Invasion of an Old-Growth Forest in New York by Ailanthus altissima: Sapling Growth and Recruitment in Canopy Gaps

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Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps[1]

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KNAPP, L. B. (Bard College, Annandale-on-Hudson, NY 12504) AND C. D. CANHAM (Institute of Ecosystem Studies, Millbrook, NY 12545). Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. J. Torrey Bot. Soc. 127:307–315. 2000.—The exotic tree *Ailanthus altissima* is known to invade open and disturbed sites. As a shade-intolerant species, it is not generally identified as a potential invader of forests. Nevertheless, *Ailanthus* saplings dominate several natural gaps within Montgomery Place South Woods, a small old-growth hemlock-hardwoods forest in the Hudson Valley region of New York State. Within these gaps, the height, diameter, and extension growth of the tallest *Ailanthus* saplings are significantly greater than those of the tallest native competitors. Although *Ailanthus* is absent from fully shaded areas, relative radial growth rates of saplings throughout Montgomery Place are not strongly affected by light availability. Pole-sized *Ailanthus* within South Woods exhibit a history of high annual radial growth, with means for individual trees ranging from 1.96–3.70 mm/yr. These results support the hypothesis that *Ailanthus* established in old-growth gaps can reach the canopy by virtue of rapid growth during a single period of release. *Ailanthus* thus exhibits a "gap-obligate" strategy of forest recruitment.

Key words: *Ailanthus altissima,* exotic species invasion, gap-phase dynamics, shade tolerance.

Disruption of native ecosystems by exotic plant species is a well-documented phenomenon (e.g., Cronk and Fuller 1995). Some 4000 exotic plants grow wild in North America (Stein and Flack 1996). The majority of U.S. National Park managers polled in 1996 identified invasive nonindigenous plant species as a problem within their parks, and the Congressional Office of Technology Assessment has estimated that exotic plants and animals have cost the United States economy at least $97 billion during the past century (Stein and Flack 1996). Still, it is probable that only a small fraction of imported species become established in their new habitats, and that only a small portion of these become actual pests (Crawley 1987; Vitousek 1990; Lodge 1993; Bright 1995). Unfortunately, there is no reliable method of predicting which species will become an invasive threat (Crawley 1987; Bright 1995; Allen 1996). The invasive potential of an exotic species cannot be studied independently of its target community, for it is the interaction of species and community that determines the success of an invasion (Lodge 1993).

Often described as a "weed tree," *Ailanthus altissima* exhibits characteristics shared by many successful exotic colonizers (see Berger 1993; Bright 1995). *Ailanthus* produces large numbers of wind-borne seeds (Hu 1979), grows quickly (Bazzaz 1979; Hu 1979; Feret 1985; Heisey 1990), tolerates stress (Graves et al. 1989), and can also reproduce asexually via root sprouts (Hu 1979). Originally introduced to North America from China in the eighteenth century (Hu 1979), its widespread occurrence in fields, along roads, and at forest edges throughout the northeastern United States bears testimony to its success as a colonizer of open and disturbed lands. *Ailanthus* has been labeled a nuisance in some urban areas (Newton 1986) and is viewed as a potential hazard along highways ("Tree that grew in Brooklyn is dying all over New York" 1996).

Although *Ailanthus* is recognized by The Nature Conservancy as an important exotic weed (Hoshovsky 1999), it is seldom identified as a threat to native forests (e.g., Cronk and Fuller 1995). *Ailanthus* is consistently described as

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shade-intolerant (e.g., Grime 1965a, 1965b, 1966; Heisey 1990). As a result, it is thought to be unable to compete with native species in a forest environment (e.g., Bordeau and Laverick 1958; Feret 1985; Newton 1986). Nevertheless, *Ailanthus* forms part of the canopy and shrub layers of an intact, secondary-growth forest near Seneca Rocks, West Virginia (Kowarik 1995). As documented in the present study, *Ailanthus* also dominates several small natural treefall gaps in Montgomery Place South Woods, a small old-growth hemlock-hardwoods forest in Dutchess County, New York. At three locations within this forest, a dozen *Ailanthus* have successfully grown to subcanopy height with dbh > 10 cm.

There are a number of mechanisms by which forest species can reach the canopy. Canham (1988b, 1989, 1990) describes two extremes in recruitment patterns for shade-tolerant trees: continuous slow growth in shade (e.g., *Tsuga canadensis*) or alternating periods of suppression and release due to small forest gaps (e.g., *Acer saccharum*). Orwig and Abrams (1994) describe species such as *A. saccharum* as "gap-facultative," able to survive under a closed canopy but capable of exploiting small gaps when they occur. A third possible pattern of recruitment into the forest canopy depends not on shade tolerance, but on rapid growth to canopy height during a single period of release in a large gap. Among native species, *Liriodendron tulipifera* is an example of such a "gap-obligate" species (Runkle 1985; Orwig & Abrams 1994).

Ailanthus may be the most rapidly growing tree species in the northeastern United States (Petrides 1978). Given a sufficient window of opportunity, *Ailanthus* might overtop its native competitors and reach canopy height in a single period of release, thus avoiding the shade it cannot tolerate. The present study addresses two sets of questions related to this hypothesis: (1) Can natural forest gaps provide suitable conditions for growth of *Ailanthus* saplings? Can *Ailanthus* saplings grow rapidly enough to compete with native species within these gaps? Can *Ailanthus* established in forest gaps survive to reach the canopy? (2) How do *Ailanthus* saplings respond to differing light levels in the field? How does this response compare to those of native species? Specifically, does *Ailanthus* fit the Michaelis Menton function used to model growth and succession of native saplings (Pacala et al. 1994)?

The ability of a species to invade a particular forest depends both on the growth characteristics of the species and the scale of disturbance relative to those characteristics (Runkle 1985). As secondary forests in the northeastern United States mature, canopy gaps may become more prevalent, and the potential for invasion by gap-obligate species may increase. Moreover, there is often a time lag between introduction and invasion (Bright 1995), and dispersal into a forest may be less rapid than dispersal across fields or along transportation corridors (Cronk and Fuller 1995; Williamson 1996). If *Ailanthus* can compete and survive within old-growth forest gaps, it may have the potential for further invasion of forest environments in the future.

Materials and Methods. STUDY SITE. All field data were collected 1–23 August 1995 on the grounds of Montgomery Place, a 176-hectare historic estate bordering the Hudson River in Dutchess County, New York. The buildings, lawns, and formal gardens of Montgomery Place are bordered by areas of old-growth hemlock-hardwoods forest, known as South Woods (approximately 29 ha at 4651.2 N, 5819.2 E) and North Woods (approximately 11 ha at 4651.9 N, 589.6 E). These stands might have been logged in the early 1700s; they have remained relatively undisturbed for the past 200 years except for removal of deadwood (Kiviat 1978). *Tsuga canadensis* dominates both forests, especially South Woods. Other species include *Quercus rubra, Quercus alba, Acer saccharum,* and *Liriodendron tulipifera*; escaped ornamentals may also be found within both areas (Kiviat 1978, 1991).

Both areas, but especially South Woods, have sparse undergrowth, with little advance regeneration of tree species. Kiviat (1978) noted a very low density of trees under 2.5 cm dbh, which he attributed to intensive browsing by deer. Montgomery Place was closed to hunting for many years, as were neighboring areas, and the deer population has grown considerably in recent decades (Kiviat 1978, 1991). Controlled hunting has been allowed on the property during the past decade, but apparently has had little impact on the deer population (Lucy Kuriger pers. comm., Talea Fincke pers. comm.).

The region experiences moderately cold winters and warm humid summers, with a growing season of 150–167 days (Secor et al. 1955). Precipitation averages 1018 mm annually (Kiviat 1978) and is distributed evenly over the year (Secor et al. 1955). Soils in the area are a mixture of clay (Hudson and Vergennes soils, glossaquic hapladulfs, fine and very fine, illitic, mesic) and sand (Knickerbocker fine sandy loam, typic dystrochrepts, sandy, mixed, mesic) (Dutchess County Soil and Water Conservation District 1991a, 1991b). Within South Woods and North Woods these two soils are interfingered to create a pattern of small scale variation in soil type (Kiviat 1978).

GROWTH OF *AILANTHUS* IN OLD-GROWTH GAPS. To document colonization of old-growth forest gaps by *Ailanthus,* we placed sample quadrats in six gaps within Montgomery Place South Woods. All open canopy gaps in South Woods that contained young *Ailanthus* saplings were included unless they were formed or bordered by footpaths. The area of each gap was estimated as an ellipse, with the gap's greatest length and perpendicular width as diameters. Based on these measurements, gaps were classified into three size categories: small (17.3–17.7 m^2), medium (24.9–26.4 m^2), and large (33.6–37.3 m^2).

We placed five quadrats within each gap along a north-south transect. To sample varying light levels within the gap, quadrats were placed in the center of the canopy opening ("Center Gap"), at the northern and southern edges of the gap ("North Gap and South Gap") and in the canopy 2 m north of the gap ("North Edge"). The distance between quadrats therefore varied depending on the length of the north-south canopy opening. A fifth quadrat was placed in the canopy 5 m south of the gap ("Canopy") to compare sapling growth under intact canopy. Each quadrat measured 1 m by 4 m and was oriented east-west across the transect.

Within each quadrat, we measured the vertical height, diameter at 10 cm above ground, and extension growth of each *Ailanthus* sapling, and of each native sapling taller than 30 cm. Extension growth for the current summer was measured using terminal bud scars as a guide. Terminal bud scars were also used to estimate the age of each *Ailanthus* sapling. *Ailanthus* saplings were then cut down and their roots excavated. Several smaller saplings in one of the gaps proved to be root sprouts from a nearby dead sapling. None of the saplings in any quadrat was a sprout from the roots of another living sapling or tree, although several showed signs of having died back from taller heights.

After all *Ailanthus* were removed, fisheye photography of the canopy was used to find the Gap Light Index (GLI) for each quadrat (Canham 1988a, 1988b). This index of the percent of seasonal total photosynthetically active radiation transmitted by the canopy takes into account both diffuse radiation and direct beam radiation (Canham 1988b). Light availability, as measured by GLI, was compared across quadrat positions and across gap sizes, using two-way analysis of variance. Because measured gap size had no significant effect on light availability, gap size was excluded from subsequent analysis of sapling size and growth in the quadrats, and data from the six gaps were treated as replicates.

We compared density, height, diameter and extension growth of *Ailanthus* saplings across quadrat positions by one-way analyses of variance. We also conducted similar analyses of variance for native saplings taller than 30 cm. In comparing height, diameter and growth rates, we considered only the tallest sapling in each quadrat, as the tallest individual is most likely to represent its species in competition for light within the gap.

In comparing *Ailanthus* and native saplings, we considered only saplings taller than 30 cm. Because of the absence of eligible saplings from some quadrats, we could perform neither a paired t-test nor a two-way analysis of variance comparing the dependent variables across both species and quadrat positions. Instead, data from all quadrats (except Canopy quadrats) were averaged for each gap, and the means treated as replicates in one-way analyses of variance. Canopy quadrats were excluded from these averages because their position 5 m south of the gap made them representative of canopy conditions rather than of gap conditions; moreover, the majority included neither *Ailanthus* nor native saplings taller than 30 cm. Although the remaining four quadrats do not represent a truly random sampling of a gap, quadrat position had no significant effect on the dependent variables for either *Ailanthus* or native species.

We cored every *Ailanthus* within South Woods with a stem diameter greater than 10 cm dbh. A total of 12 trees were cored, each at height 1–1.5 m. The cores were examined under magnification and each ring width was measured to the nearest 0.01 mm using a movable stage connected to an optical encoder (see Canham 1985).

GROWTH OF *AILANTHUS* SAPLINGS UNDER VARYING LIGHT. To measure growth response of *Ailanthus* to varying light conditions, we harvested 40 saplings from locations within Montgomery Place. Sampling sites were selected to represent

Table 1. Density, size, and growth of *Ailanthus altissima* and of native saplings across quadrat positions[1] in six forest gaps; results of one-way analyses of variance.

	Ailanthus altissima			Native species		
Dependent variable	F	df	p	F	df	P
Density	1.764	4, 25	0.168	1.713	4, 25	0.179
Vertical height[2]	2.425	4, 12	0.105	0.755	4, 12	0.574
Diameter at 10 cm[2]	1.924	4, 12	0.171	0.896	4, 12	0.496
Extension growth[2]	1.698	4, 12	0.215	0.524	4, 12	0.720

[1] Along north-south transect through gap (see text).

[2] Of tallest sapling within each quadrat; quadrats without saplings were excluded.

a variety of light conditions which ranged from full open sky to forest gap to intact canopy; however, no eligible saplings were found growing in less than 1% full sun. At each location, the individual harvested was the tallest *Ailanthus* sapling within a 5 m radius. To avoid spatial auto-correlation, no two saplings were selected within 10 m of each other. All saplings were at least two years old, and no more than 3 m tall. None was a root sprout from another currently growing sapling or tree, or from a much larger stump. A fisheye photograph was taken of the sky above each sapling after it was harvested and used to calculate the GLI for each site (Canham 1988a).

Sapling height and diameter were measured as described above. A 5–10 cm segment was then removed from the base of the stem of each sapling. These were allowed to air-dry for one year, then sanded and examined under magnification. Annual rings were counted to determine the age of each sapling, and the width of the previous full season's radial growth was measured to the nearest 0.01 mm using a movable stage connected to an optical encoder (see Canham 1985). In the case of two-year-old saplings, only woody tissue growth was measured, from the edge of the pith outward.

Relative radial growth rates were calculated for each sapling harvested. Use of relative growth was necessary because absolute growth showed a linear increase with size ($r^2 = 0.617$, slope significantly greater than zero at $p < 0.001$), introducing a potentially confounding variable into analyses of the effects of light on growth. Relative radial growth (ring width divided by starting diameter) had only a weak relationship with diameter ($r^2 = 0.234$, slope significantly greater than zero at $p = 0.002$).

We tested the effect of light availability (GLI) on relative radial growth using three models: a linear function, a logarithmic function, and a Michaelis Menton function in the form

$$\text{relative growth} = (a * \text{GLI})/((a/b) + \text{GLI})$$

where a is the asymptotic maximum relative growth rate and b is the slope at zero light. This function has been used by Pacala et al. (1994) to model the effects of light on radial growth for ten native forest species, and forms the growth submodel of the forest simulator SORTIE (Pacala et al. 1993). We also estimated models of relative growth as an inverse function of age and as a combined function of light and age.

Diameter and height data were combined with that gathered from gap quadrats in a regression analysis to check for correlation between these variables.

All regression analyses and analyses of variance were performed by SYSTAT (v. 6.1 for Windows, SPSS Inc. 1996).

Results. GROWTH OF *AILANTHUS* IN OLD-GROWTH GAPS. The six gaps containing *Ailanthus* ranged in size from 17.3–37.3 m^2, smaller than the mean gap size of 55.6 m^2 reported for South Woods by Kim (1990); this agrees with Kim's anecdotal observation that *Ailanthus* did not appear in the larger gaps. Light availability within the gaps ranged from 2% to 15% of full sun, and varied significantly with quadrat position ($F = 6.749$, $df = 4,15$, $p = 0.003$), but not with gap size ($F = 2.193$, $df = 2,15$, $p = 0.146$). In most gaps, GLI was greatest at the North Gap or North Edge quadrats, and lowest in the South Gap or Canopy quadrats.

In spite of the variation in light availability across quadrats, quadrat position had no significant effect on the density of *Ailanthus* saplings, nor on the vertical height, diameter at 10 cm, or extension growth of the tallest *Ailanthus* saplings (Table 1). The near absence of data from Canopy quadrats, however, precluded meaningful comparison of these shaded quadrats with the four quadrats within the gaps. *Ailanthus* was never present in a Canopy quadrat except as a

Table 2. Comparison of *Ailanthus altissima* and native tree saplings[1] in six forest gaps; mean of six gaps[2] with SEM and results of one-way analyses of variance.

Dependent variable	*Ailanthus*	Native[3]	F	df	p
Density (per quadrat)	1.750 (0.289)	1.625 (0.264)	0.201	1, 10	0.756
Vertical height[4] (cm)	377.5 (49.5)	111.4 (36.3)	18.801	1, 10	0.001
Diameter at 10 cm[4] (mm)	23.03 (3.40)	9.49 (2.62)	9.930	1, 10	0.010
Extension growth[4] (mm)	288.1 (38.2)	93.38 (19.7)	20.494	1, 10	0.001

[1] Only saplings >30 cm included.

[2] Each gap represented by mean of four 4-m^2 quadrats along north-south transect (see text).

[3] All native species combined into a single category for ANOVA.

[4] Average of tallest saplings within each of 4 quadrats in each gap.

single first year seedling found in one gap. By comparison, Kim (1990) found that the mean extension growth rate of *Ailanthus* in gaps was nearly three times higher than that of *Ailanthus* in forested areas of South Woods.

Quadrat position had no significant effect on the density of native saplings taller than 30 cm, nor on the height, diameter at 10 cm, or extension growth of the tallest native tree saplings (Table 1).

Among saplings taller than 30 cm, *Ailanthus* was as abundant as all native species combined (Table 2). Had smaller saplings been included, however, a different result might have arisen; several quadrats contained numerous *Acer saccharum* seedlings, but none of these was taller than 30 cm. On the other hand, *Fraxinus americana, Prunus serotina, Betula lenta,* and *Liriodendron tulipifera,* while less numerous overall, were all represented by more than one individual taller than 30 cm, and therefore were more likely than *A. saccharum* to compete directly with *Ailanthus* for light.

The dominant *Ailanthus* saplings were significantly taller than the dominant native tree saplings; the tallest *Ailanthus* saplings also had significantly greater diameter and extension growth than their tallest competitors (Table 2).

Although four quadrats in three of the gaps contained first-year *Ailanthus* seedlings, none contained two- or three-year-old saplings, which suggests the window of opportunity for successful establishment may have already closed. In three of the gaps there were no *Ailanthus* between the ages of two and seven years. Within any given gap, the estimated ages of saplings over the age of two were within a range of two to nine years (Fig. 1). The oldest saplings in each gap ranged in age from seven to sixteen years, which provides a minimum estimate of the age of each gap. Because *Ailanthus* frequently dies back between growing seasons, it is possible that sapling age may have been underestimated by relying on bud scars, especially for older saplings; overestimation, however, is unlikely.

The twelve pole-sized *Ailanthus* within South Woods were 14–23 years old, as estimated by a count of annual rings at 1–1.15 meters above ground. The trees were grouped in three separate locations within South Woods; two of the locations clearly were multiple treefall gaps. At any given site, the estimated age of the trees varied by only two to three years, which again suggests a limited recruitment window following disturbance. The trees showed high growth rates overall, with mean annual growth rates for individual trees ranging from 1.96–3.70 mm/yr. Minimum annual growth for individual trees ranged from 0.85–2.39 mm, while maximum annual growth ranged from 3.53–6.51 mm.

GROWTH OF *AILANTHUS* SAPLINGS UNDER VARYING LIGHT. Radial growth of *Ailanthus* saplings was not strongly affected by light availability. All three models of relative radial growth as a function of light provided a poor statistical fit ($R^2 = 0.131$ to 0.167; Table 3). This result contrasts sharply with results obtained by Pacala et al. (1994), who found that calibrated Michaelis Menton functions of GLI could explain 23–78% of the variance in radial growth in ten native species. Among *Ailanthus* saplings, a Michaelis Menton function of light explained less than 17% of the variation in relative radial growth (Fig. 2).

A large part of the unexplained variation in relative radial growth lies in the effect of age on growth rate; relative radial growth rates were much more accurately predicted by an inverse-age function than by models based on light alone ($R^2 = 0.354$; Table 3, Fig. 3). Combining this function with either a logarithmic or Michaelis Menton function of GLI yielded a still better fit ($R^2 = 0.471$ and 0.472, respectively; Table 3),

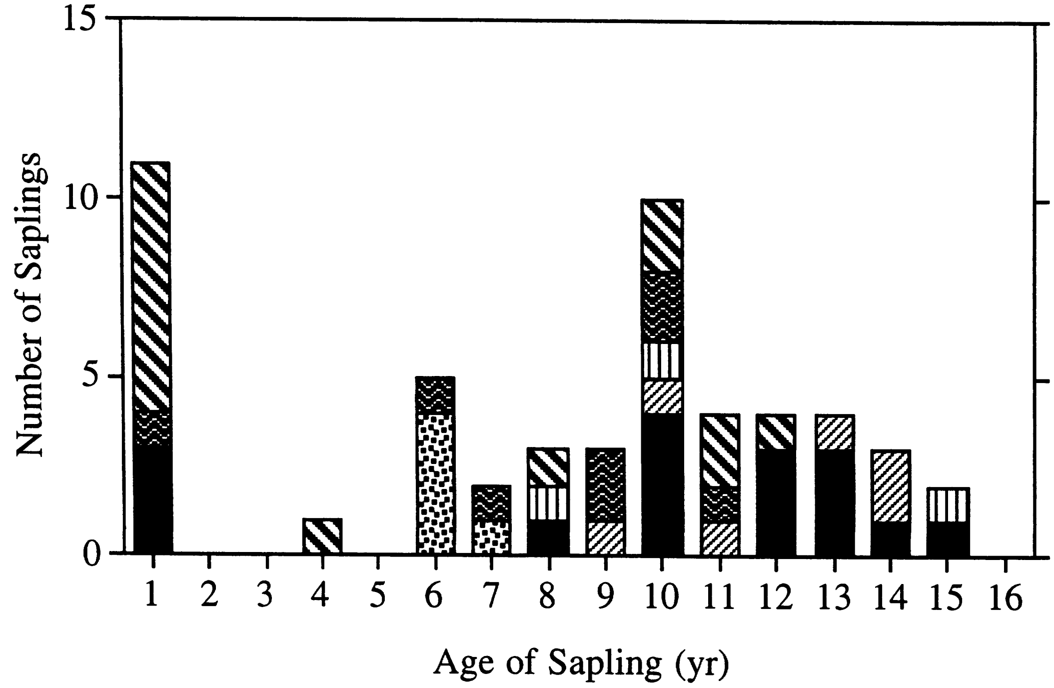

Fig. 1. Age structure of *Ailanthus altissima* saplings in old-growth forest gaps. Saplings were harvested from four 4 m^2 quadrats along a north-south transect (see text); age is based on count of terminal bud scars. Data are shown from six gaps.

comparable to results obtained with native species for functions based on light alone.

Sapling height was correlated with diameter (R = 0.79). Thus radial growth rate is a good predictor of height growth in *Ailanthus* saplings. Radial growth may be a better predictor than extension growth, because radial growth is cumulative, whereas extension growth may be lost to dieback or browsing (Pacala et al. 1994).

Discussion. A tree's success in reaching the canopy may be determined by its performance as a sapling (e.g., Canham 1988b). On this basis, it would appear that *Ailanthus* stands a good chance of eventual canopy recruitment within the six gaps surveyed; *Ailanthus* saplings outperformed native species by several measures, including height. To succeed in reaching the canopy, however, these *Ailanthus* saplings must sustain their superior performance. The data collected from subcanopy-height poles demonstrate that *Ailanthus* established in gaps within South Woods were capable of maintaining highly competitive growth rates for up to 23 years.

Both juvenile growth and survivorship may vary with light availability. A canopy gap produces a temporary increase in light availability; as the gap closes, light availability changes again. The outcome of competition in a gap may therefore be determined by interspecific variation in shade tolerance (Hibbs 1982; Pacala et al. 1994). Forest simulators such as FORET and

Table 3. Estimated models of relative radial growth in *Ailanthus altissima* saplings; parameter estimates (with 95% confidence limits) and R^2 values. GLI = Gap Light Index (Canham 1988a); see text.

Model estimated	a	b	R^2
a*GLI+b	0.009 (0.001, 0.017)	0.274 (0.112, 0.436)	0.131
a*log10GLI+b	0.365 (0.069, 0.661)	0.085 (−0.188, 0.357)	0.152
(a*GLI)/((a/b)+GLI)	1.013 (0.266, 1.760)	0.078 (0.006, 0.150)	0.167
a/age	1.992 (1.469, 2.515)	—	0.354
(a*GLI+b)/age	0.021 (−0.002, 0.044)	1.679 (1.062, 2.296)	0.385
(a*$\log_{10}$GLI+b)/age	1.369 (0.463, 2.275)	0.825 (−0.080, 1.730)	0.471
[(a*GLI)/((a/b)+GLI)]/age	3.322 (2.031, 4.613)	0.795 (0.035, 1.555)	0.472

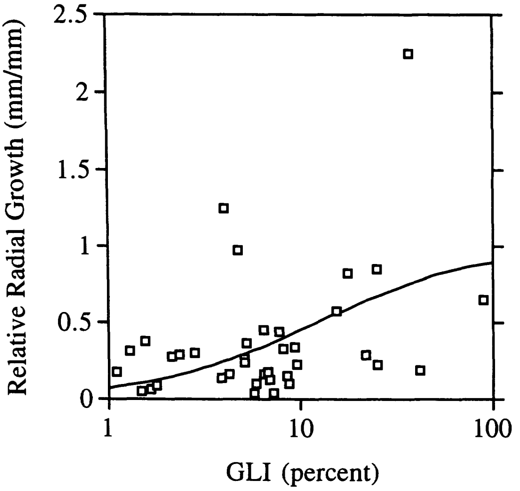

Fig. 2. Relative radial growth of *Ailanthus altissima* as a function of light availability. GLI = Gap Light Index (Canham 1988a). Curve represents estimated Michaelis Menton function, growth = (a*GLI)/((a/b)+GLI), a = 1.013, b = 0.078, R^2 = 0.167. This poor statistical fit contrasts with results obtained by Pacala et al. (1994) using a similar model for native species.

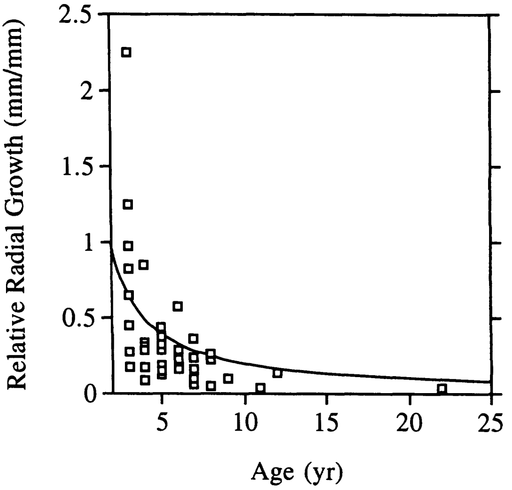

Fig. 3. Relative radial growth of *Ailanthus altissima* as a function of sapling age. Curve represents estimated inverse function, growth = a/age, a = 1.992, R^2 = 0.354.

SORTIE include shade tolerance as one of the factors that predict future forest composition (Pacala et al. 1993). Kobe et al. (1995) studied saplings of ten dominant tree species in the Great Mountain Forest (GMF), Connecticut, and found that height growth in high light was inversely correlated with survivorship in low light. The position of a species along this continuum defined its shade tolerance and accurately predicted its successional status (Kobe et al. 1995).

How might *Ailanthus* fit into this continuum of shade tolerance? When Pacala et al. (1994) estimated Michaelis Menton light-response functions for ten GMF species, the resulting functions predicted relative radial growth rates between 0.10 and 0.25 in full sun. When we estimated similar parameters for *Ailanthus,* the resulting function predicted a relative radial growth rate of 0.90 in full sun. This extraordinarily high radial growth rate implies an equally impressive height growth rate, because diameter and height are correlated.

The position of a species along the shade tolerance continuum is defined not only by its growth in high light but also by its survivorship in low light (Kobe et al. 1995). There is some evidence that *Ailanthus* seedlings may occasionally germinate but cannot survive beneath an intact canopy. Forgione (1993) found a mortality rate of over 90% for *Ailanthus* seeds experimentally planted in a closed-canopy forest. Grime (1965a) also reported high mortality of *Ailanthus* seedlings grown in shade; however, he initially germinated his seeds in full light. Kowarik (1995) studied a population of forest *Ailanthus* near Seneca Rocks, West Virginia; he found few first-year seedlings and none from previous seasons, implying 100% mortality beneath a closed canopy. Similarly, in the present study, Canopy quadrats were devoid of *Ailanthus,* except for one first-year seedling. The absence of any 2- or 3-year-old saplings in any of the gap quadrats also supports the idea that *Ailanthus* seedlings need unshaded sky in order to survive to their second year. The data thus support the traditional description of *Ailanthus* as highly shade intolerant, placing the species at the extreme early-succession end of the continuum described by Pacala et al. (1993) and Kobe et al. (1995).

On the other hand, the specific model used to define this continuum among native species did not provide a good fit when applied to our sapling data. When Pacala et al. (1994) estimated growth functions for native species, they found that variation in GLI could explain up to 73% of the variance in growth. When we estimated the same function for *Ailanthus,* we found that variation in GLI explained less than 17% of the variance in the sample. Relative radial growth was much more dependent on the age of the sapling than on the light available to it. The poor fit of the GLI function may partly reflect the fact that we compared the current year's GLI with the previous year's relative radial growth, whereas Pacala et al. (1994) compared current GLI with current growth. On the other hand, the idea that *Ailanthus* may be relatively insensitive to varying light levels seems plausible in view of the earlier findings of Bordeau and Laverick (1958) that *Ailanthus* failed to demonstrate "photosynthetic flexibility" under varying light. Rather than decrease its growth rate, *Ailanthus* may exhibit an abrupt transition to high mortality as light decreases. If so, then forest recruitment of *Ailanthus* must be gap-obligate rather than gap-facultative.

Kowarik (1995) reports an exception to this finding. He found that, unlike seedlings, rootborn shoots of *Ailanthus* were able to survive many years under intact canopy while exhibiting low growth rates. These suppressed ramets may provide an alternative, gap-facultative pathway for persistence of *Ailanthus* within a forest environment. These daughter ramets, however, were assumed to be dependent on parent trees already present in the canopy; thus initial invasion of native forest must still depend upon successful recruitment of independent, gap-obligate *Ailanthus* seedlings.

It should be noted that, even in South Woods, *Ailanthus* did not grow in every canopy opening. Wherever *Ailanthus* did occur, it dominated the gap, but there were several canopy gaps that had no *Ailanthus* growing in them at all. This suggests that some variable other than light availability may be influencing the initial establishment of *Ailanthus* seedlings within South Woods. For example, soil type varies throughout Montgomery Place, influencing local tree species composition (Kiviat 1978). *Ailanthus* itself is generally praised for its ability to tolerate even very poor soils (Hoshovsky 1999), and it spreads rapidly on both clay and sandy soils (Cronk and Fuller 1995). Variation in soil type might create varying conditions for its competitors, however, thus indirectly affecting the abundance of *Ailanthus* within a particular gap.

Gap closure rate may be important in determining the success of a gap-obligate species (Canham 1988). The closure rate of a forest gap depends on several factors, including the starting size of the gap and the lateral growth rates of surrounding canopy trees (Runkle 1985). These factors may in turn vary with the age, type, and management history of a forest. Lorimer (1989) hypothesized that gaps in older forests are less likely to close by lateral canopy growth. Rates of lateral growth into gaps may also be slower in coniferous forests (Hibbs 1982). As an old-growth forest dominated by hemlock, South Woods may be especially vulnerable to the prolonged canopy disturbance required for invasion by *Ailanthus.* On the other hand, as secondary forests age, they may become more prone to such disturbance, and therefore more vulnerable to invasion.

Forests that lack advance regeneration, due for example to high rates of herbivory by deer, may also provide a more suitable environment for the establishment of a rapid-growing, shade-intolerant species. If *Ailanthus* seedlings require unshaded sky to survive, their establishment in a gap could be successfully inhibited by significant advance regeneration of more shade-tolerant species. Herbivory may also favor those species which are least palatable (e.g., Lonsdale and Braithwaite 1988). Kiviat (1978), noting evidence of intensive browsing by deer in Montgomery Place and surrounding forests, predicted that unpalatable species might eventually become dominant there. As an apparently unpalatable species (Forgione 1993), *Ailanthus* could have a significant advantage in forests with high deer populations.

Attempts to identify invader species or invasible communities independently of each other may lead to inaccurate predictions; instead, research must focus on the interactions between both the invader and the target community (Lodge 1993). The present study supports the hypothesis that *Ailanthus altissima* can successfully invade an old-growth hemlock-hardwoods forest. Extrapolation of these results to other temperate forests must await further research.

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