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Dispersal and recruitment limitation in native versus exotic tree species: life-history strategies and Janzen-Connell effects

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Life-history traits of invasive exotic plants are typically considered to be exceptional vis-à-vis native species. In particular, hyper-fecundity and long range dispersal are regarded as invasive traits, but direct comparisons with native species are needed to identify the life-history stages behind invasiveness. Until recently, this task was particularly problematic in forests as tree fecundity and dispersal were difficult to characterize in closed stands. We used inverse modelling to parameterize fecundity, seed dispersal and seedling dispersion functions for two exotic and eight native tree species in closed-canopy forests in Connecticut, USA. Interannual variation in seed production was dramatic for all species, with complete seed crop failures in at least one year for six native species. However, the average per capita seed production of the exotic *Ailanthus altissima* was extraordinary: $>$ 40 times higher than the next highest species. Seed production of the shade tolerant exotic *Acer platanoides* was average, but much higher than the native shade tolerant species, and the density of its established seedlings ($\geq$ 3 years) was higher than any other species. Overall, the data supported a model in which adults of native and exotic species must reach a minimum size before seed production occurred. Once reached, the relationship between tree diameter and seed production was fairly flat for seven species, including both exotics. Seed dispersal was highly localized and usually showed a steep decline with increasing distance from parent trees: only *Ailanthus altissima* and *Fraxinus americana* had mean dispersal distances $>$ 10 m. Janzen-Connell patterns were clearly evident for both native and exotic species, as the mode and mean dispersion distance of seedlings were further from potential parent trees than seeds. The comparable intensity of Janzen-Connell effects between native and exotic species suggests that the enemy escape hypothesis alone cannot explain the invasiveness of these exotics. Our study confirms the general importance of colonization processes in invasions, yet demonstrates how invasiveness can occur via divergent colonization strategies. Dispersal limitation of *Acer platanoides* and recruitment limitation of *Ailanthus altissima* will likely constitute some limit on their invasiveness in closed-canopy forests.

Colonization by trees is the composite of two distinct spatial processes: supply processes of seed production and dispersal which determine the spread of propagules, and post-dispersal recruitment processes that govern the survival of seeds and seedlings (Clark et al. 1998, Nathan and Muller-Landau 2000, Wang and Smith 2002). Together dispersal and recruitment processes constitute a major determinant of the local abundance and diversity of adult trees (Ribbens et al. 1994, Tilman 1994, Clark and Ji 1995, Hurtt and Pacala 1995, Dalling et al. 1998), and dispersal and/or recruitment limitation can act as a fundamental bottleneck in the population dynamics of many species of trees (Pacala et al. 1996, Swaine 1996, Nathan and Muller-Landau 2000). Given the tight linkage between these processes, studies of colonization ideally integrate each stage of colonization, from seed production and dispersal through seedling establishment, including germination and early seedling survival (Harcombe 1987, Nakashizuka et al. 1995). Such integrated studies can detect key stages and interactions controlling colonization. For example, secondary dispersal and post-dispersal seed predation (sensu Janzen 1970, Connell 1971) can substantially alter the shape of a dispersal 'shadow' (Howe et al. 1985, Schupp 1988). Indeed, there is growing evidence that such negative density-dependent effects are common, particularly at the seedling stage (Connell and Green 2000, Harms et al. 2000, Packer and Clay 2000, Uriarte et al. 2005) and that they can decouple seedling dispersion patterns from spatial arrangement of conspecific adults.

Most studies of tree seed dispersal report highly localized patterns, with empirical estimates of average seed and seedling distances from parent trees generally less than 20 m for all but the smallest-seeded species (Ribbens et al. 1994, Clark et al. 1998, LePage et al. 2000, Uriarte et al. 2005). While long distance dispersal occurs and is critical for migration rates (Clark et al. 1999, Higgins and Richardson 1999), the predominance of short range dispersal has a fundamental influence on forest dynamics, as studies demonstrate local (e.g. stand-level) dispersal limitation can act to promote coexistence among tree species by preventing competitive exclusion (Pacala et al. 1996, Hubbell et al. 1999, Chesson and Neuhauser 2002, Papaik and Canham 2006). If these patterns hold for exotic tree species, regional and local dispersal limitation could buffer forests from invasion by exotic species.

Seed production, dispersal and seedling recruitment are likewise pivotal in the dynamics of exotic plant invasions. High fecundity, long-range dispersal, and early maturity are typically regarded as the key life-history attributes of an invasive plant (Rejmánek and Richardson 1996). Given the initial disadvantage exotic plants typically face in abundance and range in their introduced environments, high fecundity, efficient dispersal, and rapid recruitment and maturation are crucial to the rate and trajectory of invasions (Kot et al. 1996, Rouget and Richardson 2003, Hastings et al. 2005, Von Holle and Simberloff 2005), so much so that high propagule pressure is considered one of the few universal components of invasions (Lonsdale 1999, Grime 2001). Yet, little work has simultaneously examined fecundity, dispersal and recruitment of exotic invasive trees in direct comparison with natives in closed-canopy forests, where such processes undoubtedly exert a pronounced influence on invasion dynamics and where conditions are generally assumed to block recruitment by invasive plants (reviewed by Martin et al. 2009). For example, if exotic invasive tree species have predominately short range dispersal like native tree species, areas distant from exotic seed sources may be buffered from invasion; likewise, if exotic species experience recruitment limitation and negative density-dependent effects, these processes may promote coexistence between native and exotic species even on stand scales (Pacala et al. 1996, Hille Ris Lambers and Clark 2003). Exotic species, however, may be less prone to negative density-dependent processes given their presumed reduction in granivores, pests and pathogens in introduced habitats (Elton 1958). These are fundamental issues in assessing the invasive potential of exotic species, and highlight the relative importance of propagule pressure (via fecundity and dispersal) versus the invasion resistance of native communities (by limiting exotic species recruitment) in determining the long-term trajectory of exotic invasions.

We used spatially-explicit techniques and inverse modelling to explore variation in fecundity, seed dispersal and seedling dispersion of two invasive exotic and eight native tree species that are common in forests of the northeastern United States. Seed production and dispersal had not previously been characterized for either the native or exotic species in these forests using these techniques, though Ribbens et al. (1994) used inverse modelling to measure seedling dispersion for these native species. For the exotic species, we chose *Acer platanoides* (Norway maple) and *Ailanthus altissima* (tree of heaven) as two of the most common exotic invasive tree species of the eastern USA. Both species have demonstrated an ability to invade forests (Knapp and Canham 2000, Martin and Marks 2006) and are reported to have high or prolific fecundity (Hu 1979, Mitchell and Wilkinson 1982), but their seed production and dispersal have not been studied in an integrated, spatially-explicit fashion nor in natural closed-canopied forests in direct competition with native species. The primary objective of this study was to determine whether these exotic invasive tree species have life history advantages in seed production, dispersal and seedling establishment over native tree species in closed-canopy forests free of recent disturbance. We asked if there are fundamental limits on colonization and recruitment of these exotic species. In addition, we asked how native and exotic tree species regeneration patterns are influenced by negative density- and distance-dependent processes, the so-called Janzen-Connell effects. The eight native species in the study represent a wide range of life history strategies, and provide a robust basis for comparing dispersal and recruitment dynamics between native and exotic tree species in these forests.

Methods

Study species and sites

As part of a long-term study of forest dynamics, two permanent study sites (1.6 ha and 1.3 ha, respectively) were established in 1990 within Great Mountain Forest (GMF) (41°57′N, 73°15′W) in Litchfield County in northwestern Connecticut, USA. Forests in the region are transition oak–northern hardwoods, ~90–130 years in age, on sandy, acidic inceptisols and podsols derived from glacial till and schist/gneiss bedrock (Pacala et al. 1996). Because the two exotic tree species are not yet present within GMF in sufficient numbers for study, we selected six additional sites near GMF in 2003. Three of the new sites contained populations of *A. altissima*, and three contained populations of *A. platanoides*. These sites were carefully selected to have conditions similar to GMF. Specifically, all were part of larger, contiguous, unfragmented forests, where the bulk of the individual exotic species were located in the interior of closed-canopy stands and had soil parent material and topography similar to GMF. The mapped portions of the sites were 2.2 ha, 3.5 ha and 2.6 ha for the *A. platanoides* sites, and 0.8 ha, 2.5 ha and 1.6 ha for the *A. altissima* sites. The sites varied in relative basal area of the exotic species, from 5–14% for *A. platanoides* and 8–32% for *A. altissima*. Understory light levels in the exotic stands were homogeneous and low (mean [Q10%–Q90%] = 4.86% full sun [4.00%–6.21%]; Gómez-Aparicio et al. 2008).

The eight native and two exotic study species encompass both wind and faunal dispersal vectors (Appendix 1). The wind-dispersed species are the two exotic species, and five of the native species: *Acer rubrum* (red maple), *Acer saccharum* (sugar maple), *Fraxinus americana* (white ash), *Pinus strobus* (white pine), and *Tsuga canadensis* (eastern hemlock). *Prunus serotina* (black cherry) is primarily dispersed by birds and gravity. *Fagus grandifolia* (American beech) and *Quercus rubra* (northern red oak) are dispersed by gravity and caching by small mammals. *Acer saccharum*, *F. grandifolia*, *P. serotina* and *Q. rubra* are 'masting' species while the other native species are thought to produce more regular seed crops. The masting behaviour of the exotic species is unknown.

Parent tree mapping

In each site, stems ≥ 10 cm DBH of the ten species were mapped using an impulse laser rangerfinder with a digital compass. We used two mapping radii: in 1993, all individuals of the native species were mapped in a radius of at least 20 m around each sample point (seed trap or seedling quadrat). Early work showed that a mapped distance of 20 m is adequate for minimizing bias in dispersal parameter estimation for these native species (Ribbens et al. 1994).

In 2004, we used a larger map radius of 50 m for the exotic species, as the dispersal patterns of these species was unknown and Canham and Uriarte (2006) showed that a 50 m map distance effectively eliminates any potential bias in the estimation of dispersal parameters. We evaluated the potential effects of the different mapped areas in the dispersal and dispersion analyses by comparing the output using a 20 m versus 50 m radii – the effects of the different radii were consistently very small and the larger distance provided slightly better fits, so hereafter we present the results of the 50 m distance for the exotic species.

All species in this study are monoecious, except *F. americana* and *A. altissima* which are dioecious and *P. serotina* which has perfect flowers. Field determination of gender was impractical for *F. americana* as seeds were not visible when mapped; however, we noted the presence of seeds on female individuals of *A. altissima* when mapping, as its seed clusters were readily visible. Only female trees were used in the analysis of *A. altissima* seed dispersal and seedling dispersion, but male individuals were included in the dispersion analysis of root sucker sprouts. There is a potential source of bias when comparing the fecundity of female-only individuals of *Ailanthus* against other dioecious species whose fecundity was estimated using both female and male individuals (in effect, reducing the average fecundity for such a species by the percentage of male trees in the population). In this study, the only other dioecious species was *F. americana*.

Seed rain and seedling sampling

Seed rain for seven of the eight native tree species was collected over a three year period (1994–1996) in the GMF sites. We used the six new sites to sample seed rain of the two exotic species and two of the native species (*A. saccharum* and *F. americana*). Seed rain of *A. platanoides* and *A. saccharum* was collected for three years (2003–2005), while seeds of *A. altissima* and *F. americana* were collected for two years (2004–2005). We placed seed traps (0.5 m^2) in each mapped site. Locations of the seed traps were designed to capture a range of distances (0–50 m in the new sites, 0–25 m in GMF) around the target tree species. The two GMF sites had 36 seed traps each; the 6 new sites had 15 seeds traps per site in year 1, and 20 traps per site in year 2 and 3. Seed traps had a circular frame, were constructed of a tough, very fine mesh and were suspended with wire on fibreglass stakes 1 m off the ground to keep small mammals from entering the traps. The traps were sufficiently large (0.75 m deep) to prevent overflow of any leaf litter or seeds, as the dates of their fall overlap. Traps were placed in early September and left out until mid-December, except for sites with *A. altissima*, where traps were left out until early May as seeds of that species can remain attached to parents over winter until leaf out. Seeds were collected from the traps every two weeks. No evidence of rodents (e.g. faeces) was detected in the seed traps, so we assumed that predation from inside seed traps was negligible.

Seedlings of all tree species were enumerated in mid-summer in 1-m^2 quadrats (30 quadrats per site) using three age classes: 1 year old seedlings, 2 year old seedlings, and seedlings 3 years and older. Like seed traps, seedling quadrats were located to capture a range of distances (0–50 m in the new sites, 0–25 m in GMF) around the target tree species. Seedlings were aged from bud-scars. We found seedlings in sufficient numbers for modelling for *A. platanoides*, *A. rubrum* (in the GMF sites), *A. saccharum*, *A. altissima*, *F. americana* and *P. serotina*. For *A. altissima*, seedlings were noted as seed or root sucker origin based on clear morphological differences; this species often produces numerous root sucker 'seedlings' which have higher shade tolerance than seed-origin plants (Miller 1990).

Data analysis

We used inverse modelling to analyze seed dispersal and seedling dispersion around parent trees. Inverse modelling techniques represent a powerful and pragmatic approach for the study of dispersal and recruitment processes (Ribbens et al. 1994, Clark et al. 1998, Bullock and Clarke 2000, LePage et al. 2000, Uriarte et al. 2005). As with previous studies (Ribbens et al. 1994), we assumed that the potential number of seeds or seedlings produced by a tree is a function of stem diameter (DBH)

$$g(DBH) = STR\left(\frac{DBH}{30}\right)^{\alpha} \quad (1)$$

where STR is the potential number of seeds or seedlings produced by a tree with a 30-cm stem diameter at breast height (Ribbens et al. 1994, LePage et al. 2000, Uriarte et al. 2005). In our analyses, we allow STR to vary among sites, on the assumption that site quality may influence per capita seed production. Following the arguments presented by Canham and Uriarte (2006), we tested for variation in the relationship between fecundity and adult tree size by allowing α to vary, rather than fixing it at 2 as most previous studies have done. We also expect size at reproductive maturity to vary by species, and estimate an additional parameter (DBH_{min}) to determine the minimum size at which potential parents begin contributing to seed rain.

Most previous seed dispersal studies have assumed that propagule density declines monotonically with distance from a parent tree, and thus have some form of an exponential function (sometimes referred to as a Weibull function) to estimate the shape of a seed shadow (Ribbens et al. 1994, Clark et al. 1998, 1999, LePage et al. 2000). Greene et al. (2004) compared alternate dispersal functions and argued that a lognormal dispersal kernel is more amenable to a mechanistic interpretation and is more appropriate for both wind and animal-dispersed seeds. They further showed that the lognormal function often fits empirical data as well as or better than exponential functions. Thus, we tested two alternate forms for the shape of the dispersal patterns for each species. We tested the exponential function used by Ribbens et al. (1994):

$$f(d) = \frac{1}{\eta}\exp^{-\beta d^{\gamma}} \quad (2)$$

where d is the distance from a seed trap or seedling quadrat to a parent tree, β and γ are estimated parameters, and η is a normalization constant equivalent to the arcwise integration of the dispersal kernel. Previous studies have generally fixed γ at an arbitrary value ranging from 1 to 3, but more recent studies (Canham and Uriarte 2005, Uriarte et al. 2005) have allowed γ to vary, allowing the data to determine the appropriate shape. We also tested the lognormal function advocated by Greene et al. (2004):

$$f(d) = \frac{1}{\eta} \exp^{-\frac{1}{2}\left[\frac{\ln[d/X_0]}{X_b}\right]^2} \quad (3)$$

where X_0 is the distance at which maximum seed rain or seedling dispersion occurs (mode of the dispersal kernel), and X_b determines the breadth or spread of the dispersal kernel.

While previous studies of seed rain and seedling dispersion have assumed that all input is local (i.e. originating from one of the potential parent trees within the mapped area), other studies have suggested that dispersal should be analyzed in terms of both local input and a distance-independent 'bath' of seed rain from both local and regional sources. We explicitly test for this form of non-local seed rain ('bath') using a simple intercept in our model (Eq. 4). Combining Eq. 1 with Eq. 3, the potential number of seeds (S_{im}) in seed trap i in site m is:

$$S_{im} = \text{bath} + STR_m \sum_{j=1}^{n} \left(\frac{DBH_{jm}}{30}\right)^{\alpha} f\left(d_{ijm}\right) \quad (4)$$
$$\text{for } DBH_{jm} > DBH_{min}$$

where DBH_j is the diameter of j = 1… n trees in site m with diameter greater than the estimated parameter DBH_{min}, within a distance of 20 m in the GMF sites and 50 m in the six new sites, and d_{ijm} is the distance from the seed trap or seedling quadrat i to tree j in site m.

We assumed that the expected number of seeds in a seed trap or seedlings in a quadrat follows a Poisson distribution in which the mean of the distribution is given by Eq. 4. We used simulated annealing (a global optimization algorithm; Goffe et al. 1994) to find the parameter values that maximized the likelihood of observing the recorded seed trap counts. We used asymptotic 2-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 and Mangel 1997).

Results

Seed production

Seed rain was sufficient for inverse modelling in 1994–1996 for seed production and dispersal for all the native species with the following exceptions: in 1994 when *P. strobus* had a seed crop failure; in 1995 when *A. saccharum*, *A. rubrum*, *F. grandifolia*, *P. serotina*, and *P. strobus* had seed crop failures; and in 1996 when *Q. rubra* had a seed crop failure (Appendix 1, 2). In the six new sites, seed rain was sufficient for inverse modelling for all species except in 2004 and 2005 when *A. saccharum* had seed crop failures.

Prior studies using inverse modelling typically have assumed that all individual canopy trees of a given species contribute to seed production in years when a seed crop is produced (but see Clark et al. 2004). Our analysis indicates, however, that this assumption is unwarranted: six of the native species consistently had a minimum reproductive DBH of at least 22–50 cm for individuals contributing to seed production (DBH_{min}; Table 1). In contrast, *A. platanoides*, *A. saccharum*, *A. altissima* and *P. strobus* had much lower minimum size thresholds at least in some years: 11.6 cm, 7.9 cm, 12.3 cm and 9.0 cm, respectively. Those species which showed interannual variation in DBH_{min} typically saw their DBH_{min} increase in years of relatively low seed production (Table 1, Appendix 2), suggesting that larger individuals increasingly dominate seed production during low seed years. Previous studies have also typically assumed that seed production increases as a squared function of DBH (i.e. approximately linearly related to aboveground biomass, which typically scales to DBH with an exponent slightly greater than 2; Jenkins et al. 2004). The maximum likelihood estimates of α for all species ranged from 0 to 3.24 (Table 1). *Acer rubrum*, *A. saccharum*, *A. altissima*, *F. grandifolia* and *Q. rubra* all had at least one year with $\alpha > 2$. For these species, seed production can increase significantly with diameter once an adult reaches its species-specific minimum size (DBH_{min}). For the remaining species, estimates of α were low (0–1.19), meaning that seed production was effectively constant with respect to size once an individual reached its effective minimum reproductive size (DBH_{min}) (Table 1, Appendix 2). Overall, there appears to be a negative relationship between α and seed production (STR), as α was consistently higher in low seed crop years. These results indicate that tree size–fecundity relationships can vary widely among both species and among years within a species. Note the narrow support intervals around the maximum likelihood estimates of α (Table 1): unlike the earlier analyses by Ribbens et al. (1994) using a simpler annealing algorithm, we did not encounter significant parameter tradeoffs between estimates of α and the parameters of the dispersal kernel.

Intraspecific year-to-year and site-to-site variation in STR was notably high (Fig. 1, Appendix 2). All species showed some variation in STR among years; even within our 2–3 year study span, all of the native species showed evidence of masting and seed production by the native species was uniformly low in 1995, except for *T. canadensis*. Conversely, *Acer platanoides* produced reasonable numbers of seeds in all three years sampled, and its seed production was much less variable between sites than most native species (Appendix 2). The fecundity estimates for *A. altissima* were particularly striking, with an overall average STR > 1 million seeds; individuals in one site in 2005 averaged almost 4 million seeds per 30 cm DBH tree. Recall that *A. altissima* STR values were calculated for female trees only, which comprised 13%, 100% and 18% of the individuals in sites 1, 2 and 3, respectively.

Table 1. Seed dispersal models with maximum likelihood parameter estimates and 2-unit asymptotic support intervals (in parentheses) of eight native and two exotic tree species in northwestern Connecticut, USA. Dispersal models were fit to seed rain in each year individually and for all years simultaneously. Exponential (E.P.; Eq. 2) and lognormal (L.N.; Eq. 3) dispersal models were compared; the model with a lower AIC_c is reported. Two measures of model fit are reported: R^2 and slope of the relationship between observed and predicted values. See Eq. 1–4 for definitions of the parameters. Also reported is the mean dispersal distance in meters (MDD), the estimated minimum reproductive size in cm of a parent tree (DBH_{min}), and 'bath' seed rain inputs (seeds m^{-2}) from non-local parent trees (i.e. trees outside the mapped stand). Only years with seed rain sufficient for model estimation are shown.

Species	Slope	R^2	Model	α	β/X_0	γ/X_b	MDD	DBH_{min}	Bath
Acer platanoides									
2003	0.90	0.26	L.N.	0 (0–0.06)	1.42 (1.31–1.56)	0.89 (0.87–0.92)	5.0	27.0	4.5 (2.9–6.2)
2004	1.06	0.52	L.N.	0.04 (0–0.85)	4.56 (3.98–4.94)	0.57 (0.51–0.61)	7.4	22.5	0 (0–0.3)
2005	1.01	0.37	L.N.	0 (0–0.12)	3.50 (3.31–3.73)	0.59 (0.57–0.62)	6.1	11.6	0.4 (0–1.3)
All Years	0.92	0.35	L.N.	0 (0–0.02)	1.15 (1.07–1.22)	0.99 (0.97–1.00)	5.5	27.2	1.1 (0.6–1.6)
Acer rubrum									
1994	1.10	0.31	L.N.	2.48 (2.44–2.51)	4.11 (4.08–4.14)	0.40 (0.39–0.41)	5.2	29.5	61.3 (57.7–64.9)
1996	1.10	0.32	L.N.	3.13 (3.08–3.19)	4.42 (4.34–4.50)	0.67 (0.66–0.68)	8.6	28.4	19.7 (17.7–22.0)
All years	1.10	0.33	L.N.	2.76 (2.73–2.79)	4.25 (4.22–4.29)	0.49 (0.48–0.50)	6.1	29.6	36.8 (34.9-39.0)
Acer saccharum									
1994	0.95	0.56	E.P.	1.89 (1.70–2.28)	1.49 (1.34–2.28)	3.33 (3.29–3.49)	7.0	7.9	1.7 (1.2–2.8)
1996	0.98	0.44	E.P.	0.44 (0.32–0.65)	11.59 (10.45–12.11)	2.60 (2.49–2.64)	6.3	30.3	0.2 (0.1–0.7)
2003	1.02	0.92	L.N.	3.04 (2.95–3.11)	0 (0-0.01)	2.60 (2.54–2.66)	6.2	67.2	2.9 (1.7–3.9)
All years	0.93	0.61	E.P.	1.69 (1.49–1.98)	104.43 (96.04–113.46)	1.79 (1.77–1.82)	7.6	8.8	0.4 (0.3–0.7)
Ailanthus altissima									
2004	1.01	0.84	L.N.	2.11 (1.55–2.56)	0 (0–0)	2.45 (2.43–2.47)	4.9	28.1	169.8 (163.5–176.9)
2005	0.99	0.71	L.N.	0 (0–0.05)	0 (0-0.01)	3.89 (3.87–3.91)	16.1	12.3	0 (0–4.4)
All Years	0.99	0.59	L.N.	0 (0–0.05)	0 (0–0)	3.74 (3.72–3.75)	15.2	13.5	0 (0–4.6)
Fagus grandifolia									
1994	1.08	0.75	L.N.	3.22 (2.11–3.79)	0.0001 (0.0001–0.0002)	3.14 (3.08–3.24)	5.6	21.6	0.1 (0–0.36)
1996	1.05	0.79	L.N.	0.05 (0–0.75)	0.0001 (0.0001–0.0002)	2.73 (2.65–2.79)	4.3	37.3	0.1 (0–0.3)
All Years	1.04	0.67	L.N.	3.24 (2.92–3.49)	0.0001 (0.0001–0.0002)	3.12 (3.08–3.19)	4.9	29.7	0.1 (0–0.2)
Fraxinus americana									
2003	1.03	0.54	L.N.	0 (0–0.05)	5.68 (5.36–6.00)	0.81 (0.78–0.83)	13.4	26.1	0 (0–3.1)
2004	1.10	0.51	E.P.	0 (0–0.06)	0.01 (0.01–0.01)	3.99 (3.96–4.00)	14.7	25.1	0 (0–0.7)
All Years	1.05	0.53	E.P.	0 (0–0.03)	0.01 (0.01–0.02)	4.0 (3.96–4.00)	14.4	26.2	0 (0–1.0)
Pinus strobus									
1996	1.00	0.55	E.P.	0 (0–0.06)	0.31 (0.20–0.52)	3.95 (3.85–4.00)	6.6	9.0	21.1 (18.8–23.6)
Prunus serotina									
1994	1.01	0.83	L.N.	0.16 (0–0.32)	1.39 (1.26–1.56)	0.81 (0.78–0.85)	4.1	38.3	0.8 (0.6–1.4)
1996	1.02	0.95	L.N.	0 (0–0.17)	0.02 (0.02–0.02)	1.29 (1.27–1.30)	2.2	34.1	0.4 (0.2–0.7)
All years	1.03	0.85	L.N.	0 (0–0.14)	0 (0–0)	2.09 (2.06–2.12)	3.1	38.4	0.7 (0.5–1.0)

(Continued)

Table 1. *(continued)*

Species	Slope	R^2	Model	α	β/X_0	γ/X_b	MDD	DBH_{min}	Bath
Quercus rubra									
1994	0.90	0.22	L.N.	0 (0–0.09)	0.0001 (0.0001–0.0002)	2.58 (2.55–2.63)	5.5	46.4	2.3 (1.7–2.9)
1995	0.91	0.15	L.N.	3.07 (2.32–3.48)	2.02 (1.79–2.43)	0.41 (0.35–0.44)	2.6	44.0	0.5 (0.4–1.3)
All years	0.91	0.25	L.N.	0 (0–0.09)	0 (0–0)	3.01 (2.97–3.04)	4.3	46.4	1.4 (1.1–1.8)
Tsuga canadensis									
1994	0.98	0.86	L.N.	0 (0–0.12)	0.41 (0.37–0.45)	1.07 (1.04–1.09)	3.5	48.4	0.5 (0.2–0.8)
1995	1.04	0.76	L.N.	1.19 (1.02–1.35)	3.21 (3.08–3.39)	0.50 (0.47–0.54)	4.7	48.2	0.7 (0.4–1.0)
1996	0.92	0.11	L.N.	0 (0–0.44)	7.63 (6.93–9.09)	0.31 (0.30–0.41)	5.8	50.0	3.5 (2.9–4.3)
All years	0.98	0.76	L.N.	0.52 (0.39–0.61)	0.59 (0.56–0.65)	1.07 (1.05–1.09)	4.3	48.2	2.3 (2.0–2.6)

Spatial variation in seed dispersal

Seed dispersal was a 'local' process in these sites, with most seeds falling directly beneath or near the crown (Table 1, Fig. 2). Mean dispersal distances (MDD) were < 10 m for eight species, and in most cases showed a steep, nearly monotonic decline with increasing distance from a parent tree (Fig. 2). Mean dispersal distances of seeds conformed well to expectations based on seed weight (Appendix 1). *Ailanthus altissima* and *F. americana* had a MDDs > 14 m while the heavy-seeded species all had a MDDs < 5 m. Only *P. strobus* (6.6 m) and *T. canadensis* (4.7 m) were anomalous, with MDDs much shorter than their seed weights would suggest.

The maximum likelihood models produced good to excellent fits (R^2 = 0.22–0.95) for all species, except for one year of *T. canadensis* (R^2 = 0.11) and *Q. rubra* (R^2 = 0.15). The most parsimonious dispersal model (i.e. the unbiased model with the lowest AIC_c) for *A. saccharum*, *F. americana* and *P. strobus* usually was an exponential dispersal function (Eq. 2) while the remaining species were best fit with a lognormal function (Eq. 3) (Table 1, Fig. 2).

Seedling dispersion

The abundance of seedlings was much more irregular than seed rain, perhaps due to the low understory light levels in the sites. This limited our analyses of seedling dispersion to six species (Fig. 3, Table 2). Our analyses revealed markedly different seedling dispersion and recruitment patterns for the six species, and seedling abundances appear to reflect not only parental seed production but also life history strategy (Table 2, Appendix 3, Fig. 4). In particular, both of the shade intolerant species (*A. altissima* and *F. americana*) had the longest dispersion tails for 1 year old seedlings, while the two most shade tolerant species (*A. platanoides* and *A. saccharum*) had the density of ≥ 3 year-old

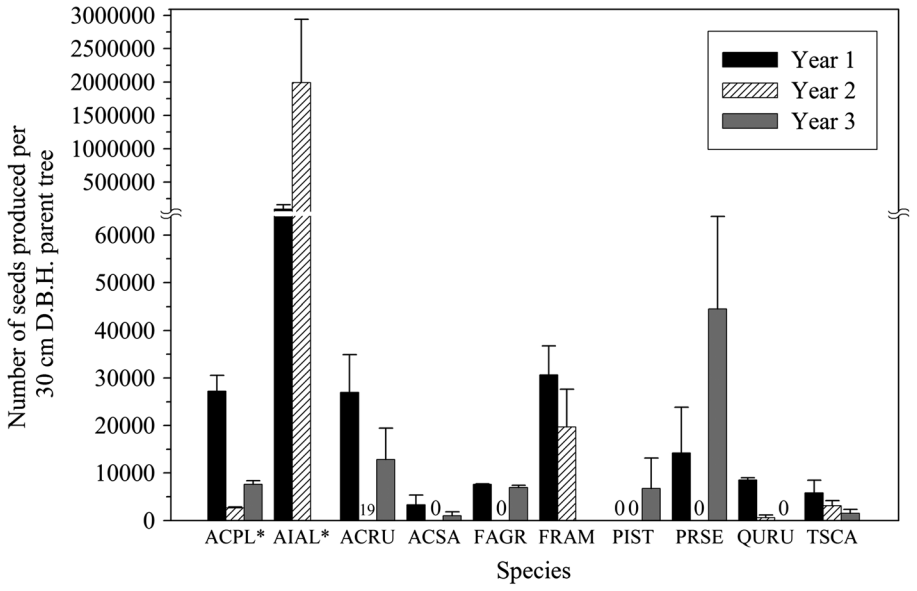

Figure 1. Average seed production (STR) of two exotic and eight native tree species in closed-canopy forests in northwestern Connecticut, USA. STR is the annual seed production for a 30 cm DBH individual of given species, averaged across sites. The exotic species are denoted with an asterisk (*). Species codes are taken from the Latin names, e.g. ACPL = *Acer platanoides* (Norway maple). AIAL and FRAM have only two years of data. Those species with no or very low seed production in a year are labelled with a zero or the amount (19 for ACRU). Note the break on the Y-axis. Bars are 1 SE.

Table 2. Seedling dispersion models with maximum likelihood parameter estimates and two-unit asymptotic support intervals (in parentheses) of four native and two exotic tree species in northwestern Connecticut, USA. Dispersion models were fit to seedlings in each year individually and for all years simultaneously, when the data allowed. Exponential (E.P.; Eq. 2) and lognormal (L.N.; Eq. 3) dispersion models were compared; the model with a lower AIC_c is reported. Two measures of model fit are reported: R^2 and slope of the relationship between observed and predicted values. See Eq. 1–4 for the definitions of the parameters. Also reported is the mean dispersal distance in meters (MDD), the estimated minimum reproductive size in cm of a parent tree (DBH_{min}), and 'bath' seedling inputs (seedlings m^{-2}) from non-local parent trees (i.e. trees outside the mapped stand). Only those species with seedlings in sufficient numbers for parameter estimation were analyzed.

Species	Slope	R^2	Model	α	β/X_0	γ/X_β	MDD	DBH_{min}	Bath
Acer platanoides									
One year-olds 2004	1.03	0.52	L.N.	2.26 (1.76–2.52)	3.48 (3.48–3.13)	0.78 (0.74–0.81)	8.4	19.2	0 (0–0.6)
One year-olds 2005	1.09	0.39	L.N.	4.54 (3.86–4.98)	9.96 (7.71–12.30)	0.43 (0.31–0.59)	13.1	10.5	0 (0–0.3)
One year-olds 2006	0.99	0.52	L.N.	2.41 (1.22–2.95)	9.19 (8.09–11.18)	0.38 (0.32–0.51)	11.2	41.9	0.1 (0–0.1)
All one year-olds	1.06	0.58	L.N.	1.96 (1.61–2.29)	3.99 (3.61–4.39)	0.74 (0.71–0.77)	8.9	20.6	0 (0–0.1)
Two year-old seedlings 2005	1.09	0.43	L.N.	4.87 (4.71–4.93)	5.64 (4.97–6.65)	0.67 (0.62–0.73)	10.8	18.7	1.3 (0.8–1.9)
≥ three year-old seedlings 2006	1.00	0.71	L.N.	1.97 (1.79–2.13)	8.62 (7.78–9.32)	0.66 (0.62–0.69)	16.0	43.7	2.3 (1.9–2.8)
All seedlings 2006	1.04	0.72	L.N.	4.89 (4.86–4.99)	8.15 (7.56–8.64)	0.58 (0.55–0.61)	13.3	20.4	8.9 (7.6–10.2)
Acer rubrum									
One year-olds 1995	1.07	0.42	L.N.	0 (0–0.09)	5.61 (5.27–5.86)	0.36 (0.32–0.40)	6.8	35.9	4.7 (3.9–5.3)
Two year-old seedlings 1996	0.93	0.26	L.N.	0.25 (0.21–0.29)	7.60 (7.12–8.05)	0.47 (0.43–0.51)	10.6	35.8	2.5 (1.5–3.4)
Acer saccharum									
One year-olds 2004	0.97	0.37	L.N.	0 (0–0.11)	2.44 (1.76–3.33)	1.02 (0.94–1.10)	10.8	53.9	0 (0–0.1)
Two year-old seedlings 2005	1.06	0.44	L.N.	0.36 (0.16–0.74)	8.74 (7.60–11.14)	0.51 (0.46–0.61)	12.8	53.7	0 (0–0.1)
≥ three year-old seedlings 2006	1.03	0.28	L.N.	0 (0–0.14)	15.25 (14.34–16.24)	0.32 (0.30–0.37)	15.0	34.4	0.2 (0.1–0.5)
All seedlings 2006	1.05	0.28	L.N.	0 (0–0.12)	15.32 (14.58–16.19)	0.36 (0.31–0.38)	18.6	31.8	0 (0–0.4)
Ailanthus altissima									
One year-olds 2005	0.92	0.12	L.N.	1.07 (0.04–1.49)	19.16 (16.87–24.94)	0.81 (0.75–0.90)	26.6	35.4	0 (0–0.4)
Root suckers 2005	1.06	0.35	L.N.	0 (0–0.39)	0.01 (0.01-0.03)	2.05 (1.97–2.15)	7.2	40.1	0.8 (0.6–1.1)
Fraxinus americana									
One year-olds 2004	1.08	0.29	E.P.	0.01 (0–0.45)	1107.96 (307.4–1570.4)	1.66 (1.23–1.85)	8.1	15.9	0.3 (0.2–0.6)
One year-olds 2005	1.01	0.37	L.N.	0 (0–0.14)	9.34 (8.98–9.83)	0.55 (0.43–0.59)	14.4	34.9	2.9 (2.5–3.4)
One year-olds 2006	1.00	0.31	L.N.	0.01 (0–0.25)	9.81 (8.91–11.19)	0.65 (0.61–0.70)	17.0	36.8	0 (0–0.4)
All one year-olds	1.00	0.40	L.N.	0 (0–0.11)	7.07 (6.67–7.67)	0.67 (0.65–0.70)	13.3	32.5	0.3 (0.2–0.5)
≥ three year-old seedlings 2006	1.09	0.33	L.N.	0.03 (0–0.24)	11.20 (10.52–12.11)	0.35 (0.32–0.37)	13.5	68.3	1.3 (0.9–1.7)
All seedlings 2006	0.96	0.39	L.N.	0 (0–0.05)	2.21 (2.11–2.31)	0.34 (0.32–0.38)	10.3	19.7	15.2 (13.9–16.4)
Prunus serotina									
One year-olds 2004	0.90	0.42	L.N.	4.81 (4.62–4.95)	3.36 (2.87–3.50)	0.35 (0.31–0.39)	4.0	32.5	2.1 (1.8–2.8)
One year-olds 2005	1.10	0.19	L.N.	4.77 (3.73–4.98)	0.97 (0.34–2.04)	1.52 (1.34–1.69)	7.3	24.8	0 (0–0.2)
Two year-old seedlings 2005	1.00	0.10	L.N.	1.53 (0–2.39)	7.22 (2.67–25.37)	0.37 (0.31–0.89)	8.8	38.8	0.9 (0.6–1.2)
≥ three year-old seedlings 2006	0.99	0.45	L.N.	0.98 (0.57–1.31)	4.19 (3.82–4.63)	0.34 (0.31–0.40)	4.9	43.2	2.0 (1.6–2.5)
All seedlings 2006	0.98	0.23	L.N.	3.73 (3.36–3.96)	2.21 (1.59–2.84)	0.97 (0.89–1.06)	8.5	31.2	0 (0–0.7)

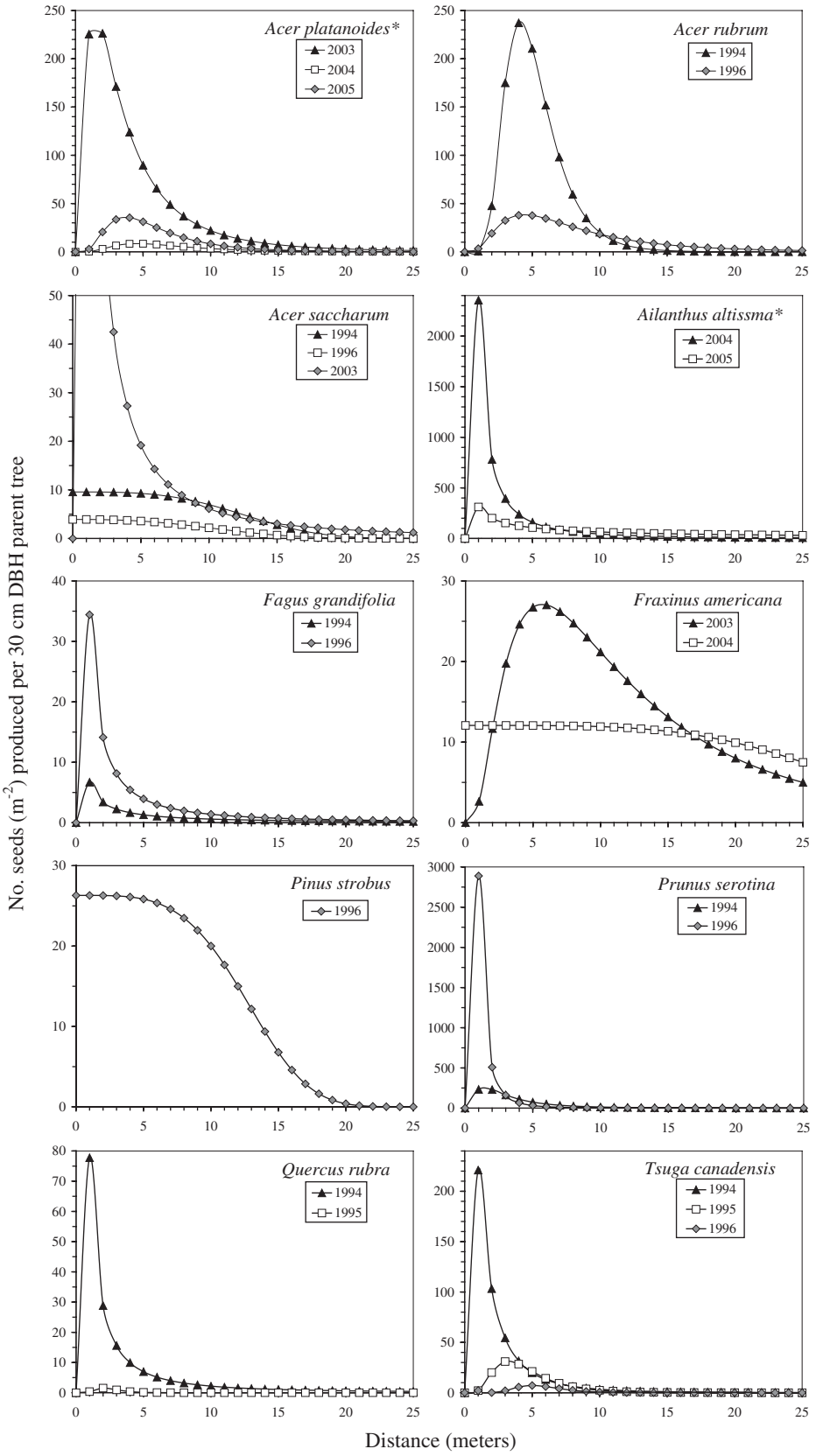

Figure 2. Predicted seed rain (no. m^{-2}) as a function of distance from a single 30 cm DBH parent tree for two exotic and eight native tree species tree species in closed-canopy forests in northwestern Connecticut, USA. The exotic species are denoted with an asterisk (*). Only years with sufficient seed rain to fit dispersal models are shown. Note the different scales of the Y-axes for all species. The functions do not include the predicted bath input (if any).

seedlings exceeding seed rain inputs at distances ≥ 13 m from parent trees (Fig. 4). Interestingly, the density of *A. altissima* 1 year-old seedlings in 2005 was higher than the preceding year's seed rain input at distances of ≥ 20 m. However, this species had no seed-origin seedlings survive into the 2nd year, probably due to the low light levels.

Mean seedling dispersion distances were approximately double the MDDs of seeds for all species except for *F. americana* whose MDD remained effectively the same between stages. All six species, both native and exotic, displayed evidence of negative distance- and/or density-dependent processes as evidenced by the increasing displacement of MDD and the mode of dispersion for a seedling cohort from parent trees with each successive year (Fig. 4, Table 2). For example, the mode of dispersion for a cohort of *A. platanoides* seedlings increased with each year, from 2 m in 2003 to 9 m by 2006. Perhaps in part because of this successive displacement, all but one year of the seedling analyses were best fit with a lognormal dispersal kernel.

Discussion

Our study linked fecundity, seed dispersal and seedling dispersion and establishment for native and exotic trees in the northeastern USA, and demonstrates that the processes which generate these patterns are manifold: parent size, interannual variation in seed production, distance from local seed sources, non-local 'bath' seed inputs, and negative density-dependent effects of parent trees on conspecific regeneration were all important influences on seed dispersal and seedling recruitment in both native and exotic tree species.

Seed and seedling production

Though our study spans two-to-three years of seed rain, this period is too short to categorically characterise the observed temporal variation in seed production in terms of classic masting cycles. Nevertheless, variation in seed production by the native trees was dramatic, with complete seed crop failures in at least one year for six of the eight native species. While the two exotic species had no seed crop failures, both showed sizeable interannual variation in fecundity, with peak per capita seed production over 10 times higher than the year of lowest production. Despite such interannual variation, it is clear that *Ailanthus altissima* is exceptionally fecund even in competitive, closed-canopy forest stands. The seed production of *Acer platanoides*, however, is unremarkable (but, see below), despite its reputation for fecundity.

Many studies have shown that seed production, subsequent seedling germination and seedling establishment are influenced by seed mass (Westoby et al. 1992, Greene and Johnson 1994, 1998, Muller-Landau et al. 2008). Greene and Johnson (1994, 1998) developed an empirical model of average seed production based on seed mass. This approach works reasonably well for most of the native species (Papaik and Canham 2006), but based on our calculations with the model (see Greene and Johnson 1994, 1998 for model details), it appears to seriously underestimate the seed production of the exotic species: mean seed production of *A. platanoides* (with a high seed mass) and *A. altissima* (with a medium seed mass) were almost 20 times and 600 times higher respectively in our study compared to fecundity–seed mass estimates based on the Greene and Johnson model. These dramatic differences indicate that exotic invasive tree

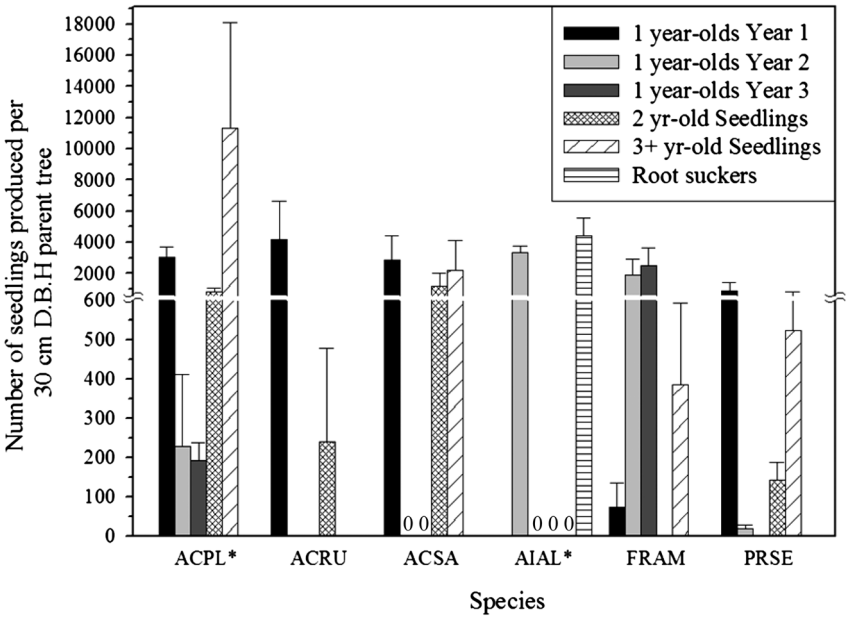

Figure 3. Average seedling production (STR) of two exotic and four native tree species in closed-canopy forests in northwestern Connecticut, USA. STR is the annual seedling production for a 30 cm DBH individual of given species, averaged across sites. The exotic species are denoted with an asterisk (*). Species codes are taken from the Latin names, e.g. ACPL = *Acer platanoides* (Norway maple). Those species with no seedling production in a year are labelled with a zero; empty columns indicate no data. Note the break on the Y-axis. Bars are 1 SE.

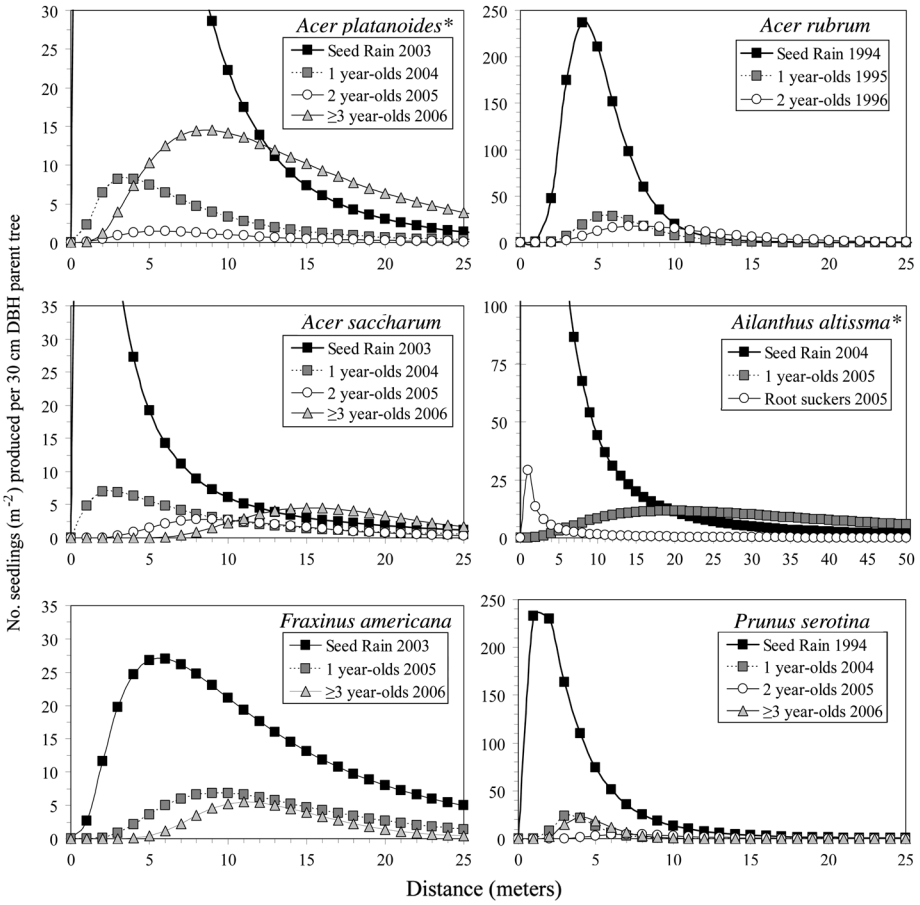

Figure 4. Predicted number of seedlings (no. m^{-2}) in age class cohorts as a function of distance from a single 30 cm DBH parent tree for two exotic and four native tree species in closed-canopy forests in northwestern Connecticut, USA. The exotic species are denoted with an asterisk (*). Note the different scales of the Y-axes for all species, the different X-axis for *A. altissima*, and that the ≥ 3 year-old seedling group is not a single cohort. The functions do not include the predicted bath input (if any). Seeds of *F. americana* do not germinate until two years after dispersal, so there is an additional year between its seeds and 1 year old seedlings. For *P. serotina*, there was inadequate seed rain and seedling data to analyze patterns from the same site, so different sites (and thus years) are shown for this species.

species may have fundamentally different life history strategies, allocating resources to reproduction in a way which departs from fecundity–seed mass relationships in native species. Mason et al. (2008) found that across the globe, woody invasive species produced on average > 26 times more seeds per individual per year than native species for a given seed mass, suggesting our exotic study species fit into a global pattern of invasiveness.

There was a great deal of variation in the effective minimum size (DBH_{min}) of reproductive trees, both among species and among years within species. The most notable patterns in DBH_{min} were across seed and seedling cohorts. In four of six species, DBH_{min} increased from seed production to seedling production (Table 1, 2). Within a species, DBH_{min} also tended to increase (four species) with the increasing age of the seedling cohort (1 year old to ≥ 3 year-old seedlings), suggesting that seedlings produced by larger trees had higher survivorship. There are a number of possible mechanisms that could result in such a pattern, including size-dependent effects of adult trees on microsite and understory favourability (e.g. soil resource availability; Gómez-Aparicio and Canham 2008). Moreover, the two species that did not exhibit an increase in DBH_{min} between seed and seedling production (*A. platanoides* and *P. serotina*) were the two species that did show large increases in *alpha* (α) between stages, again suggesting that larger trees predominate as the sources of successful seedling recruitment.

Dispersal patterns

The appropriate shape for the dispersal kernels of trees has received considerable attention (reviewed by Greene et al. 2004). Greene et al. (2004) compared a number of different functional forms, and advocated for a lognormal dispersal kernel on both empirical and mechanistic grounds. We tested both exponential and lognormal models, and found that overall the lognormal kernels provided the best fits for both seed dispersal and seedling dispersion patterns. The better fit of the lognormal function was probably due in part to its 'fat tail' (Clark et al. 1999) relative to the exponential model. There was no clear relationship between the shape of the estimated dispersal kernel and the life-history traits of individual species. For example, both the pioneer *A. altissima*

and the late successional species *F. grandifolia*, whose seed weights differ by an order of magnitude, were best fit by the lognormal.

Ribbens et al. (1994) argued that while temporal variation in seed production (i.e. masting) should result in significant variation in STR not captured by a short-term study, these variations should only affect the intercept, not the shape, of a dispersal kernel. Furthermore, they argued that temporal variation in mean dispersal distance (MDD) is unlikely, as MDD reflects the physics of seedfall and secondary dispersal, though seed predation could interact with temporal variation. In general, our results suggest that this viewpoint is reasonable. Two species – *A. saccharum* and *F. americana* – did show interannual variation in the 'best' dispersal kernel, shifting between the exponential and the lognormal, but this was the exception. MDDs were very consistent from year to year for most species, except in the exotic *A. altissima*, where MDD more than tripled in the year with the highest per capita seed production.

Overall, mean dispersal distances were short, although there were notable differences between species (Table 1, 2). The short MDDs reduced the likelihood of bias in parameter estimation: Canham and Uriarte (2006) demonstrated that as long as the minimum mapped distance is greater than MDD, any bias in parameter estimation is small. An examination of Table 1 shows that the MDDs of the native species were all less than the 20 m map radius used in those stands. Canham and Uriarte (2006) also showed that any bias resulting from smaller mapped distances would slightly elevate bath estimates. The bath term was unimportant (< 5) for all species except *A. rubrum*, *A. altissima* and *P. strobus*. That is, patterns of seed dispersal for most species were attributable to parent trees within the mapped neighbourhoods alone. While the different mapped areas in this study could influence the bath term (i.e. smaller mapped areas can increase the bath term, as more distant parent trees are not directly included in the analysis), the generally low bath term and its narrow support intervals indicate this was not an issue in these analyses (Table 1).

Our seedling dispersion distances match reasonably well with Ribbens et al. (1994), except for *A. saccharum* whose seedling dispersion was 5.7 m greater in our results. Seedling densities were consistently lower than seed inputs, except in three notable instances. The densities of ≥ 3 year-old *A. platanoides* seedlings were higher than annual seed inputs at distances ≥ 13 m, indicating the accumulation of a seedling bank, but only at distances displaced away from parents (Fig. 4). *Acer platanoides* is reported to form a 'seedling bank' in invaded stands (Webb and Kaunzinger 1993, Martin 1999, Martin and Marks 2006). *Acer saccharum* showed the same pattern between 13–18 m from parents. Finally, the density of 1 year old seedlings of *A. altissima* exceeded seed inputs at 20 m and up, suggesting significant amount of secondary dispersal, a large non-local 'bath' input, and/or a seed bank mechanism. Root suckers of *A. altissima* can survive in the shade, but this species is not thought to regenerate from seed in a shaded understory (Miller 1990, Kowarik and Säumel 2007). However, it can establish short-term seed banks, with seeds remaining viable on (Hildebrand 2006) and in the soil (Kota et al. 2007) for at least 1 year. In our sites, older wingless *A. altissima* seeds – which were super abundant beneath recent leaf litter – appeared to germinate primarily where the forest floor litter layer was even slightly disturbed (Martin and Canham unpubl.). This abundant seed bank may reflect in part the very low seed predation of *A. altissima* seeds in these forests (Martin unpubl.).

Negative density-dependent recruitment

The evidence for negative density-dependent recruitment processes in this study, although observational, is compelling. With each successive step in the dispersal and recruitment process, from seed to established seedling, surviving individuals were displaced further from conspecific parent trees. Interestingly, these patterns were evident for the exotic species as well as the natives. Evidence for the importance of negative density-dependent mortality at both seed and seedling stages continues to accumulate (Harms et al. 2000, Packer and Clay 2000, 2003, Hille Ris Lambers et al. 2002, Hille Ris Lambers and Clark 2003, Reinhart et al. 2003), and hence the shape and abundance of seedling recruitment patterns can look quite different from the original seed dispersal shadow.

Our results are consistent with a study where first-year *A. platanoides* seedling survivorship was positively associated with increasing distance from *A. platanoides* trees but not soil nutrients or light levels (Gómez-Aparicio et al. 2008). Such spatial patterns correspond well with evidence that *A. platanoides* seedlings experience 'enemy' effects in their introduced range: Reinhart and Callaway (2004) reported that the biomass of 1-year-old *A. platanoides* seedlings was greater when the seedlings were grown in sterilized soils versus soils collected under conspecific trees, suggesting the accumulation of inhibitory soil biota under adults, and Morrison and Mauck (2007) found no general decrease of foliar insect herbivory and disease symptoms for *A. platanoides* in forests in New Jersey, USA in comparison with the native *Acer saccharum*. Overall, the patterns in our study strongly suggest the existence of negative distance and/or density-dependent processes associated with conspecific adults due to host-specialized herbivores, parasites or pathogens (Janzen-Connell effects; Janzen 1970, Connell 1971), and adds to the evidence that Janzen-Connell effects are more important in temperate forests than once thought (Hille Ris Lambers et al. 2002).

Invasion implications

Given *A. altissima's* extraordinary seed production and comparatively long range dispersal, this exotic tree possesses the dispersal traits of a problematic invasive. However, its failure to recruit established seedlings (≥ 2 years-old) in our sites suggests that it will be dependent on disturbance to colonize new areas of closed-canopy forest, though it may not require large openings. Knapp and Canham (2000) found that this species can reach the canopy in a single period of release in gaps by virtue of its unrivalled height growth. Moreover, this species' seed bank potential and its production of shade tolerant juveniles from root suckering suggests that it can invade forests by several means. Overall, we expect that its rate of invasion into closed-canopy forests will likely be much more

limited by the rate of gap formation and other disturbances than by dispersal limitation.

Acer platanoides displays a very different dispersal and recruitment pattern than *A. altissima*, one contrary to common generalizations of the life-history traits of invasives (Martin et al. 2009). Foremost, it is shade tolerant (Martin and Marks 2006). It has mean seed dispersal distances that are comparable to the dominant native tree species, suggesting that its spread in closed-canopied forests will be partially dispersal-limited. Its seed production is also unexceptional vis-à-vis the natives collectively, although its mean STR is 3.6–8.6 times higher than any of the three native shade tolerant species, and as noted, its fecundity is much higher than a seed-mass model might predict. Indeed, *Acer platanoides'* high per capita seed production for a shade tolerant species combined with its relatively low DBH_{min} and its rapid growth rates (Kloeppel and Abrams 1995) creates a species with elements of both mid- and late-successional life history strategies. This combination enables it to aggressively invade forest understories, at least on small scales – in this study, it produced densities of established seedlings ($\geq$ 3 years old) that were more than five times greater than the seedlings densities of the native shade tolerant congener *A. saccharum*. At one site, we estimated that a single 30-cm DBH *A. platanoides* produces over 26350 $>$ 3 years old seedlings (Appendix 3). However, this exotic must reach the canopy before it can challenge native trees for dominance, and the stages from seedling establishment to canopy recruitment typically unfold over many decades and are often dependent on additional factors like herbivory and soil fertility (Martin and Marks 2006, Martin et al. 2009).

These two exotic tree species have important, yet divergent life-history advantages over natives. Clearly, there is more than one way to be a successful invader of closed-canopy forests, and neither species appears to require unusual, large or anthropogenic disturbances. However, our results suggest that recruitment limitation of *A. altissima* and dispersal limitation of *A. platanoides* will keep their rate of invasion slow, and that Janzen-Connell effects may promote co-existence with natives.

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Appendix 1. Number of seed traps, number of seedling quadrats, minimum tree map radius (m) around a sample point, number of adult stems in the mapped area (≥ 2 cm DBH; ≥ 10 cm DBH *A. platanoides* and *A. altissima*), maximum tree diameter (cm), mean number of seeds sampled by year (m^2), mean number of one year-old seedlings sampled by year (m^2), cleaned seed weight (g), and successional status. Years 1, 2 and 3 are 1994–1996 for sites WGM and WMP, and 2003–2005 for sites GR, NL, SC, AM, DF and NM. As the number, distances and sizes of parent trees sampled varied between species, seed and seedling values in this table are best used for interannual and life-stage comparisons within a species. Seed weights are from the USDA Woody Plant Seed Manual (2002). Values for adult *A. altissima* are female individuals only. No data is shown with a dash (–).

							Seeds m^{-2}			One year-olds m^{-2}				
Species site	No. traps	No. quadrats	Map radius	No. adult stems in mapped area	Max. diameter	Median diameter	year 1	year 2	year 3	year 1	year 2	year 3	Seed weight	Status
Acer platanoides													0.158	Exotic
GR	15-20	30	50	89	81.2	18.1	51	5	36	6	1	1		
NL	15-20	30	50	113	71.5	32.1	60	9	34	21	<1	2		
SC	15-20	30	50	119	47.7	18.6	76	10	49	10	2	1		
Acer rubrum													0.019	Early
WGM	36	36	20	129	69.3	31.0	468	3	189	–	33	–		
WMP	36	36	20	345	79.4	25.4	314	1	103	–	19	–		
Acer saccharum													0.065	Late
WGM	36	36	20	733	81.0	11.2	64	0	22	–	9	–		
WMP	36	36	20	113	63.6	23.7	6	0	1	–	<1	–		
GR	15-20	30	25	314	71.7	16.1	3	0	0	0	0	0		
NL	15-20	30	25	420	113.4	17.6	16	0	0	2	0	0		
SC	15-20	30	25	891	81.6	17.8	99	0	0	8	0	0		
Ailanthus altissima													0.026	Exotic
AM	20	30	50	22	48.2	28.6	–	180	529	–	4	1		
DF	20	30	50	20	37.9	27.3	–	419	328	–	6	14		
NM	20	30	50	28	43.2	23.2	–	–	115	–	–	0		
Fagus grandifolia													0.284	Late
WGM	36	–	20	189	51.4	13.9	3	<1	3	–	0	–		
WMP	36	–	20	352	54.7	4.5	1	0	1	–	0	–		
Fraxinus americana													0.012	Early
GR	15-20	30	25	137	71.5	30.7	146	55	–	2	38	15		
NL	15-20	30	25	62	99.7	28.7	87	83		1	5	4		
SC	15-20	30	25	114	66.6	19.6	69	70	–	2	17	8		
Pinus strobus													0.017	Mid
WGM	36	–	20	0	–	–	0	0	1	–	0	–		
WMP	36	–	20	47	72.4	28.0	0	0	43	–	0	–		
Prunus serotina													0.107	Mid
WGM	36	–	20	27	59.7	40.6	14	0	15	–	<1			
WMP	36	–	20	179	67.6	34.0	9	0	10	–	1			
GR	15-20	30	25	114	75.5	35.9	<1	2	1	3	<1	<1		
NL	15-20	30	25	57	69.0	29.2	0	0	0	3	1	1		
SC	15-20	30	25	53	62.8	28.3	0	<1	<1	6	1	<1		
Quercus rubra													3.629	Early
WGM	36	–	20	77	82.8	46.8	8	<1	<1	–	0	–		
WMP	36	–	20	101	71.5	46.3	12	3	1	–	0	–		
Tsuga canadensis													0.002	Late
WGM	36	–	20	287	62.9	24.4	15	10	3	–	<1	–		
WMP	36	–	20	203	82.3	29.9	16	12	7		7			

Appendix 2. Seed production as standardized total recruits (STR) and two-unit asymptotic support intervals (in parentheses) for eight native and two exotic tree species in northwestern Connecticut, USA. STR is the annual seed production for a 30 cm DBH individual of a given species. STR was estimated in each site and in each year, except in year-site combinations with insufficient seed rain to allow model estimation (denoted with an n/a). Combinations with no data are denoted with a dash (–).

	Standardized total recruits 30 cm DBH								
Species	Year 1 site 1	Year 1 site 2	Year 1 site 3	Year 2 site 1	Year 2 site 2	Year 2 site 3	Year 3 site 1	Year 3 site 2	Year 3 site 3
Acer platanoides									
2003	23355 (20966–26203)	24372 (21981–26857)	33883 (30471–36482)	–	–	–	–	–	–
2004	–	–	–	2203 (1657–2890)	2686 (2166–3313)	3032 (2361–3546)	–	–	–
2005	–	–	–	–	–	–	6188 (5514–6824)	8452 (7431–9289)	8295 (7543–9051)
All years	28614 (24669–30783)	25090 (22628–27408)	36993 (34773–41693)	2567 (1701–3249)	2910 (2376–3800)	4179 (3535–5610)	18411 (16626–20647)	12286 (10844–13585)	25181 (23305–28203)
Acer rubrum									
1994	34895 (34007–35726)	19107 (18479–19658)	–	–	–	–	–	–	–
1995	–	–	–	n/a	n/a	–	–	–	–
1996	–	–	–	–	–	–	19457 (18750–20171)	6234 (5862–6593)	–
All years	36618 (35862–37623)	19141 (18550–19675)	–	n/a	n/a	–	14648 (14130–15261)	4511 (4226–4826)	–
Acer saccharum									
1994	5365 (5150–5885)	1245 (1010–1583)	–	–	–	–	–	–	–
1995	–	–	–	n/a	n/a	–	–	–	–
1996	–	–	–	–	–	–	1837 (1766–2015)	205 (167–261)	–
2003	0 (0–224)	2909 (2241–3508)	26134 (23932–27884)	n/a	n/a	n/a	–	–	–
All years	6920 (6567–7403)	1964 (1365–2203)	–	n/a	n/a	–	2375 (2147–2635)	190 (121–454)	–
Ailanthus altissima									
2004	33029 (28765–37346)	159938 (152463–167847)	–	–	–	–	–	–	–
2005	–	–	–	3793020 (3673285–3883389)	1613251 (1559837–1672729)	563964 (538192–605413)	–	–	–
All years	1065012 (1016602–1117202)	1710081 (1655698–1761341)	–	3144371 (3071549–3247677)	1335600 (1292299–1385939)	478625 (452774–507991)	–	–	–
Fagus grandifolia									
1994	7583 (5313–9399)	7714 (4522–10510)	–	–	–	–	–	–	–
1995	–	–	–	n/a	n/a	–	–	–	–

(Continued)

Appendix 2. *(continued)*

Species	Standardized total recruits 30 cm DBH								
	Year 1 site 1	Year 1 site 2	Year 1 site 3	Year 2 site 1	Year 2 site 2	Year 2 site 3	Year 3 site 1	Year 3 site 2	Year 3 site 3
1996	–	–	–	–	–	–	6489 (4748–8931)	7398 (4556–11885)	–
All years	5189 (3360–6203)	4292 (2826–6476)	–	n/a	n/a	–	4125 (2899–5430)	3740 (1928–5201)	–
Fraxinus americana									
2003	25343 (23891–26960)	26011 (23884–27953)	40623 (37079–44229)	–	–	–	–	–	–
2004	–	–	–	8040 (7360–8729)	20684 (19376–22281)	30384 (28191–32808)	–	–	–
All years	23013 (21380–24178)	23238 (20852–24585)	40825 (37415–44631)	8208 (7524–8923)	21626 (19896–22916)	33379 (31165–36304)	–	–	–
Pinus strobus									
1994	n/a	n/a	–	–	–	–	–	–	–
1995	–	–	–	n/a	n/a	–	–	–	–
1996	–	–	–	–	–	–	n/a	13175 (11787–14744)	–
Prunus serotina									
1994	23871 (20827–27376)	4575 (3339–4980)	–	–	–	–	–	–	–
1995	–	–	–	n/a	n/a	–	–	–	–
1996	–	–	–	–	–	–	63938 (56703–72661)	25108 (21045–28908)	–
All years	48883 (41444–54847)	14509 (12153–16950)	–	n/a	n/a	–	56433 (50912–65583)	15209 (13162–18220)	–
Quercus rubra									
1994	9023 (7384–10544)	8072 (6507–9491)	–	–	–	–	–	–	–
1995	–	–	–	1 (0–52)	1186 (783–1568)	–	–	–	–
1996	–	–	–	–	–	–	n/a	n/a	–
All years	7218 (5953–10233)	6458 (5489–7735)	–	0 (0–475)	927 (364–1090)	–	n/a	n/a	–
Tsuga canadensis									
1994	8507 (7419–9542)	3114 (2755–3499)	–	–	–	–	–	–	–
1995	–	–	–	4204 (3587–4969)	1979 (1708–2256)	–	–	–	–
1996	–	–	–	–	–	–	705 (0–2205)	2356 (1780–3336)	–
All years	7756 (6580–8575)	3033 (2665–3405)	–	4578 (3561–5156)	2205 (1899–2538)	–	0 (0–401)	216 (80–383)	–

Appendix 3. Seedling production as standardized total recruits (STR) and two-unit asymptotic support intervals (in parentheses) for five native and two exotic tree species in northwestern Connecticut, USA. STR is the annual seedling production for a 30 cm DBH individual of a given species. STR was estimated in each site and in each year where seedlings abundance was sufficient to allow model estimation. Combinations with no data are denoted with a dash (–).

	Standardized total recruits 30 cm DBH								
Species	Year 1 site 1	Year 1 site 2	Year 1 site 3	Year 2 site 1	Year 2 site 2	Year 2 site 3	Year 3 site 1	Year 3 site 2	Year 3 site 3
Acer platanoides									
One year-olds 2004	1910 (1549–2357)	4096 (3262–4143)	3181 (2532–3595)	–	–	–	–	–	–
One year-olds 2005	–	–	–	27 (10–132)	63 (47–150)	594 (393–852)	–	–	–
One year-olds 2006	–	–	–	–	–	–	276 (61–345)	128 (87–223)	177 (5–454)
All one year-olds	1093 (969–1322)	2100 (1782–2236)	1796 (1529–1963)	21 (7–100)	117 (64–172)	342 (196–442)	232 (137–345)	169 (99–228)	121 (46–188)
Two year-old seedlings 2005	–	–	–	473 (341–679)	819 (702–953)	1193 (867–1586)	–	–	–
≥three year-old seedlings 2006	–	–	–	–	–	–	7617 (5330–10870)	26350 (24641–29281)	62 (0–1708)
All seedlings 2006	–	–	–	–	–	–	1999 (1621–2432)	4628 (4282–4876)	3237 (2610–4059)
Acer rubrum									
One year-olds 1995	6663 (6022–7373)	1708 (1343–2064)	–	–	–	–	–	–	–
Two year-old seedlings 1996	–	–	–	2 (0–45)	478 (320–615)	–	–	–	–
Acer saccharum									
One year-olds 2004	0 (0–66)	5522 (3745–7397)	2970 (2538–3674)	–	–	–	–	–	–
Two year-old seedlings 2005	–	–	–	0 (0–44)	2827 (2120–4991)	735 (586–1027)	–	–	–
≥ three year-old seedlings 2006	–	–	–	–	–	–	519 (331–826)	5988 (5249–6766)	180 (112–273)
All seedlings 2006	–	–	–	–	–	–	569 (389–800)	5446 (4710–5930)	1198 (1054–1393)
Ailanthus altissima									
1 year-olds 2005	2878 (1902–4293)	3784 (2883–5139)	–	–	–	–	–	–	–
Root suckers 2005	–	–	–	3269 (2453–3925)	5586 (4570–6743)	–	–	–	–
Fraxinus americana									
One year-olds 2004	24 (17–79)	0 (0–18)	198 (98–257)	–	–	–	–	–	–
One year-olds 2005	–	–	–	2501 (2279–2763)	0 (0–75)	3235 (2627–3912)			

(Continued)

Appendix 3. *(Continued)*

Species	Standardized total recruits 30 cm DBH								
	Year 1 site 1	Year 1 site 2	Year 1 site 3	Year 2 site 1	Year 2 site 2	Year 2 site 3	Year 3 site 1	Year 3 site 2	Year 3 site 3
One year-olds 2006	–	–	–	–	–	–	1848 (1601–2095)	1010 (758–1268)	4699 (3996–5796)
All one year-olds	96 (50–175)	0 (0–111)	540 (362–948)	3240 (3023–3601)	920 (657–1133)	6266 (5439–7089)	1285 (1080–1438)	635 (472–895)	2894 (2245–3395)
≥ three year-old seedlings 2006	–	–	–	–	–	–	117 (57–155)	790 (676–1054)	252 (113–326)
All seedlings 2006	–	–	–	–	–	–	2275 (2009–2499)	1225 (676–1054)	3195 (1581–2820)
Prunus serotina									
One year-olds 2004	182 (132–255)	462 (348–636)	1995 (1639–2469)	–	–	–	–	–	–
One year-olds 2005	–	–	–	1 (0–9)	19 (5–27)	35 (18–70)	–	–	–
Two year-old seedlings 2005	–	–	–	48 (32–83)	203 (95–245)	173 (91–261)	–	–	–
≥ three year-old seedlings 2006	–	–	–	–	–	–	683 (501–851)	887 (549–1334)	0 (0–1313)
All seedlings 2006	–	–	–	–	–	–	168 (150–223)	246 (201–303)	295 (186–355)