area accumulation was greatest there (Table 3), and most surviving seedlings were in that site (31.4% of survivors).

Superior performance of natives over invaders is widely 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 the future timber value as well as affect species composition historically found on that site.

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 species success in reaching the canopy. This is especially applicable to opportunistic, 'gap obligate' pioneers such as *A. altissima* and *L. tulipifera* (Knapp and Canham 2000; Orwig and Abrams 1994) that must quickly take advantage of available light and resources.

The general dissimilarity among species responses to sites demonstrates that categorical definitions of disturbances (i.e. clearcut versus selective cut) are not necessarily accurate indicators of expected differences among disturbance levels as environmental factors at 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 × 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 seven 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 an invader. The relatively low

establishment rate of *A. altissima* in comparison with *L. tulipifera* may help to explain why the invasive was described as ''becoming a great nuisance'' by Millspaugh in 1892 (Strausbaugh and Core 1977), and it could still be described in those terms over a century later. Native *L. tulipifera* may have successfully outcompeted the invader when there was a sufficient seed source, limiting the spread of *A. altissima* to highly disturbed road, river, and rail corridors. Nevertheless, as of the beginning of this century there are frequent sites where *A. altissima* dominates the vegetation (Kota, McGraw and Landenberger, pers. observation, 2005), and concerns about allelopathic suppression of native tree regeneration on these sites warrants further experimental investigation of this potentially noxious exotic.

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