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Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests

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Summary

1. The study of invasiveness typically emphasizes early successional life-history traits in exotic plants, which enable the capture of high resources in disturbed environments and rapid growth. A key issue in invasion dynamics is whether such behaviours come at the expense of traits such as low-light survivorship, which allow species to become more dominant later in succession.

2. We used maximum-likelihood analysis to compare the growth and survivorship of two exotic trees, *Ailanthus altissima* and *Acer platanoides*, with nine dominant native tree species in closed-canopy forests in Connecticut, USA. Growth was modelled as a function of light and survivorship as a function of recent growth; combining models yielded estimates of light-dependent mortality.

3. The exotic species had strikingly high growth rates, exceeding all native species at light levels ≥ 10% full sun, and growing 2.6 times faster than the *fastest*-growing native species at 80% full sun. At low-light levels (< 3% full sun), however, growth rates of five native species exceeded both exotics. Exotic species survivorship (as a function of light-driven growth) was strongly dependent on the degree of shading: at 1% full sun, the annual mortality rate of *A. platanoides* was 10% and *A. altissima* was 17%; only two native species had higher mortalities. However, at 5% full sun, *A. platanoides*' mortality was < 1%, superior to all but three native species. Mortality of all species dropped to < 1% by 10% full sun, except *A. altissima* whose mortality remained high at *c.* 10%.

4. A life-history trade-off analysis (based on radial growth, height allometry and low-light survivorship) shows a nearly linear trade-off for most species. The native species and *Ailanthus* follow the common life-history trade-off of low-light survivorship vs. high-light growth. However, *A. platanoides* diverges from this trade-off pattern by combining very high growth rates with moderately high shade tolerance.

5. Simulations with SORTIE-ND (a forest dynamics model) indicate that poor survivorship of *A. altissima* will limit it to disturbed sites, whereas *A. platanoides*' unusual combination of traits makes it invasive in both disturbed and undisturbed forests. Overall, native shade-tolerant trees and slow stand dynamics make undisturbed forests highly resistant to invasion by exotic trees that are intolerant of shade.

6. *Synthesis*. This study showcases the importance of rapid growth in invasive plants, holding even for exotic tree species known to invade established forests. For *A. altissima*, high growth rates were accompanied by poor low-light survivorship. *A. platanoides* departs from the general trade-off pattern that exists among native species and *A. altissima*, and consequently it can be highly invasive in closed-canopy forests.

Key-words: *Acer platanoides, Ailanthus altissima,* biological invasions, enemy release, growth, invasive species, life-history trade-off, mortality, northern hardwoods, shade tolerance

Introduction

The scope of plant invasion ecology continues to expand, building on the fundamental hypothesis of 'enemy release'

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(Elton 1958) to incorporate a wide range of mechanisms that account for the exceptional life-history and demographical traits displayed by exotic invasive species. These mechanisms include plasticity in resource allocation (Claridge & Franklin 2002; Richards *et al.* 2006; Funk & Vitousek 2007), allelopathy and 'novel weapons' (e.g. Callaway & Ridenour 2004), and evolutionary factors (e.g. founder effects; Lambrinos 2004). At its foundation, however, the success of an exotic plant species results directly from the invader's demographic advantages relative to native species. Hence, where in the life-history relationships of a native community an exotic plant species fits will to a large degree determine the pattern of its invasiveness.

Grime's (1977) classic work on plant life-history strategies maintains that species are constrained by fundamental 'compromises between the conflicting selection pressures resulting from particular combinations of competition, stress and disturbance', and this inescapably involves the sacrifice of fitness in one scenario for another. A key question in invasion dynamics is whether exotic species are subject to trade-offs that constrain the life histories of native plants, especially tree species. In conditions which support forest growth, life-history trade-offs largely occur between 'ruderal' and 'competitor' life histories (*sensu* Grime 1977). In particular, there is a well-known interspecific trade-off between high survivorship under low light vs. rapid growth under high light (e.g. Pacala *et al.* 1994; Kobe *et al.* 1995). Here, shade-intolerant, early successional species typically have a suite of morphological and ecophysiological traits that support high rates of carbon gain under high light, whereas shade-tolerant, late-successional species are characterized by traits that allow positive carbon gain at much lower light levels, but that limit their ability to maximize carbon gain under high light (Bazzaz 1979). Plasticity across light levels is constrained by the very different physiological (e.g. low respiration rates) and morphological (e.g. planar leaf display) requirements for optimizing growth in low light vs. high light (Canham 1988a). Pacala *et al.* (1996) determined that such interspecific trade-offs are necessary for realistic predictions of successional dynamics in native forests, and like Grime (1977), that design constraints prevent the evolution of a hypothetical 'super' species efficient at utilizing the high-to-low light levels found in the forest. If exotic invasive plants are not constrained by this life-history trade-off, this would offer a powerful explanation of the invasiveness of exotic species in forest ecosystems. There is scant evidence in invasion ecology for a super-species *sensu* Pacala *et al.* (1996), perhaps in part because the study of survivorship and shade tolerance in invasive plants has received comparatively little attention (see review in Martin, Canham & Marks 2009). Rather, numerous studies of invasives have emphasized early successional traits – typified by rapid growth, low shade tolerance, early reproduction and a short life span – as the source of invasiveness (e.g. Bazzaz 1986; Lodge 1993; Rejmánek & Richardson 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997). A ruderal, early successional life-history paradigm has important implications for invasions: if early successional traits are intrinsic to most invasive plants, invasions will be uncommon in undisturbed communities where life-history traits favouring competitive ability predominate. Recent research is challenging this paradigm, highlighting the role that 'competitor' traits – such as shade tolerance and high resource use efficiency – play in the invasion of low resource environments like shady forest understoreys (Martin & Marks 2006; Reinhart *et al.* 2006; Funk & Vitousek 2007; Martin, Canham & Marks 2009).

In this study, we ask if exotic invasive tree species are constrained by classic life-history trade-offs such as high-light vs. low-light growth, and growth vs. survivorship. Do forest invaders show early successional life-history patterns that predominate in the invasions of other ecosystems? If evident, does rapid growth in exotic plants come at the expense of survivorship? Is shade tolerance necessary to invade unfragmented forests? If exotic species diverge from typical life-history trade-off patterns, what are the implications for invasiveness? We address these questions by examining the life-history patterns of exotic and native tree species by directly comparing their growth and survivorship in forests. We used *in situ* techniques to quantify sapling growth and survivorship of two invasive exotic and nine dominant native tree species in forests of the north-eastern United States. An *in situ* approach integrates the potentially numerous factors behind invasiveness, and focuses on the net demographic patterns key to forest invasions. We chose *Acer platanoides* L. (Norway maple) and *Ailanthus altissima* Mill. (tree of heaven) as two of the most common exotic invasive tree species in the eastern United States. Their life-history patterns are not as well known as those of the natives, but both species are reported to have high growth rates (Kloeppel & Abrams 1995; Knapp & Canham 2000), and *A. platanoides* also shows seedling recruitment patterns that suggest it is shade-tolerant (Webb & Kaunzinger 1993; Martin 1999; Martin & Marks 2006; Gómez-Aparicio, Canham & Martin 2008). As in Pacala *et al.* (1994) and Kobe *et al.* (1995), we focus on saplings because a tree's success in reaching the canopy is largely determined by its performance as a sapling (e.g. Canham 1988a; Clark & Clark 1992; Pacala *et al.* 1996) and allocation trade-offs are confined to growth and survivorship as saplings are pre-reproductive in the forest understorey. The native species in the study represent a wide range of life-history strategies and provide a robust basis for comparing demographics between native and exotic tree species in closed-canopy forests.

Materials and methods

SITES AND STUDY SPECIES

As part of a long-term study of forest dynamics, two permanent sites were established in 1990 in Great Mountain Forest (GMF; 41º57′ N, 73º15′ W) in Litchfield County in north-western Connecticut, USA. The core study area of these sites is 1.8 and 1.5 ha, respectively. Forests in the region are transition oak-northern hardwoods, predominately 90–130 years in age, on sandy, acidic inceptisols and spodsols derived from glacial till and schist/gneiss bedrock (Pacala *et al.* 1996). Nine native tree species were previously characterized for growth (Pacala *et al.* 1994) and survivorship (Kobe *et al.* 1995). These native species include the majority of the dominant and subdominant species in the region and span a wide range of life-history strategies (listed in order of a traditional classification of shade tolerance; Baker 1949): *Fagus grandifolia* Ehrh. (American beech), *Tsuga canadensis* (L.) Carr. (eastern hemlock), *Acer saccharum* Marsh. (sugar maple), *Acer rubrum* L. (red maple), *Betula alleghaniensis* Britton (yellow birch), *Pinus strobus* L. (white pine), *Quercus rubra* L. (northern red oak), *Prunus serotina* Ehrh. (black cherry) and *Fraxinus americana* L. (white ash). The exotic species are invading GMF, but because introductions to the region have been fairly recent, saplings are not yet present within GMF in sufficient numbers for study. Hence, we selected six additional sites nearby in 2004 – three with populations of *A. altissima* and three with populations of *A. platanoides*. The minimum and maximum distances were 6.7–16.9 km, respectively, between the native and exotic study sites. As growth and mortality can be sensitive to soil and site conditions (e.g. Kobe *et al.* 1995), the exotic sites were carefully selected to have conditions similar to GMF: part of large, healthy, unfragmented forests with a native forest composition similar to GMF; where the bulk of exotic species individuals were located in the interior of closed-canopy stands with understorey light conditions ranging from deep shade to high light in large natural gaps; where topography and soil parent material were the same as in the GMF stands, as determined by United States Geological Survey (USGS) topographic maps and a fine-scale bedrock geology map of Connecticut (Rodgers 1985); and where the exotic species were a relatively minor component of the adult overstorey as reflected in dominance (relative basal area ranged from 5% to 14% for *A. platanoides* and 8% to 32% for *A. altissima*). The core study area of each exotic study site was *c.* 2.5 ha. Sampling for growth rates was conducted throughout the core area of each of the six exotic sites; sampling for mortality was conducted in a nested subsite in each core area where conditions promoted shade-induced mortality (see next). As a partial validation of results, we compared *A. platanoides* growth and mortality models from north-western Connecticut with models developed from an *A. saccharum–A. platanoides* forest site near Mason, Michigan, USA (J.M. Eickwort & R.K. Kobe, unpubl. data). Although we lack detailed information for the Michigan site, we expect it to have soils of higher pH and base cation availability based on parent material but lower mean annual precipitation (750 vs. 1350 mm) than the sites in Connecticut.

DATA COLLECTION

Radial growth

Field methods follow Pacala *et al.* (1994). For the native species, we did not collect new data, but re-analysed the original radial growth data from Pacala *et al.* (1994) (see next). To quantify radial growth of exotic saplings (defined as ≥ 1.4 m tall and < 10 cm d.b.h.), we harvested 48–50 sapling cross-sections of each exotic species at 10 cm above the ground (Table S1 in Supporting Information); in Michigan, we harvested 30 *A. platanoides* saplings for stem cross-sections. Saplings were harvested in mid-September 2004 after cessation of radial growth. Locations from which saplings were harvested were selected to span a wide range in light levels as determined by overstorey canopy conditions, from low light under a closed canopy to high light in large gaps. Collected samples represented five categories of light intensity (from very low to very high) to ensure replicates were balanced across the range of light levels. Light levels were quantified *post hoc* (see next). Cross-sections were sanded with a series of progressively finer abrasive belts so that growth rings were clearly visible. The 10 most recent annual growth rings were measured along a representative radius (the radius bisecting the angle formed by the longest and shortest radius of the cross-section) to 0.001 mm accuracy using a stereo microscope ocular micrometre and a computer-assisted mechanical stage. As in Pacala *et al.* (1994), only the most recent growth ring was used in the analysis as it provided the best fit with light.

Height–diameter relationships

We measured heights (1.4–33 m) and diameters (at 10 cm above the ground) of 96 *A. altissima* and 101 *A. platanoides* forest-grown individuals. We sampled from closed forests rather than open conditions because allometric relationships can change with local tree density and our goal was to characterize intact forest stands. Heights were measured using a 7.5-m pole where possible and with an Impulse laser rangefinder and digital clinometer otherwise (Laser Technology Inc., Centennial, CO, USA). We also measured extension growth for the exotic species, although we emphasize radius as a superior predictor of height as radial growth is cumulative, whereas extension growth can be lost to dieback or browsing.

Light availability

We estimated integrated whole-growing season light levels for each sapling with canopy photographs taken on overcast days. Photographs were taken with a camera fit with a fish-eye hemispherical lens, levelled and oriented to true North. After the sapling was cut down, the camera was raised on a telescoping tripod to the height of where the centre of the sapling's foliage had been (up to 7 m high), as an average of the sapling's overall light levels. Photographs were analysed with gap light analyzer (GLA) software (Frazer, Canham & Lertzman 1999) to calculate the gap light index (GLI) of the combined incident diffuse and direct beam radiation over a growing season expressed as a percentage of full sun (Canham 1988b).

Mortality

Species-specific mortality functions of the exotic species were estimated using the sampling methods and maximum-likelihood estimator of Kobe & Coates (1997). These methods provide field-calibrated models of mortality probability as a function of recent radial growth. For the native species, we re-analysed the data in Kobe *et al.* (1995) with the maximum-likelihood estimator of Kobe & Coates (1997) to ensure that all species were fit to a common mortality model (see next).

Sampling of the exotic species mortality occurred in one subsite per species. In addition to the aforementioned criteria, a subsite was chosen for adequate sample sizes of dead saplings. For *A. altissima*, this occurred in dense, self-thinning patches with no mature canopy influence but where dead individuals had been overtopped and shaded by neighbouring *A. altissima* individuals; for *A. platanoides*, we sampled for recently dead saplings in a mature, closed-canopy stand. To ensure adequate sample sizes, we used variable-length belt transects 10-m wide until *c.* 50 recently dead individuals of each species were sampled (dead individuals were less common than live individuals), resulting in sample areas of 550 m^2 for *A. platanoides* and 575 m^2 for *A. altissima*.

In the transects, we tallied the total number of live individuals of each species and collected stem cross-sections at 10 cm above the ground for a random subsample of live individuals and for the entire population of dead individuals. For both exotic species, the subsample of live individuals included all living saplings in the transect, except those with nearly complete dieback (basal sprouters, etc.). Application of these criteria resulted in cross-sectional samples of 47 dead and 55 live individuals for

A. platanoides, and 56 dead and 58 live individuals for *A. altissima*. In Michigan, applying these criteria resulted in 34 dead and 30 live *A. platanoides* saplings. These live and dead samples were collected in addition to the cross-sections collected for growth. We measured the 10 most recent growth rings on these cross-sections following the same methods as before.

As per Kobe & Coates (1997), we determined the time period over which sampled saplings had died (criterion of 'recently dead'). The recently dead threshold for *A. altissima* was determined in the laboratory by comparing the maximum age of the live saplings with the age of the dead saplings, resulting in a 'recently dead' threshold of 3 years for *A. altissima.* The maximum age was consistent as the site was colonized by *A. altissima* seed in a single episode after a small logging operation. The stand history and distance from the nearest adults (> 75 m) also indicated that the saplings were not connected via roots to adult *A. altissima* trees. For *A. platanoides*, we used the field determination method developed for sugar maple (see Kobe *et al.* 1995), resulting in a 'recently dead' threshold of 5 years.

DATA ANALYSIS

Radial growth as a function of light

We used a size-dependent Michaelis–Menten function to model the relationship between light and radial growth:

$$w = r^D(p(L)) + \varepsilon, \qquad \text{eqn 1}$$

where $p(L) = \frac{AL}{(A/S)+L}$,

$$\varepsilon \sim N(0, C[r^D p(L)]).$$

Here, w is the ring width of an individual with radius r, L is the light level and D, A and S are parameters estimated from the data. The parameter D characterizes departures from strictly proportional effects of tree radius on radial growth. In contrast, Pacala *et al.* (1994) modelled radial growth as a constant proportion of sapling radius (i.e. fixed $D = 1$). Although many trees do grow geometrically when small, this may not be realistic for larger individuals as the effect of size on growth rates may level off or become negative (MacFarlane & Kobe 2006). The parameter A defines the rate of asymptotic (or high light) growth and S corresponds with the slope of the growth function at zero light, thus summarizing low-light growth. Large A values indicate that saplings grow rapidly when light levels are high. Large S values indicate that when light is low, a small increase in resource availability leads to a large increase in growth. Observed ring widths are assumed to be normally distributed around the mean ($r^D p(L)$) with variance $C[r^D p(L)]$. We estimated A, S, C and D for each species using maximum-likelihood estimation and simulated annealing (a global optimization algorithm; Goffe, Ferrier & Rogers 1994). We used asymptotic two-unit support intervals (Edwards 1992) to assess the strength of evidence for individual maximum-likelihood parameter estimates. A two-unit support interval is roughly equivalent to a 95% support limit defined using a likelihood ratio test (Hilborn & Mangel 1997). These statistical analyses were performed in R.

Height–Diameter relationships

We estimated the relationship between height and diameter for the exotic species with the exponential Michaelis–Menten regression function used in Pacala *et al.* (1994):

$$H = \alpha(1 - e^{-(\beta/\alpha)2r}) + \varepsilon, \qquad \text{eqn 2}$$

where

$$\varepsilon \sim N(0, \delta[\alpha(1 - e^{-(\beta/\alpha)2r})^\gamma]).$$

Here, H is the height (m) of an individual with radius r (cm) at 10 cm above the ground, α is the asymptotic height, β is the slope of the function at radius zero and δ and γ govern the dependence of the variance on the mean. We estimated the parameters in eqn 2 with the same maximum-likelihood techniques used for radial growth (see before).

Mortality model parameter estimation

We summarize the main features of our analysis here; the reader should refer to Kobe & Coates (1997), which we generally followed, for additional details. We modelled mortality probability as a cumulative distribution function of an exponential random variable, fit to the new data for the two exotic species and re-analyzed the native species data originally collected to develop the fixed time interval mortality models [probability of mortality for a 2.5-year period $= \mathrm{A}e(-B \times \mathrm{gr})$] reported in Kobe *et al.* (1995). A sapling's probability of dying over time interval t is:

$$m(g) = P(\text{death} < t) = 1 - \exp[-\mathrm{t}(\mathrm{z}\mathrm{e}^{-(C \times \mathrm{gr})})], \qquad \text{eqn 3}$$

where z and C are parameters estimated from the data. Parameter z influences mortality at zero growth (where the function crosses the y-axis) and C represents the sensitivity of mortality probability to changes in growth or whole-plant carbon status (and controls the function's decay). We modified the model in Kobe & Coates (1997) by including parameter z, which allows for lower mortality rates at zero growth (thus accommodating shade-tolerant species) than when $z = 1$ [as in eqn 7 of Kobe & Coates (1997)].

We used the arithmetic mean of the five most recent and complete growth rings, which consistently resulted in higher likelihoods than averages of the 2–4 most recent years. For the live samples, we excluded the current growth ring (mortality sampling was conducted in early-to-mid summer before radial growth was completed) to ensure that live growth measurements represented a full growing season.

Interspecific life-history trade-offs and SORTIE-ND simulations

The outcome of competition among saplings in a gap depends primarily on height growth, which is governed by five parameters in our analysis (A, S, D, α, β). Saplings must also survive to compete in height growth. To highlight competitive traits, we calculated two metrics that integrate key aspects of growth and mortality: (i) following Pacala *et al.* (1996), the time to grow from a seedling (diameter at 10 cm above the ground $= 2$ mm) to 3 m in height in deep shade (GLI $= 2\%$), moderate shade (GLI $= 5\%$), a small gap (GLI $= 10\%$) and very high light (GLI $= 80\%$); and (ii) survivorship over 5 years of a 1-cm diameter sapling of each species growing at 1%, 2% and 5% full sunlight, based on the mortality (eqn 3) and radial growth models (eqn 1); saplings growing in higher light levels generally have growth rates large enough to make mortality rates negligible.

To explore the long-term invasion dynamics of the exotic species in native tree communities, we introduced the exotics into virtual forest communities in SORTIE-ND (http://www.sortie-nd.org/), a spatially explicit individual-based model of forest dynamics based on the earlier SORTIE model (Pacala *et al.* 1996). SORTIE-ND simulates forest community dynamics with species-specific submodels that predict a tree's light-based growth and mortality, light extinction (i.e. shade cast by adults) and recruitment (i.e. fecundity, dispersal and seedling establishment). We ran 500-year simulations in a 16-ha area with species-specific growth, mortality, allometry and light extinction parameters. Recruitment was set to an intermediate value (represented by *A. saccharum*; Ribbens, Silander & Pacala 1994) for both exotic and native species to isolate four key traits directly connected to growth and mortality: low-light growth, high-light growth, low-light survival and shade cast. In these simulations, disturbance was modelled as a function of canopy tree controls on understorey light availability. Disturbance can affect resources and exotic species invasions in other ways (e.g. Lozon & MacIsaac 1997), but we did not incorporate alternative effects into the model. Simulations were run with three initial stand conditions: (i) *open field* with seedlings only and equal initial abundances of exotic and native species (density = 25 seedlings species^{-1} ha^{-1}), representing conditions directly after a large, stand-replacing disturbance; (ii) *closed-canopy stand* of mature-sized individuals (mean d.b.h. = 25 cm) with equal initial abundances of exotic and native species (density = 47 trees species^{-1} ha^{-1}); (iii) *incipient invasion* in a closed-canopy stand of mature-sized individuals (mean d.b.h. = 25 cm) with a small population of exotic species (density = 12 trees species^{-1} ha^{-1}) and a large population of natives species (density = 55 trees species^{-1} ha^{-1}). Both closed-canopy scenarios had an initial basal area of 25 m^2 ha^{-1}. Each scenario was simulated with and without a disturbance regime: at years 150 and 300, 100% of adults ($\geq$ 10 cm d.b.h.) in one-quarter of the area were killed, an event analogous to an intermediate-severity windstorm (Papaik & Canham 2006). We replicated each scenario five times with different random-number seeds.

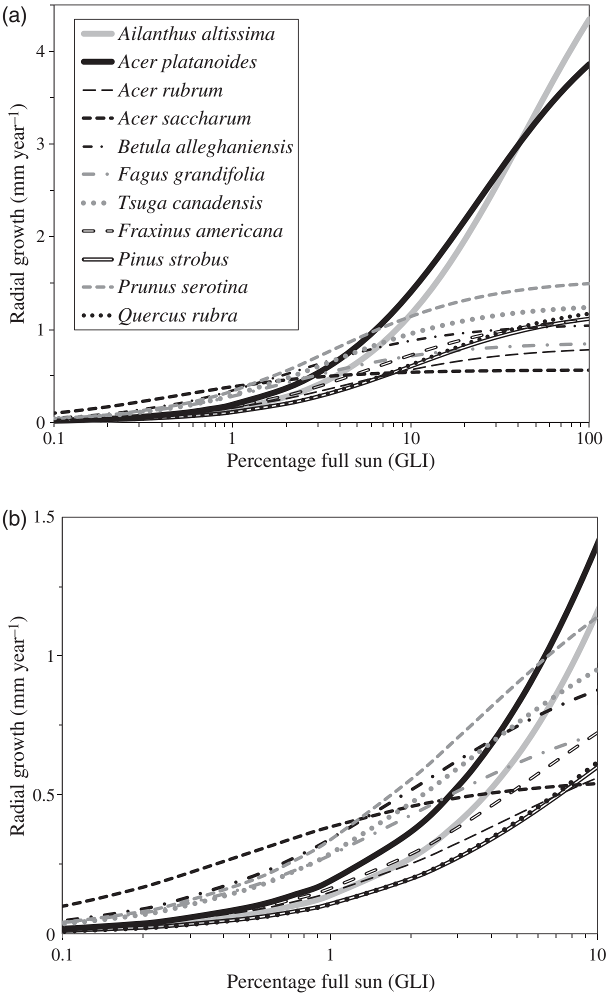

Fig. 1. (a) Estimated radial growth as a function of light intensity for a 1-cm diameter sapling (at 10 cm above the ground) for two exotic and nine native tree species in the north-eastern United States. Growth functions were estimated with a size-dependent model which allows the influence of size on growth rates to vary. Parameters were estimated using eqn 1 and are listed in Table 1. GLI is a gap light index which combines diffuse and direct beam radiation over a growing season expressed as a percentage of full sun. (b) An enlargement of the radial growth from 0.1% to 10% full sun light levels. Note the different scale of the *y*-axis.

Results

SAPLING RADIAL GROWTH RESPONSES

For all species, variation in sapling radial growth was related to variation in light availability (Fig. 1). Depending on species, light explained 25–78% of the variation in growth (Table 1). Light was a better predictor of growth for the two exotic species (average 68%); on average, it explained only 49% of native species growth, perhaps because of higher levels of genetic variation, herbivory or pathogens in native populations. The strength of the growth vs. light patterns in the exotics (across three sites per species) suggests that the role of site-level influences was minor. For *A. platanoides*, the Connecticut and Michigan sites yielded nearly identical irradiance–radial growth relationships for the lower range of irradiance values (Table 1); predicted growth at 1% and 4% full sun differed by $<$ 10% and 1%, respectively, between the Connecticut and Michigan models. We cannot assess correspondence for growth rates associated with light availability $>$ 5% full sun because of limited sampling in Michigan.

The highest irradiances measured for *A. platanoides* and *A. altissima* were 60% and 80% full sun, respectively; the average highest irradiance measured for the native species was *c.* 70% full sun (Table S1). This lack of data $>$ 80% full sun is not an issue in most contexts, as such light levels are very unusual in most forest conditions, even in large blowdowns (e.g. Papaik & Canham 2006), and the growth rates of the native species level off within the measured range of light (Fig. 1). However, the exotic species growth rates did not level off over the measured range of light. Hence, we focus on light levels from $<$ 1–80% full sun.

Species differed with respect to both high (*A*) and low-light (*S*) growth (Table 1). Both exotic species had strikingly higher high-light growth rates (*A*) than the native species, with their average high-light growth rates being 1.7, 2.3 and 2.6 times higher than the *fastest*-growing native species at light levels of 25%, 50% and 80% full sun, respectively. Mean radial growth rates of both exotics exceeded all native species when light levels exceeded 10% full sun (Fig. 1a); between 6% and 10% full

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Table 1. Growth models with maximum-likelihood parameter estimates and two-unit asymptotic support intervals (in parentheses) of two exotic and nine native tree species in the north-eastern United States. Data for the native species came from Pacala *et al.* (1994), but were re-analysed here. Radial growth rates (mm year^{-1}) by light (% full sun) were fit using a Michaelis–Menten function which included a size-dependent parameter (D); this allows the influence of diameter on growth rates to vary with size. See eqn 1 for full definitions of parameters. Two measures of model fit are reported: R^2 and slope of the relationship between observed and predicted values. The two exotic species are listed first

Species	A	S	D	R^2	Slope
Acer platanoides	3.489 (2.478–5.58)	0.145 (0.120–0.175)	0.197 (0.151–0.243)	0.64	1.01
Ailanthus altissima	3.683 (2.615–6.399)	0.084 (0.072–0.102)	0.328 (0.285–0.378)	0.72	1.01
Acer rubrum	0.295 (0.224–0.375)	0.066 (0.045–0.105)	0.630 (0.529–0.718)	0.26	0.98
Acer saccharum	0.213 (0.192–0.238)	0.451 (0.388–0.601)	0.605 (0.559–0.658)	0.25	1.09
Betula alleghaniensis	0.348 (0.279–0.431)	0.165 (0.119–0.274)	0.693 (0.624–0.794)	0.40	1.03
Fagus grandifolia	0.250 (0.212–0.292)	0.120 (0.085–0.174)	0.774 (0.716–0.833)	0.54	1.01
Fraxinus americana	0.360 (0.245–0.512)	0.058 (0.041–0.081)	0.733 (0.665–0.817)	0.49	1.05
Pinus strobus	0.303 (0.249–0.383)	0.029 (0.023–0.039)	0.869 (0.822–0.921)	0.78	1.00
Prunus serotina	0.459 (0.391–0.553)	0.128 (0.098–0.174)	0.756 (0.711–0.808)	0.62	0.99
Quercus rubra	0.264 (0.209–0.320)	0.024 (0.018–0.034)	0.988 (0.916–1.038)	0.57	0.99
Tsuga canadensis	0.378 (0.329–0.432)	0.110 (0.073–0.165)	0.757 (0.711–0.799)	0.52	1.00

*For the Michigan population of *A. platanoides*, which was sampled from < 0.5 to 4% full sun, $w = \text{radius}^D \times 0.126 \times \text{GLI}$ ($R^2 = 0.75$), where D is set to 1 because of the narrow range of tree radii (5–30 mm). For a hypothetical sapling of 1-cm diameter, predicted growth over 0–4% full sun is nearly identical between the Michigan and Connecticut models.

sun, *A. platanoides* had the highest growth rate of any species. At light levels below 3% full sun, however, the average growth of the five native species was faster than that of either exotic species (Fig. 1b).

SAPLING SIZE EFFECTS ON GROWTH

The exotic species' extraordinary advantage in high-light growth was tempered by smaller effects of increased size on growth rates; that is, D was much smaller for the exotics than any native species (Table 1). As sapling diameter increased, all the native species markedly increased growth at a given light level compared with the exotics. At ≥ 5 cm diameter (at 10 cm above the ground; diameter hereafter refers to this) radial growth of four native species (*P. serotina, P. strobus*, *Q. rubra*, *T. canadensis*) began to equal or exceed the growth of the exotics except at the highest light levels; the growth rates of the other five native species did not exceed the exotics at light levels ≥ 40% full sun even for the largest saplings (5–10 cm in diameter). The ecological significance, however, of this size-effect advantage is unclear as the native species data set does not include very large saplings that would ensure robust estimation of D, and the same native species are reported to experience a reduction in size effects on growth at larger sizes in Michigan (Kobe 2006). Overall, the average diameter in the native sample was 17 mm (SD ± 12 mm), much smaller than the range for the exotics (Table S1). Hence, we concentrate on small saplings, although the natives' advantage in size effects are reflected in the SORTIE-ND simulations (see next).

HEIGHT–DIAMETER RELATIONSHIPS

For saplings, the average individual of *A. altissima* at a given radius is shorter than four native species (*B. alleghaniensis*, *F. americana*, *A. rubrum*, *A. saccharum*) and *A. platanoides* is shorter at a given radius than all the natives except for *P. strobus* and the region's late-successional species, *F. grandifolia* and *T. canadensis* (based on value rankings of β in Table S2). These relationships change at larger diameters, as the height of the species with low asymptotic heights (α) level off by d.b.h. 30 (Table S2). *A. platanoides* has a maximum height greater than that of any native species except for *F. grandifolia* and *P. strobus*. From a competitive interactions standpoint, allometric relationships link diameter growth with height growth, which summarizes overtopping relationships and competitive hierarchies for irradiance (Table 2). For example, despite relatively fast radial growth under high light, the squat architecture of *T. canadensis* results in relatively slow height growth, limiting its ability to overtop other species. However, *A. altissima*'s very high radial growth rates at high-light levels compensate for its rather typical height–diameter relationship (smaller β than four native species), and its height growth overtops all species in large openings (Table 2). The exotic species also displayed high height extension growth rates: *A. altissima*'s extension growth was as high as 1730 mm in 21% full sun, with an average of 681 mm in 10% full sun and 1620 mm in 75% full sun; *A. platanoides*' highest extension growth was 782 mm in 17% full sun, with an average of 305 mm in 10% full sun and 586 mm in 55% full sun.

MORTALITY

Three native species (*F. grandifolia*, *T. canadensis* and *P. strobus*) have lower mortality than either exotic species for all observed growth rates (Fig. 2 and Table 3). Across observed growth rates, *A. platanoides* has intermediate mortality at both the Connecticut and Michigan sites. At growth rates > 0.1 mm (the minimum growth rate for the Michigan saplings), the Connecticut and Michigan mortality functions were very similar (Table 3). Given the distance between and differences in sites, the correspondence of light-driven *A. platanoides* growth and mortality in the two sites is strong (if indirect)

Table 2. Metrics of interspecific variation in competitive strategies of two exotic and nine native tree species in the north-eastern United States. GLI is a gap light index which combines diffuse and direct beam radiation over a growing season expressed as a percentage of full sun. The two exotic species are listed first

	Time to 3 m height (years)				Growth (mm year^{-1})			Survivorship (5-year)		
	Light level (GLI):				Light level (GLI):			Light level (GLI):		
	2%	5%	10%	80%	2%	5%	10%	2%	5%	10%
Acer platanoides	31.5	15.2	9.4	3.4	0.37	0.82	1.41	0.77	0.98	1.00
Ailanthus altissima	36.8	16.9	9.9	2.8	0.27	0.64	1.16	0.22	0.37	0.55
Acer rubrum	37.2	22.5	17.6	12.3	0.25	0.43	0.56	0.68	0.93	0.98
Acer saccharum	21.2	18.0	18.2	16.6	0.46	0.52	0.54	0.87	0.92	0.94
Betula alleghaniensis	19.6	14.1	12.2	9.6	0.52	0.75	0.88	0.76	0.89	0.94
Fagus grandifolia	32.3	23.1	19.0	16.3	0.43	0.61	0.72	0.97	0.98	0.98
Fraxinus americana	36.5	20.8	15.5	9.9	0.29	0.52	0.72	0.56	0.95	0.99
Pinus strobus	70.1	35.9	24.5	13.5	0.20	0.40	0.60	0.79	0.94	0.98
Prunus serotina	22.4	14.5	11.9	9.6	0.55	0.90	1.14	0.95	1.00	1.00
Quercus rubra	65.3	33.3	22.6	12.2	0.20	0.40	0.62	0.71	0.98	1.00
Tsuga canadensis	35.1	22.6	18.4	13.8	0.47	0.76	0.95	0.99	1.00	1.00

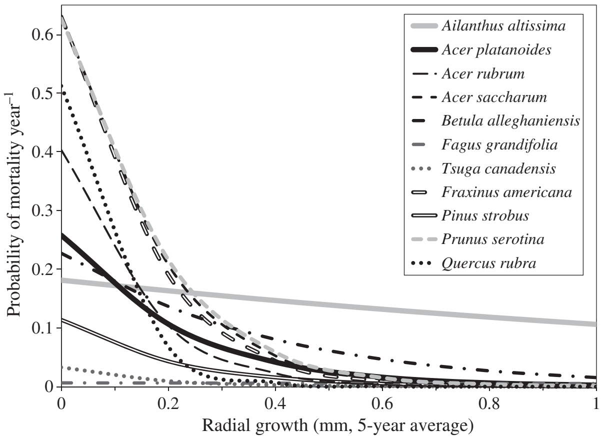

Fig. 2. Species-specific probabilities of mortality per year as a function of radial growth for two exotic and nine native tree species in the north-eastern United States. Parameter estimates are in Table 3.

evidence of the robustness of the pattern for this species. At radial growth rates < 0.2 mm year^{-1} in the Connecticut site (considered suppressed in these forests; Kobe *et al.* 1995), its mean mortality rate ranks lower than that of five native species. *A. altissima* has relatively high probabilities of mortality at high growth rates, arising from a rather flat relationship between mortality and growth (Fig. 2).

Table 3. Mortality model parameter estimates and two-unit asymptotic support intervals (in parentheses) of two exotic and nine native tree species in the north-eastern United States. Data for the native species are from Kobe *et al.* (1995), but are re-analysed here using the annual mortality estimator in Kobe & Coates (1997). Z influences the annual probability of mortality at zero growth and C represents the sensitivity of mortality probability to changes in growth. The two exotic species are listed first

Species	Z	C
Acer platanoides	0.298 (0.216–0.393)	4.870 (3.587–6.357)
Ailanthus altissima	0.200 (0.159–0.247)	0.577 (0.316–0.818)
Acer rubrum	0.516 (0.372–0.710)	7.703 (6.548–8.996)
Acer saccharum	0.997 (0.762–1.572)	7.268 (6.066–8.510)
Betula alleghaniensis	0.257 (0.182–0.353)	2.806 (2.188–3.522)
Fagus grandifolia	0.006 (0.002–0.011)	0.091 (-2.833–3.483)
Fraxinus americana	0.994 (0.635–0.1.577)	7.732 (6.192–9.617)
Pinus strobus	0.121 (0.062–0.207)	5.001 (3.073–7.287)
Prunus serotina	0.986 (0.559–1.737)	7.193 (5.425–9.532)
Quercus rubra	0.717 (0.369–1.197)	11.588 (9.104–14.787)
Tsuga canadensis	0.033 (0.013–0.069)	6.361 (3.603–9.467)

*For *A. platanoides* sampled in Michigan, Z = 1.169 (0.533–2.202) and C = 15.60 (12.46–19.25); the Michigan and Connecticut models result in similar estimates of mortality probability between 0.1 and 0.2 mm growth.

Based on the combination of the growth and mortality models, the rankings of low-light mortality for the exotic species were strongly dependent on the degree of shading; for example, at very dark light levels of 1% full sun, annual mortality probability for *A. platanoides* saplings was *c.* 10%, and the mortality probability for *A. altissima* was nearly 17% (Fig. 3). At this light level, only two natives (*P. serotina* and *F. americana*) had higher mortality. However, at 5% full sun, *A. platanoides* had < 1% probability of mortality per year, and the mortality rates of only three natives ranked lower. The mean annual mortality probability of all species dropped to < 1% by 10% full sun, except for *A. altissima* which still had a mortality rate of 9% year^{-1} at this light level (Fig. 3).

INTERSPECIFIC LIFE-HISTORY TRADE-OFFS AND SORTIE-ND SIMULATIONS

Among species, low-light survivorship vs. high-light height growth was inversely correlated along an approximately linear axis (Fig. 4): as the ability to persist in low light increased, height growth rates in high light decreased. This axis ordered the native species according to their successional status (Kobe *et al.* 1995) and provided a quantitative measure of the exotic species rankings in this hierarchy. Clearly, the exotic species

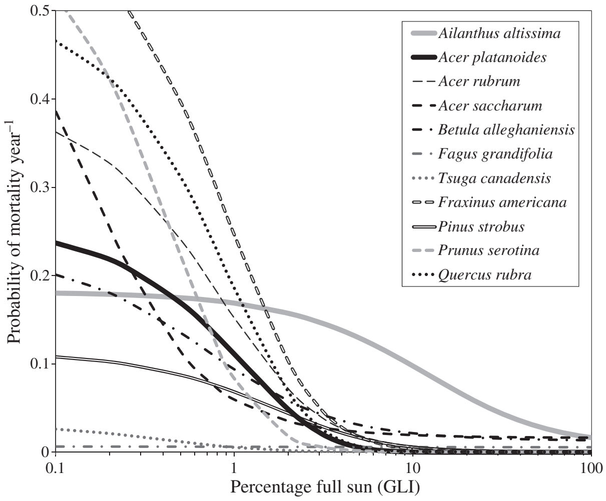

Fig. 3. Species-specific annual probabilities of mortality as a function of light intensity based on average growth light response of a 1-cm diameter sapling (at 10 cm above the ground) for two exotic and nine native tree species in the north-eastern United States. GLI is a gap light index which combines diffuse and direct beam radiation over a growing season expressed as a percentage of full sun.

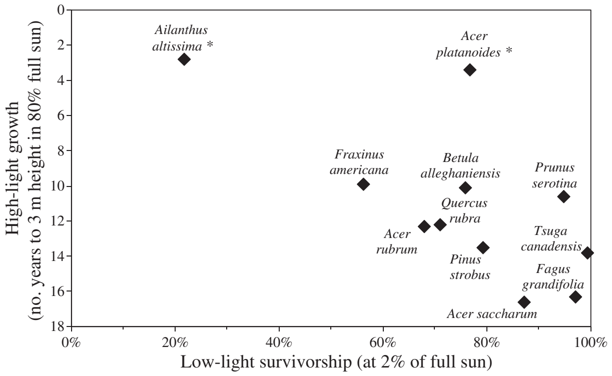

Fig. 4. Species trade-off between high-light growth and low-light survivorship for two exotic and nine native tree species in the north-eastern United States. The *x*-axis is 5-year survivorship (%) of a 1-cm diameter sapling growing at 2% full sunlight. The *y*-axis represents the number of years necessary for a 2-mm diameter seedling to reach 3 m in height in 80% full sunlight. The exotic species are denoted with an asterisk (*).

have exceptional growth rates in high light, but for *A. altissima* high growth was associated with low survivorship under low light. In contrast, *A. platanoides* diverged from this trade-off pattern, with higher than expected high-light growth based on its low-light survivorship.

Initial conditions strongly influenced long-term invasion dynamics, based on the SORTIE-ND simulations. In the *open field* scenario, the exotics' rapid high-light growth translated into a large early advantage through year 165 when their joint basal area peaked at 68% of total basal area. After year 165, *A. altissima* (Fig. 5a) declined in basal area, although disturbance notably delayed the decline (Fig. 5d). *A. platanoides* remained dominant throughout the *open field* simulations with or without disturbance. In the *closed-canopy stand* scenario, native shade-tolerant species eventually dominated without disturbance, but *A. platanoides* remained at least third in total basal area throughout the run (Fig. 5b). In this scenario, *A. altissima*'s abundance was limited. With disturbance, however, both exotics invaded far more successfully (Fig. 5e). In the *incipient invasion* scenario, the exotics remained minor components with or without disturbance, although *A. platanoides* gradually increased over the run in both scenarios (Fig. 5c,f). In the *incipient invasion*, the exotics were unable to aggressively colonize owing to the closed conditions and larger native populations especially of shade-tolerant species which dominate the *incipient invasion* simulations. In general, the disturbances favoured the exotics, but also native shade-tolerant species whose regeneration was released by overstorey mortality.

Discussion

EXOTIC SPECIES LIFE-HISTORY TRADE-OFFS

The central questions posed were whether exotic invasive tree species are constrained by trade-offs between growth and survivorship, and where these exotic species fit into the life-history hierarchies of the native forest community. This study provides a quantitative analysis of these issues and in the process highlights the main invasion 'strategies' of these species: we conclude that by combining rapid high-light growth and intermediate low-light survivorship – characteristics of both early and mid-successional species – the invasiveness of *A. platanoides* results at least in part from its departure from the trade-off constraints experienced by the native species. Conversely, *A. altissima* invaded via its very high growth rates which directly trade-off with its survivorship along the line defined by the native community (Fig. 4). Thus, *A. altissima* invades as an early successional species, albeit a particularly extreme one. The departure of *A. platanoides* from the growth–survival trade-off may result from its high levels of physiological plasticity – for example, *A. platanoides*' rates of photosynthesis and light saturation at the leaf level were twice those of *A. saccharum*, whereas both species had similar respiration rates and light compensation points (Kloeppel & Abrams 1995). Similar evidence for such 'trade-off plasticity' has been reported elsewhere for *A. platanoides* (Reinhart *et al.* 2006) and other exotic invasive plants (Ridenour *et al.* 2006). Still, the plasticity of these exotic species is not without limitation, as even *A. platanoides* failed to combine high survivorship under low light with high growth at high light.

RAPID GROWTH AND INVASIVENESS

This study highlights the role of rapid growth as the *principal* source of invasiveness by these exotics species. In moderate to high-light levels, *A. altissima* and *A. platanoides* had growth rates far higher than those of even the fastest-growing native tree species. *A. altissima* required 23% full sun and *A. platanoides* 16% full sun to reach 50% of maximum radial growth, and neither exotic species' growth appeared to saturate at high light. To maintain high growth rates in high light, the exotics likely have adaptations to temperature and moisture stress

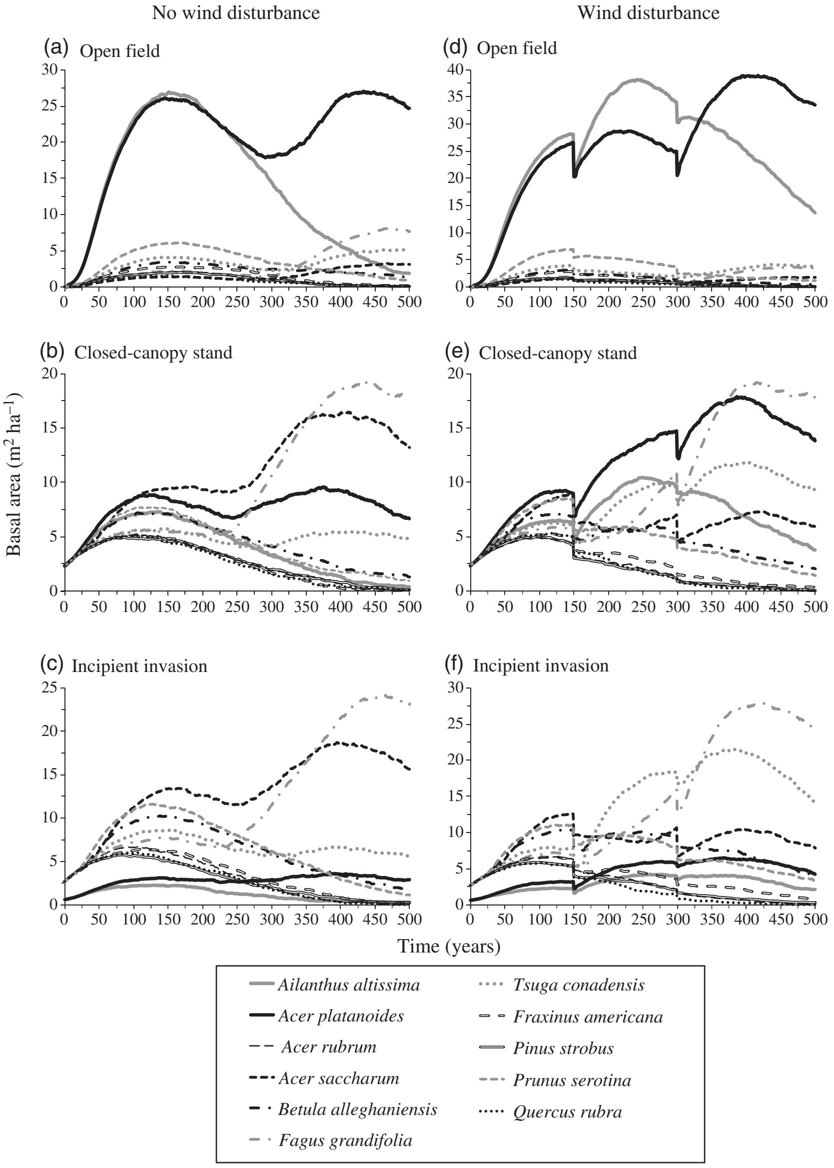

Fig. 5. The long-term invasion dynamics of *Acer platanoides* and *Ailanthus altissima* in 500-year SORTIE-ND simulations in closed-canopy forest in the north-eastern United States. Simulations were run with three initial stand conditions: *open field*, *closed-canopy stand* and an *incipient invasion* in a closed-canopy stand. Each scenario was run with and without a wind disturbance regime. Five replicates per scenario were run; the average is shown. Note the different scales of the *y*-axes.

associated with exposure to full sunlight. Recall that conservative inferences about the exotics' growth should be confined to the range of light we measured: up to 60% for *A. platanoides* and 80% full sun for *A. altissima*. In contrast, native species growth was highly sensitive to light levels < 10% but fully saturated by moderate light levels of *c*. 20% full sun, which is well below the maximum measured light levels (Table S1).

In general, unusually rapid growth rates are a common characteristic of exotic invasive plants (e.g. Rejmánek & Richardson 1996; Reichard & Hamilton 1997) and such life-history patterns have been found in other exotic invasive trees: for example, genetic modifications in exotic populations of *Sapium sebiferum* increased growth and reproduction at the expense of defence and survivorship (Siemann & Rogers 2001, 2003). Such patterns indicate that important modifications to an exotic's life-history strategy can occur in its introduced range, and given the striking advantages in growth displayed by the exotics in this study, we hypothesize that similar changes may have occurred in the introduced range of these two species. However, evidence for such changes in these exotics is limited and mixed. In its introduced range, *A. platanoides* does experiences three times less herbivory than in its native range (Adams *et al.* 2009), and in the United States it suffers less leaf damage than the native *A. saccharum* (although both species have low levels of damage, 0.4–2.5%; Cincotta, Adams & Holzapfel 2009). Alternatively, Morrison & Mauck (2007) reported nearly identical rates of foliar insect herbivory and disease for *A. platanoides* and *A. saccharum* in some forests in the United States. Likewise, *A. platanoides* seedlings grow more slowly in non-sterilized vs. sterilized soil gathered from beneath conspecific mature trees in Montana, USA, suggesting the accumulation of inhibitory soil biota under adults in its introduced range (Reinhart & Callaway 2004). The enemy ecology of *A. altissima* is relatively unknown. Historically, the species was considered relatively resistant to insects and pathogens (Goor & Barney 1968; Hepting 1971), although there is now documented evidence of stand-scale mortality of *A. altissima* by a wilt (*Verticillium albo-atrum*) and other pathogens (Schall

& Davis 2009). Both exotics were introduced to the United States over 200 years ago, so they may have acquired enemies, as occurs for other exotic plants with a long period of introduction (e.g. Siemann & Rogers 2001).

Given the contrary evidence, more common garden and biogeographical studies (see Hierro, Maron & Callaway 2005) are needed to further explore the patterns and mechanisms of life-history changes in exotic plant invasions of forests before we can conclude that forest invasions are predominately the result of rapid growth patterns by 'weedy' or ruderal exotic plant species. Indeed, a review by Martin, Canham & Marks (2009) found a surprisingly high number of shade-tolerant invaders in forests, suggesting that invasiveness does not necessarily result in the loss or diminishment of survivorship traits in exotic plants.

SHADE TOLERANCE AND FOREST INVASIONS

Both of the studied exotic tree species can invade unfragmented forests (our personal observations); thus, we assumed that shade tolerance would be an important component of their invasiveness. Our study only partially confirms this expectation. Kobe *et al.* (1995) and Pacala *et al.* (1996) argued that interspecific differences in juvenile low-light survivorship are critical to predict native forest succession. Likewise, our results show that survivorship in low light (i.e. shade tolerance) is essential for exotic invasions of forests, largely determining long-term invasion abundance.

We quantified the shade tolerance level of *A. altissima* saplings, confirming the long-held view of its intolerance to shade (Grime 1965). Nevertheless, *Ailanthus'* growth rates enable it to reach the canopy in a single release provided by a treefall gap before gap closure from lateral crown expansion (Knapp & Canham 2000); species growing more slowly must be sufficiently shade-tolerant to survive repeated periods of suppression (Canham 1989). Kowarik & Säumel (2007) report higher shade tolerance in *A. altissima* root suckers than in true seedlings which may allow the species to invade shadier areas via its root system. It was somewhat surprising that *A. platanoides* was not more shade tolerant in our study given its super abundant and highly shade-tolerant seedlings (e.g. Webb & Kaunzinger 1993; Martin & Marks 2006; Gómez-Aparicio, Canham & Martin 2008). Shade tolerance can be higher in seedlings than saplings, conferred by size-dependent changes in whole-plant carbon balance (Kneeshaw *et al.* 2006) or by carbon subsidies via a high seed mass (Martin & Canham, 2010). A high seed production also allows *A. platanoides* to replenish the seedling bank faster than native shade-tolerant species (Martin & Canham, 2010). Finally, in the absence of highly shade-tolerant native species, the moderate shade tolerance of *A. platanoides* may enable it to successfully invade the understorey (Reinhart, Greene & Callaway 2005).

ALTERNATIVE SOURCES OF INVASIVENESS

Life histories in exotic invasive and native species vary in ways not described in this study, including seed production, dispersal (e.g. Ribbens, Silander & Pacala 1994), adult tree longevity, crown allometry and modification of understorey light environments (Pacala *et al.* 1996). Both of the exotic species are highly fecund, so it is unlikely that high growth or survivorship come at the expense of fecundity (Martin & Canham, 2010). Modification of soils and soil microbes by exotic species also can be an important factor in invasions (e.g. Vitousek & Walker 1989; Ehrenfeld & Scott 2001; Ehrenfeld 2003; Callaway & Ridenour 2004). Both of these exotic species are known to modify soil chemistry (Gómez-Aparicio & Canham 2008*a* Gómez-Aparicio & Canham 2008*b*) in ways that feedback on invasion success (Gómez-Aparicio, Canham & Martin 2008). These alternative factors of invasiveness were not explicitly incorporated into our field data or simulations, and thus the results do not capture the full invasion dynamics of these species. However, these omissions make our current results conservative, as the native species were studied in sites without invasive exotic species and thus without any such potentially negative influences.

LONG-TERM INVASION DYNAMICS

In the SORTIE-ND simulations, *A. altissima* abundance was limited even with a moderate disturbance regime because of its poor shade tolerance. After a large disturbance, however, *A. altissima* becomes super dominant owing to its rapid growth. In contrast, *A. platanoides* demonstrated the uncommon combination of traits needed to invade and dominate some closed-canopy forests. The simulations highlight the importance of stand conditions at the time of invasion and the role of biological inertia in the dynamics of forests (*sensu* Von Holle, Delcourt & Simberloff 2003), where the longevity of most tree species and positive feedbacks on recruitment from adult trees can translate into centuries of dominance by the species that occupy the canopy. Short-range dispersal (e.g. Ribbens, Silander & Pacala 1994) and inherently slow growth rates in the shade (e.g. Canham 1985) also contribute to slow dynamics in forests, even where strong competitive asymmetries exist between species. Such dynamics can create the impression that even highly invasive exotics with mid- to late-successional life-history traits are weakly or non-invasive without disturbance. The simulations also reveal the importance of community composition to the resistance and recovery of native communities to invasion – the three native shade-tolerant species created conditions that excluded or slowed the spread of the exotics, making them especially important in these forests as fast-growing, less shade-tolerant natives do not compete well with the exotics.

The prevailing natural disturbance regime of eastern US forests – small canopy gaps (e.g. Lorimer 1989) – will directly influence invasion dynamics. Gaps are typically small and are unlikely to lead to high overall abundance by *A. altissima* but could enable patchy invasion and persistence (Knapp & Canham 2000). Small canopy gaps will favour *A. platanoides*, because of its high growth and survivorship in light levels typical of small gaps (Canham *et al.* 1990). A period without disturbances could delay incipient invasions, creating an apparent 'lag phase', and making some stand structures (e.g.

dense, early successional stands with smaller gaps; Lorimer 1989) temporarily more resistant to invasion. However, perturbations which increase canopy openings such as native and introduced pests and pathogens (e.g. hemlock woolly adelgid, beech bark disease) are likely to accelerate invasions (e.g. Eschtruth & Battles 2009), while also reducing invasion resistance by removing native shade-tolerant tree species. We stress that disturbance can promote and influence exotic species invasions in ways not incorporated in our SORTIE-ND simulations (e.g. via soil resources; Davis & Pelsor 2001). Given the prominence of light in the dynamics of closed-canopy forests, however, we expect that our light-based approach accounts for much of the potential influence of disturbance on the invasion dynamics of exotic tree species.

Conclusions

This study showcases the importance of rapid growth in invasive plants, and for *A. platanoides*, divergence from the low-light survivorship vs. high-light growth trade-off that drives native forest succession (Kobe *et al.* 1995; Pacala *et al.* 1996). Forests with native shade-tolerant species may be well suited to resist invasions by *A. altissima* or species with similar early successional attributes. However, *A. platanoides* diverges from the growth–survival trade-off displayed by the native species, and its relatively high growth and survivorship combined with high fecundity (Martin & Canham, in press) could endow *A. platanoides* with the ability to invade both disturbed and undisturbed forest ecosystems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Mean, standard deviation, median and ranges of the growth data used in this study.

Table S2. Height–diameter relationships with 95% confidence limits of two exotic and nine native tree species in the north-eastern United States.