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# Intact forests provide only weak resistance to a shade-tolerant invasive Norway maple (*Acer platanoides* L.)

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## Summary

**1** Intact, closed canopied forests appear highly resistant to exotic plant invasions, but there are few experimental studies of this observation. To test this issue and explore the conditions that foster resistance, we experimentally added Norway maple (*Acer platanoides* L.) seeds to intact forests for 3 years and monitored emergence, survivorship and height growth for 5 years.

**2** Seed additions (250 seeds<sup>-1</sup> m<sup>2</sup>) were replicated *in situ* in combinations of light (deep shade vs. small gaps), soil fertility (NO<sub>3</sub> and pH), and variation in soil moisture as influenced by topography (hill slopes vs. flat areas at slope bases) in five eastern deciduous forests in central New York and southern Connecticut. We then parameterized a model with this data to project long-term rates of sapling recruitment.

**3** Seedlings had high survival and low growth rates in the deep shade, suggesting that this species readily forms a seedling bank in intact forests. By age 5, annual survivorship reached 93% in deep shade and 98% in small gaps. Median seedling heights were ≤ 10 cm in all treatments after 5 years, though the largest seedlings were markedly taller in gaps. Mean year 5 densities of all experimental seedlings (ages 3–5 years) were 14 seedlings<sup>-1</sup> m<sup>2</sup> (± 2.4 SE) in the shade and 19 seedlings<sup>-1</sup> m<sup>2</sup> (± 3.5 SE) in small gaps.

**4** While seedlings colonized in all conditions, resistance to invasion varied markedly; resistance was highest in deeply shaded, acidic conditions (pH < 4.5). Small gaps initially promoted invasion, but by age 4 shade survivorship rates were equivalent to gaps. Higher soil pH (especially > 6) also significantly increased survivorship, particularly in deep shade. Shading's main effect was to suppress height growth. Overall, the model predicted impressive sapling recruitment; even in deeply shaded, acidic conditions, approximately 1% of seeds emerge and survive to become saplings.

**5** Intact forests only weakly resisted *A. platanoides* colonization, but strongly suppressed its rate of invasion. As such, the frequency of disturbance, though ultimately unnecessary for *A. platanoides* invasions, will strongly influence its near-term invasiveness. Dispersal limitation and slow stand dynamics appear to be the primary constraints on its current distribution.

*Key-words:* *Acer platanoides*, biological invasions, biotic resistance, gap dynamics, invasive species, Norway maple, seedling demography, shade tolerance, tree seedlings

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## Introduction

Resistance to invasion, usually in the form of competition from the native community, is commonly assumed to be a primary determinant of exotic plants invasions

(Levine 2000; Seabloom *et al.* 2003; Meiners *et al.* 2004). Elton (1958) championed the concept of biotic resistance, maintaining that resistance to invasion is greater in intact or undisturbed communities. Intact forests in particular are considered highly resistant to invasion (e.g. Fox & Fox 1986; Pimm 1989; Rejmánek 1989; McNaughton 1993; Rejmánek 1996; Richardson & Higgins 1998; Naeem *et al.* 2000; Fine 2002; Von Holle

*et al.* 2003) and the deep shade they cast has been highlighted as the source of this resistance (Cavers & Harper 1967; Crawley 1987; Rejmánek 1989; Fine 2002). Recent studies continue to find that most invasive plants do not spread into intact forests even when found in adjacent disturbed forests (e.g. Fine 2002; Von Holle *et al.* 2003; Martin *et al.* 2004), suggesting that robust resistance to invasion is indeed an emergent property of this ecosystem (*sensu* Lonsdale 1999).

These observations raise important questions: are intact, undisturbed forests inherently resistant to invasion, even from exotic plants with late-successional life-history traits, especially shade tolerance? Or have factors such as dispersal limitation and slow growth rates obscured an inexorable invasion into intact forests by late-successional exotics? This remains an open issue, as little experimental research on invasion resistance has addressed forests (Levine *et al.* 2004). Furthermore, most studies of invasion resistance have been retrospective, focused on extant or ongoing invasions (Levine *et al.* 2004). While useful, such studies have important limitations for addressing this issue, mainly because the conditions at the time of invasion are usually unknown (e.g. extent of disturbance). Retrospective studies also necessarily focus on areas where exotics have already established, typically human-dominated settings, and may not be indicative of general invasiveness as many exotics were intentionally introduced to thrive in unusual environments (e.g. high pollution tolerance; Bassuk 1985; Moffat 1987). In such areas, exotic plants can have more seed sourced from surrounding ornamental plantings than native species (e.g. Martin 1999), and resistance mechanisms of forests may be highly altered in these settings (e.g. very high populations of seed predators (Nupp & Swihart 1998) and herbivores (Stickney 1983)). Instead, *in situ*, experimental studies of resistance to invasion in natural, healthy intact forests are needed.

Conditions driving invasion resistance in intact forests are more complex than a deep-shade vs. no-shade dichotomy. Moderate light levels found in small gaps (< 25 m<sup>2</sup> to c. 0.1 ha) are common in intact forests, as small gaps are the most frequent natural disturbance in eastern deciduous forests (e.g. Romme & Martin 1982; Runkle 1982; Lorimer 1989). Other factors may be important as well; recent research has indicated that resistance to invasion is significantly lower in ecosystems with higher soil fertility (Stohlgren *et al.* 1998; Kalkhan & Stohlgren 2000; Williamson & Harrison 2002; Howard *et al.* 2004; Gilbert & Lechowicz 2005), particularly higher soil calcium, pH and nitrogen (Howard *et al.* 2004; Gilbert & Lechowicz 2005). Areas with finer textured soils and higher soil moisture also appear to have lower resistance (Stohlgren *et al.* 1998; Kalkhan & Stohlgren 2000). How these factors influence resistance in intact forests is unclear as little is known about the effects of variation in resources on invasibility (Howard *et al.* 2004).

To explore these issues, we conducted a 5-year *in situ* experiment on Norway maple (*Acer platanoides* L.)

establishment from seed in intact forests. *A. platanoides* is a common exotic tree species with a high potential to invade intact forests in the eastern USA. Its pattern of spread suggests that it is shade tolerant and capable of dominating some forest stands (Webb & Kaunzinger 1993; Kloeppel & Abrams 1995; Martin 1999; Webster *et al.* 2005), yet existing research is equivocal on its invasiveness into intact forests as it is found in sites that were relatively open when it established. Conversely, *A. platanoides*' wind-dispersed seeds have fairly short-range dispersal (Matlack 1987), suggesting that its current distribution could be dispersal limited. The absence of long-term studies of *A. platanoides* colonization is also problematic, as the propagules of many species establish briefly but fail to persist (e.g. seedlings of *Fraxinus americana*; Wright 1959). As such, we consider *A. platanoides* an ideal exotic species to test resistance in forests to exotic plant invasion: while its traits appear adapted to invade intact forests, its pattern of invasion suggests it may not be able to invade this ecosystem.

This study had three objectives: (i) to determine if intact forests resist invasion by a shade-tolerant exotic; (ii) to improve our understanding of the key components of resistance in intact forests; and (iii) to increase our knowledge of the ecology and invasiveness of *A. platanoides*. In particular, are biotic or abiotic conditions more important in resistance? Does resistance increase or decrease with time since invasion? Are small gaps necessary for initial seedling establishment? Testing *A. platanoides* recruitment over a range of light and soil conditions will indicate the types of forests vulnerable to *A. platanoides* invasion.

## Materials and methods

### STUDY SITES

*Acer platanoides* seeds were added in five intact, eastern deciduous forests dominated by mid and late successional tree species, particularly sugar maple (*Acer saccharum* Marsh.) (Table 1). Four sites were located in the northern Allegheny plateau in Tompkins and Chemung counties in central New York and one in southern Connecticut in New Haven county. These sites were located to span a range of plant life-zones indicated by USDA Hardiness Zones, which are classified by average annual minimum temperatures. The New York sites were transition Allegheny hardwoods (oak, cherry, hickory)–northern hardwoods (beech, maple, birch) forests. The Connecticut site, added in the second year of the study, was a transition oak–northern hardwood forest. Though previously logged, all sites have been free of human disturbance for decades, and are now dominated by trees 40–70 cm in diameter at breast height. White-tailed deer were observed regularly in all five sites.

Sites were selected to meet the following criteria: all were deeply shaded, closed-canopied deciduous forests, comprised of a healthy community of native tree species, and part of large contiguous forests, except Site 1, which

**Table 1** Study sites: locations, environmental description and dominant vegetation. Each hardiness zone number, classified by the USDA, corresponds to a 10°F (c. 5.5 °C) change in average annual minimum temperatures; each letter corresponds to a 5°F change in average annual minimum temperatures

Site	Township	Hardiness zone	Elevation (m)	Slope	Dominant tree species (alphabetical)
1	Dryden, New York	5b	293 (slope) 289 (flat)	10% 0%	<i>Acer saccharum</i> , <i>Fraxinus americana</i> , <i>Magnolia acuminata</i> , <i>Quercus</i> spp., <i>Ulmus</i> spp.
2	Van Etten, New York	5a	555 (slope) 545 (flat)	25% 0%	<i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Quercus rubra</i>
3	Ithaca, New York	5b	152–167 (slope) 137 (flat)	45% 0%	<i>Acer saccharum</i> , <i>Carya</i> spp., <i>Fraxinus americana</i> , <i>Liriodendron tulipifera</i> , <i>Tilia americana</i>
4	Dryden, New York	5b	427–430 (slope)	25%	<i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Quercus rubra</i>
5	Branford, Connecticut	6b	445 (flat) 24–27 (slope) 20 (flat)	0% 30% 0%	<i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Carya ovata</i> , <i>Quercus</i> spp., <i>Sassafras albidum</i> , <i>Pinus strobus</i>

was a 12-ha forest surrounded by open land. Sites free of *A. platanoides* were used to assure only experimentally introduced seeds were present and to avoid the potential effects of canopy trees on seedling establishment (e.g. facilitation).

#### SEED COLLECTION AND SEED ADDITION EXPERIMENTAL DESIGN

*Acer platanoides* seeds were collected in late October from 1999 to 2001 from street trees in Ithaca, NY. Seeds were collected from 25 individual trees from all parts of the crown using a pole pruner. Only seeds with an embryo were used. The seeds were thoroughly mixed to create a homogenous sample and divided into batches of 250 seeds. Our design focused on the main known sources of resistance: light, soil fertility (pH and nitrogen) and soil moisture. In November, seed batches were spread evenly on the forest floor in randomly placed 1-m<sup>2</sup> quadrats in one of two light-levels: deep shade under full canopies with no side light, or recently formed, small canopy gaps (c. 100 m<sup>2</sup> in size). Where necessary, gaps were augmented with felling (3 of 10 gaps). Augmented gaps did not differ from the natural gaps in any evident manner (e.g. soil disturbance). Estimates of natural seed rain densities in a native congener, red maple (*Acer rubrum* L.) (Schnurr *et al.* 2004), indicate that this seed density was reasonable. Light-level treatments were also laid out to combine with variation in soil fertility as indicated by USDA Soil Surveys and soil moisture as influenced by topography (hill slopes vs. flat areas at slope bases). Each light level had 16 quadrats in year 1, and 20 quadrats in years 2 and year 3, giving a total of 14 000 seeds in 56 m<sup>2</sup> per light level over the 3 years of seed additions. Seeds were added for 3 years to incorporate interannual variation in conditions (e.g. weather, seed viability). As quadrats were placed randomly within a treatment area (e.g. deep shade), no effort was made to control for differences in ground cover (e.g. forest floor herbs) between quadrats.

Seedling emergence was recorded for each cohort in late May. We chose this date to ensure that most seeds had germinated, and hence we measured seedling emergence and not germination as an unknown portion of seeds may have already germinated and died. At the end of each growing season in late October, seedling height and survivorship were measured. The census was repeated from 2000 to 2004 (five growing seasons). The presence and type of herbivory, and causes of mortality, were also noted.

#### ENVIRONMENTAL CHARACTERIZATION

A suite of environmental variables were measured to determine the factors controlling *A. platanoides* seedling growth and survivorship. Light levels were measured for each quadrat with fish-eye canopy photographs taken in August and early September from 2000 to 2002. Photographs were taken using a levelled, orientated camera mounted on a tripod at 0.3 m directly over the quadrat. Photos were processed using GLI/C software (Canham 1988), which provides a 'gap light index' (GLI) of the combined incident diffuse and direct-beam radiation over a growing season expressed as a percentage of the light available to a seedling growing in full sun. Soils were measured for NO<sub>3</sub> and pH in each quadrat in Augusts 2000–02. Leaf litter was brushed away and the top 15 cm of soil was sampled with a volumetric probe (17.5 mm diameter). Four cores were taken per quadrat and combined as a composite sample. Soils were analysed using standard laboratory techniques at Cornell University's Nutrient Analysis Laboratories (methods described at: <http://www.css.cornell.edu/soil-test>). We did not quantify soil moisture between topography (slope vs. flat) and instead treated topography as a categorical variable. The *in situ* conditions of this study integrated all other forms of resistance as well (e.g. seed predation, herbivory, etc.), providing a measure of total biotic and abiotic resistance to invasion in these forests.

## DATA ANALYSIS

To evaluate resistance in intact forests to *A. platanoides* invasion, we simultaneously analysed: (i) seed emergence; (ii) cumulative seedling survivorship post-emergence years 1–5; and (iii) seedling height from years 1–5 with a multivariate analysis of variance (MANOVA) with sequential repeated measures on seedling age. The ‘between-subjects factors’ (main effects) analysed were: (i) light; (ii) soil pH; (iii) topography; (iv) nitrate (NO<sub>3</sub>); (v) site (a random effect); (vi) cohort (a random effect); and (vii) the interactions of these factors. Post-hoc testing for statistically significant differences was performed with linear contrasts (Lehman *et al.* 2005). We only used multivariate *F*-tests as the univariate requirement of sphericity of the covariance matrices was not met for our analysis (Mauchly criterion,  $P < 0.0000$ ; Lehman *et al.* 2005). A MANOVA assumes the data have a multivariate normal distribution, but no standard tests of this assumption are available (Gotelli & Ellison 2004). As an alternative, we examined the normality of each response variable individually with a Shapiro-Wilk Goodness of Fit test (Gotelli & Ellison 2004); all response variables had satisfactorily normal distributions. All statistical analyses were performed with JMP In Version 5.1 software (SAS Institute, Cary, NC).

## MODELLING LONG-TERM INVASION

Adapting an approach from Hill *et al.* (1995) we used the parameters estimated from the multivariate fit of the field data (emergence, survivorship, and mean and maximum height growth per quadrat) to model the long-term rates of sapling establishment of *A. platanoides* in intact forests in six combinations of light (shade and gaps) and pH (< 4.5, 4.5–6, > 6). Maximum height growth was calculated as the average maximum height per quadrat. Saplings are defined as 1.4 m in height. We used light and pH as these were the only statistically significant environmental effects in the multivariate analysis (see below). As some patterns were clearly non-linear (e.g. survivorship; Fig. 1a), we compared the fit of four regression models (linear, logistic, exponential and power), selected the model with the highest  $R^2$ , and used this equation for long-term modelling. The model predicts several aspects of invasion: (i) the percentage of seedlings surviving for 100 years; (ii) the number of saplings recruited per 250 seeds; (iii) seed/sapling ratio (S/S), the ratio of seed input to number of sapling recruits; and (iv) time to first sapling (TFS), the time for the fastest growing individual to reach sapling size.

This model allows us to evaluate the cumulative effects of both biotic and abiotic resistance, identify key stages of resistance to invasion, and provide forward-looking projections of *A. platanoides* establishment given the current conditions. Actual, long-term rates of invasion obviously will be influenced by any future age-related shifts in demographics and/or changes in conditions, such as continued crown closure in gaps or new disturbances.

## Results

## OVERALL MANOVA AND ENVIRONMENTAL CHARACTERIZATION

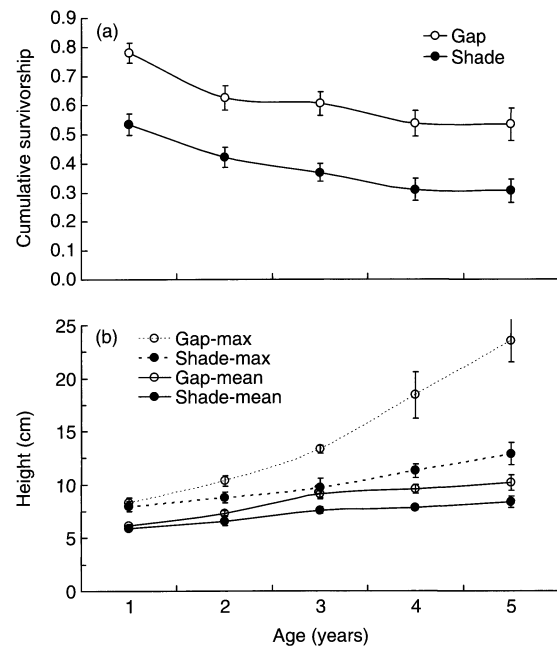
The overall MANOVA was significant ( $F_{10,80} = 10.53$ ,  $P = 0.001$ ). Analysis of demographic categories and post-hoc tests are detailed below. Mean light levels in the shade were 1.9 GLI ( $\pm 0.8$  SD), with a range of 0.8–3.6 GLI. Mean light levels in gaps were 14.3 GLI ( $\pm 4.4$  SD), with a range of 9–18 GLI. Variations in NO<sub>3</sub> and pH were large. NO<sub>3</sub> averaged 16.7 p.p.m. ( $\pm 32.8$  SD), with a range of 0–227 p.p.m. Soil pH averaged 5.0 ( $\pm 1.1$  SD), with a range of 3.4–7.6.

## SEEDLING EMERGENCE

Mean seedling emergence rates were 15.9% in 2000, 19.3% in 2001, and 8.9% in 2002. Seedling emergence did not vary significantly with light, pH, topography or NO<sub>3</sub>, but did vary significantly by site and cohort (Table 2a), with rates significantly lower in 2002 than 2000 and 2001 (post-hoc contrast,  $F_{1,80} = 10.53$ ,  $P = 0.0017$ ). A notably poor seed crop (P. H. Martin and P. L. Marks, personal observations) in *A. platanoides* street trees in 2001 preceded this modest emergence in 2002. In general, seedling emergence was patchy, with a range of 0–62% per quadrat.

## SEEDLING SURVIVORSHIP

Seedling survivorship was high, attaining average annual (year-to-year) survivorship rates of 93% in deep shade



**Fig. 1** (a) Cumulative seedling survivorship post-emergence of Norway maple (*Acer platanoides*) seedlings in deep shade and small gaps in intact forests. (b) Maximum and mean seedling height growth in deep shade and small gaps in intact forests. Maximum height growth was calculated as the average maximum height per quadrat. Bars are  $\pm 1$  SE.

**Table 2** Repeated measures MANOVA of 5 years of *Acer platanoides* invasion from seed into intact forests: (a) seedling emergence; (b) cumulative survivorship; and (c) cumulative height growth. Standardized canonical coefficients are the relative contribution of each variable to the pattern within a demographic category; larger values indicate a larger contribution to the overall explanatory power of the MANOVA. Statistically significant *P*-values are shown in bold face. There were no significant between-subjects interactions (data not shown), and there are no within-subjects results for emergence as it had no repeated measures

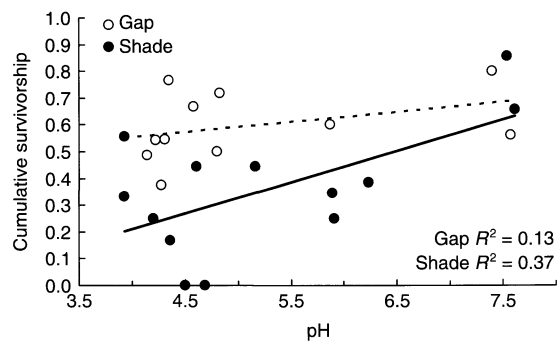
Demographic category	d.f. (numerator, denominator)	<i>F</i> -statistic	Standardized canonical coefficients	<i>P</i> -value
<b>(a) Emergence</b>				
<i>Between subjects</i>				
Site	4, 80	9.82	0.57	<b>0.0001</b>
Cohort	2, 80	4.76	0.33	<b>0.0111</b>
Light	1, 80	0.89	0.10	0.3497
pH	2, 80	0.10	0.04	0.7497
NO <sub>3</sub>	1, 80	0.59	0.08	0.4539
Topography	1, 80	1.32	0.13	0.2543
<b>(b) Survivorship</b>				
<i>Between subjects</i>				
Site	4, 80	0.47	0.28	0.7082
Cohort	2, 80	9.15	0.53	<b>0.0033</b>
Light	1, 80	7.66	0.57	<b>0.0137</b>
pH	2, 80	3.81	0.41	<b>0.0443</b>
NO <sub>3</sub>	1, 80	0.21	0.11	0.6549
Topography	1, 80	0.04	0.05	0.8502
<i>Within subjects</i>				
Age	5, 78	4.29	0.76	<b>0.0198</b>
Age × site	15, 206	1.79	0.67	0.0903
Age × cohort	10, 156	0.81	0.49	0.5041
Age × light	5, 78	1.73	0.59	0.2028
Age × pH	10, 156	3.01	0.69	0.0605
Age × NO <sub>3</sub>	5, 78	1.51	0.56	0.2573
Age × topography	5, 78	0.72	0.43	0.5952
<b>(c) Height growth</b>				
<i>Between subjects</i>				
Site	4, 80	0.60	0.01	0.6217
Cohort	2, 80	9.15	0.11	<b>0.0003</b>
Light	1, 80	13.96	0.22	<b>0.0001</b>
pH	2, 80	3.81	0.06	<b>0.0443</b>
NO <sub>3</sub>	1, 80	2.67	0.01	0.2434
Topography	1, 80	0.62	0.01	0.4445
<i>Within subjects</i>				
Age	5, 78	35.76	0.30	<b>0.0001</b>
Age × site	15, 206	2.24	0.08	0.0700
Age × cohort	10, 156	0.10	0.00	0.9043
Age × light	10, 156	9.87	0.08	<b>0.0020</b>
Age × pH	5, 78	6.39	0.05	<b>0.0124</b>
Age × NO <sub>3</sub>	5, 78	0.07	0.00	0.7919
Age × topography	10, 156	0.18	0.00	0.6760

and 98% in small gaps by year 5. Survivorship in the first growing season post-emergence was markedly lower in deep shade (54%) than in small gaps (76%), and this was the main reason gaps had higher cumulative 5-year survivorship. After year 2, decreases in survivorship slowed and then levelled off by year 4 (Fig. 1a). Hence, the repeated measures factor seedling age was a significant predictor of cumulative survivorship (Table 2b; MANOVA,  $P = 0.0198$ ). By year 4, survivorship rates were statistically equivalent between shade and gaps (post-hoc contrast,  $F_{4,78} = 62.09$ ,  $P = 0.228$ ).

The MANOVA detected several significant between-subjects effects on survivorship: light, pH and cohort were significant, while topography, NO<sub>3</sub> and site were not (Table 2b). Light and pH had a positive effect on

survival. Based on standardized canonical coefficients, light, cohort and pH (in decreasing order) explained the largest proportion of the between-subjects variation (Table 2b). There were no significant interactions with age. Despite providing the strongest fit, light levels alone were only weakly predictive of survivorship, in part because shade survivorship increased markedly at a higher pH (Fig. 2). The highest cumulative 5-year survivorship (86%) in any treatment occurred in the deep shade (GLI 0.92), which also had a very high pH (7.5). However, a high pH was not essential for shade survivorship; cumulative 4-year survivorship was as high as 89% in some quadrats with strongly acidic soils.

The composite of emergence and survivorship produced notably high mean 5-year-old seedling



**Fig. 2** The relationship between soil pH and 5 year cumulative survivorship of Norway maple (*A. platanoides*) seedlings in deep shade and small gaps. Each  $R^2$  is based on a linear regression of shade survivorship (solid line) and gap survivorship (dashed line).

densities: 8.3 seedlings<sup>-1</sup> m<sup>2</sup> ( $\pm 3.2$  SE) in the shade and 9.1 seedlings<sup>-1</sup> m<sup>2</sup> ( $\pm 1.9$  SE) in gaps. Due to higher emergence and survivorship rates in the second cohort, mean densities of 4-year-old seedlings were higher: 17.6 seedlings<sup>-1</sup> m<sup>2</sup> ( $\pm 3.9$  SE) in the shade and 23.9 seedlings<sup>-1</sup> m<sup>2</sup> ( $\pm 2.4$  SE) in gaps. The second cohort had quadrats with densities as high as 90 seedlings<sup>-1</sup> m<sup>2</sup> in the shade and 114 seedlings<sup>-1</sup> m<sup>2</sup> in small gaps.

Mammal herbivory, probably by deer, resulted in some mortality, especially in the gap treatments. Many seedlings recovered, however, from browsing injury by resprouting from dormant buds, even when all leaves were eaten. Small mammal browsing, however, tended to result in mortality as seedlings were chewed off at the base.

#### HEIGHT GROWTH

Height growth was modest (Fig. 1b), with a mean height of 9.1 cm (SD  $\pm 3.2$ ) for all 5-year-old seedlings, though maximum height growth was markedly higher in gaps. As the patterns were very similar for both maximum height growth and mean height growth,

hereafter we only present the results in detail for mean height growth. Despite modest growth, mean height across all treatments increased significantly with age at a rate of 0.8 cm year<sup>-1</sup> (MANOVA  $F_{5,78} = 35.76$ ,  $P < 0.0001$ ), with significant year-to-year increases each year except between years 3 and 4 (post-hoc contrasts within MANOVA).

The MANOVA analysis detected several significant between-subjects effects on cumulative height growth: again, light, pH and cohort were significant, while topography, NO<sub>3</sub> and site were not (Table 2c). Light had a positive effect on height growth while pH had a negative effect. Post-hoc contrasts showed that light was significant in year 2 ( $F_{1,80} = 7.77$ ,  $P = 0.0102$ ) through year 5 ( $F_{1,80} = 5.47$ ,  $P = 0.0358$ ). Based on standardized canonical coefficients, light, cohort and pH (in decreasing order) explained the largest proportion of the between-subjects variation in height (Table 2c). There were significant interactions between seedling age and light and pH, indicating that light's positive effect on height growth increased with age, as did pH's negative effect. Herbivory tended to moderate height growth as larger seedlings were browsed more often than smaller seedlings.

#### MODELLING LONG-TERM INVASION

The model predicts slow but steady *A. platanoides* invasion at current demographic rates. Invasion is slow due to the long lag time between seedling establishment and sapling recruitment. Based on rates of maximum height growth, the minimum time to first sapling (TFS) was 40 years in the shade and 23 years in gaps. This disparity was driven by the large difference in maximum height growth rates between shade and gaps (Fig. 1b), with gaps attaining notably higher rates. Mean height growth rates had a TFS of 141 years in the shade and 105 years in gaps (Table 3). The importance of height growth rate was amplified by the comparatively small

**Table 3** *Acer platanoides* sapling invasion from seed in intact forests, as predicted by a demographic model of emergence, survivorship and height growth rates in combinations of light (deep shade vs. small gaps) and soil pH (strongly acidic, pH < 4.5; moderately acidic, pH 4.5–6; and neutral, pH > 6). These rates were parameterized directly from 5 years of field data using one of four regression model fits (linear, logistic, exponential and power) selected with the highest  $R^2$ . Height growth was modelled for both the maximum and mean rates. Maximum height growth was calculated as the average maximum height per quadrat

Treatments (light, pH)	100-year % survivorship*	No. saplings†		S/S ratio‡		TFS§		Regression model¶			
		Maximum	Mean	Maximum	Mean	Maximum	Mean	Survivorship	$R^2$	Height	$R^2$
Gap, neutral	25%	13	9	10	15	23	105	Negative power	0.99	Linear	0.97
Gap, moderately acidic	15%	11	6	12	20	23	105	Negative power	0.96	Linear	0.98
Gap, strongly acidic	7%	7	3	17	38	23	105	Negative power	0.94	Linear	0.98
Shade, neutral	9%	5	3	28	48	40	141	Negative power	0.99	Linear	0.99
Shade, moderately acidic	3%	3	1	54	120	40	141	Negative power	0.98	Linear	0.97
Shade, strongly acidic	1%	2	0	85	230	40	141	Negative power	0.99	Linear	0.99

\*Percentage of post-emergence seedlings surviving after 100 years.

†The number of seeds per 250 seed batch that survive to become saplings, based on maximum height growth (Maximum) and average height growth (Mean).

‡Seed/sapling ratio = minimum number of seeds needed to recruit a single sapling, based on maximum height growth (Maximum) and average height growth (Mean).

§TFS = time for the fastest growing (Maximum) and average growing (Mean) seedling to reach sapling height.

¶All survivorship combinations were best fit with a negative power model as survivorship decreased with time.

variation in rates of seedling emergence and survivorship between treatments, except for the low rates in shaded treatments with strongly acidic soils (pH < 4.5). Overall, the model projects a relatively large percentage of *seeds* emerging, surviving and growing to become saplings in all treatments, even in the shade and strongly acidic combination (Table 3).

## Discussion

### SOURCES OF RESISTANCE

Despite a reputation as highly resistant to invasion, intact forests provided only weak resistance to *Acer platanoides* invasion even in deep shade, suggesting they are vulnerable to invasion by late successional invasives over the long term. Certainly, this study addressed only one invasive species that is comparatively suited to invade intact forests. We therefore, do not reject the idea of generally robust invasion resistance in intact forests, but instead emphasize that intact forests are vulnerable to invasion by shade-tolerant exotics such as *A. platanoides*. Indeed, the limited research on shade-tolerant exotics to date suggests that this assertion may be true (e.g. Woods 1993; Nuzzo 1999; Martin *et al.* 2004; Gilbert & Lechowicz 2005). In contrast to the general paradigm of strong invasion resistance in intact systems, this suggests that the traits of an exotic invasive plant species, if adapted to a given system, are at least as important as the competitive effects of the native plant community, even in intact forests. Moreover, such well-adapted invasives are not dependent on disturbance or resource-enrichment (*sensu* Davis *et al.* 2000), though these may facilitate invasion. An important and unanswered question is how common are exotic species which combine both invasiveness and late successional traits. If this combination of traits is rare, than strong resistance by intact systems may be a reasonable generality, though not one that addresses all invasive species.

Controls on resistance to invasion in intact forests are a combination of biotic and environmental resistance (Lodge 1993), as gradients in understory light (biotic) and soil pH (environmental) were the primary drivers of resistance to *A. platanoides* invasion. The combination of deep shade and strongly acidic soils offered the highest resistance. In contrast, increased pH circumvented the effects of deep shade by markedly increasing shade survivorship (Fig. 2, Table 3), indicating that base-rich soils can significantly reduce invasion resistance. In the light of other recent studies (Howard *et al.* 2004; Gilbert & Lechowicz 2005), it would appear that pH or calcium-facilitated invasibility may be widespread. For height growth, however, light's influence was paramount, resulting in modest height growth over 5 years. This prolonged slow growth rate should increase the chances of mortality due to pathogens, defoliation or episodic drought (Canham 1989), interacting with other sources of resistance over time. pH was negatively

associated with growth, which is somewhat surprising. This probably reflects the common trade-off between growth and survivorship (e.g. Crawley 1997); seedlings may respond to reduced shade tolerance in acidic soils by allocating more resources to growth. It is notable that our results showed non-significant effects for water (as influenced by topography) and nitrogen. As both nitrogen and water are thought to be limiting resources in north-eastern forests (e.g. Rastetter *et al.* 1991), we anticipate that the effects of both resources would be more apparent if a broader range of conditions (e.g. droughty ridges) or measurements (e.g. total N) were included.

### SEEDLING DEMOGRAPHY AND INVASION RESISTANCE

Resistance to *A. platanoides* occurred primarily in the initial stages of invasion, during seedling emergence and first-year survivorship. Indeed, *in situ* *A. platanoides* seedling emergence rates were much lower than controlled germination rates, which routinely exceed 90% (Hong & Ellis 1990; Finch-Savage *et al.* 1998). Nevertheless, the emergence rates reported here (mean 14.7%) were high compared with native trees (Shibata & Nakashizuka 1995; Clark *et al.* 1998; Houle 1998; Schnurr *et al.* 2004). For example, Schnurr *et al.* (2004) found only a c. 4% seedling emergence rate for *A. rubrum* after a good seed crop. Seed predation, an important source of biotic resistance in intact forests (e.g. Whelan *et al.* 1991; Schnurr *et al.* 2002; Schnurr *et al.* 2004), could play a role in this high rate, as *A. platanoides* has been shown to undergo less seed predation than *A. saccharum* (Meiners 2005). Likewise, its high seed mass (65% higher than *A. saccharum*, Meiners 2005) should lower mortality in newly emerged seedlings (Saverimuttu & Westoby 1996).

In contrast, *A. platanoides* total median height growth was  $\leq 10$  cm in any treatment or cohort. Height growth is important as it determines the *rate* of sapling and canopy recruitment. The rates observed here created a minimum rate of sapling recruitment of c. 40 years in deep shade (Table 3). This slow growth in deep shade is not surprising, however, and reflects a common adaptation of shade-tolerant species to low light (Kitajima 1994; Kobe 1996; Marks & Gardescu 1998). Furthermore, *A. platanoides* height growth in gaps suggests it may be an effective small gap colonizer, particularly in comparison with *A. saccharum* and *A. rubrum* (Sipe & Bazzaz 1995; Marks & Gardescu 1998). Of course, 30% of the gaps in this study were augmented at the time of seed addition, potentially inflating its apparent rate of gap colonization. Overall, invasiveness in intact forests would appear highly sensitive to survivorship, as height growth rates were slow enough to prevent any sapling recruitment in the shade at annual survivorship rates  $\leq 80\%$ . This sensitivity makes *A. platanoides*' high shade survivorship all the more notable, equivalent by age 4 to c. 12-year-old *A. saccharum* seedlings at a



base-rich site (Marks & Gardescu 1998). Its slow growth and high survivorship suggests *A. platanoides* is a 'seedling bank' species in intact forests (*sensu* Marks & Gardescu 1998) with attendant high seedling densities in deep shade. These notably high seed densities indicate that it may be even better than local 'seedling bank' species. For example, *in situ* seedling densities of native shade-tolerant species (all age classes combined) can be much lower: 13 for *Tsuga canadensis* (L.) Carr., 2.5 for *A. rubrum*, 1.5 for *A. saccharum*, and 0.6 for *Fagus grandifolia* Ehrh. (Ribbens *et al.* 1994).

#### LONG-TERM INVASION DYNAMICS

Once established in the understory, the ability of *A. platanoides*, and of shade-tolerant trees in general, to recruit into the canopy is highly sensitive to the frequency of small disturbances and the duration of suppression-and-release intervals (Canham 1989). Survivorship rates in our *shade* treatments suggest that from 1 to 9% of emerged seedlings can tolerate intense suppression for at least 100 years (Table 3), well within the typical 20–30 years return-interval of small-scale release events in forests of the eastern USA (Canham 1985, 1990). Such periods of release are typically required for appreciable increases in height, making shade-tolerant invasions into intact forests comparatively slow given these return intervals. In this way, a lack of release events could substantially delay invasions, creating an apparent 'lag phase', and making some stands (e.g. dense, early successional stands) temporarily more resistant to invasion. Alternatively, perturbations that create diffuse or discrete canopy openings such as introduced pests and pathogens (e.g. woolly adelgid) are likely to noticeably accelerate invasions. The lack of a sufficient release history may explain the shortage of *A. platanoides* saplings in many invaded stands in the north-eastern USA (P. H. Martin & P. L. Marks, personal observations), as it was only first planted widely in the 1950s and 1960s to replace dying American elms (*Ulmus americana* L.) (Nowak & Rowntree 1990). It should be stressed that release events, by increasing survivorship and growth, would most likely increase long-term invasion rates over those in our model as the model does not account for release events. Even without incorporating releases, the model still predicts very high rates of sapling recruitment.

The sapling recruitment model illustrates the potential influence of propagule pressure on invasions; high seed inputs may counteract strong biotic resistance by increasing the odds that some seedlings will survive longer (see Von Holle & Simberloff 2005). In this way, our model is conservative, as propagule pressure from a mature *A. platanoides* tree would most likely be higher in an actual invasion than in this study, albeit in a more spatially patchy pattern. Furthermore, actual seed inputs would occur most years for decades or longer, ensuring that the invasiveness of certain cohorts would interact with favourable conditions (weather, disturbance, etc.),

as suggested by the marked importance of cohort found in this study with only 3 years of seed inputs. Intact forests, however, are probably *comparatively* insulated from propagule pressure from all but very shade-tolerant invasives, as decades of suppression may render ephemeral the initial advantages of high propagule pressure.

*Acer platanoides* is known to regenerate far better under its own canopy than do native species (Wyckoff & Webb 1996; Martin 1999). In light of its vigorous colonization of native understories reported here, it appears to be capable of not only invading intact forests, but also dominating them over the long-term by displacing native regeneration. Further studies that integrate other aspects of its ecology (e.g. canopy effects on light levels) will better address this possibility. *A. platanoides* robust invasion into intact forests suggests the main controls on its current distribution are dispersal limitation and its suppressed growth in shady understories, not any fundamental imperviousness to invasion in intact forests.

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