

STAGES AND SPATIAL SCALES OF RECRUITMENT LIMITATION IN SOUTHERN APPALACHIAN FORESTS

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Abstract. Recruitment limitation of tree population dynamics is poorly understood, because fecundity and dispersal are difficult to characterize in closed stands. We present an approach that estimates seed production and dispersal under closed canopies and four limitations on recruitment: tree density and location, fecundity, seed dispersal, and establishment. Consistent estimates are obtained for 14 canopy species using 5 yr of census data from 100 seed traps and several thousand mapped trees and seedlings from five southern Appalachian forest stands that span gradients in elevation and moisture. Fecundity (seed production per square centimeter of basal area) ranged over four orders of magnitude, from 10^0 cm² basal area/yr (*Carya*, *Cornus*, *Nyssa*, *Quercus*) to $>10^3$ cm²/yr (*Betula*). Mean dispersal distance ranged from <5 m (*Cornus*, *Nyssa*) to >20 m (*Acer*, *Betula*, *Liriodendron*, *Tsuga*) and was positively correlated with fecundity. Species also differ in the degree of seed clumping at fine (1 m²) spatial scales. Dispersal patterns can be classed in two groups based on dispersal vector: wind-dispersed taxa with high fecundities, long-distance dispersal, and low clumping vs. animal-dispersal taxa with low fecundities, short-distance dispersal, and a high degree of clumping. “Colonization” limitations caused by sizes and locations of parent trees, fecundity, and dispersal were quantified as the fraction of sites receiving seed relative to that expected under null models that assume dispersal is nonlocal (i.e., long-distance) and not clumped (i.e., Poisson). Difference among species in colonization levels ranged from those capable of saturating the forest floor with seed in most stands (*Acer*, *Betula*, *Liriodendron*) to ones that leave much of the forest floor without seed, despite presence of adults (*Carya*, *Cornus*, *Nyssa*, *Oxydendrum*). Seedling establishment is one of the strongest filters on recruitment in our study area. Taken together, our results indicate (1) that fecundity and dispersal can be resolved, even under a closed canopy, and (2) that recruitment of many species is limited by the density and location of source, dispersal patterns, or both.

Key words: dispersal; establishment; fecundity; forest dynamics; negative binomial; recruitment; seed rain; southern Appalachians.

INTRODUCTION

Field studies and simulation models of forest dynamics have long assumed that seed is ubiquitous (reviewed by Clark 1993, Pacala and Hurtt 1993, Ribbens et al. 1994, Clark and Ji 1995, Schupp and Fuentes 1995) and, thus, that tree population growth rates are limited at other life history stages. The assumption that seed is always available allows one to overlook seed production and dispersal and focus instead on microsites for seedling establishment, resource limitations on growth, and factors causing mortality. Seed rain tends to be ignored, because it is difficult both to quantify seed production in closed canopies, where seed shadows from individual crowns overlap (Willson 1993), and to track dispersal by wind (Augspurger 1986, Matlack 1987, Johnson 1988) and animals (Smith and Follmer 1972, Darley-Hill and Johnson 1981,

Schupp 1993, Ribbens et al. 1994). Moreover, mechanistic models are hard to apply in forest understories, because variable winds, seed release heights, and microtopographic relief are difficult to characterize (e.g., Greene and Johnson 1989).

Growing realization that seed may often be in short supply has led to increased interest in understanding life history stages where recruitment limitation can occur, including seed arrival at the ground, seed predation, germination, and early seedling survival (Harcombe 1987, Schupp et al. 1989, Nakashizuka et al. 1995). Seed arrival depends on: (A) density and dispersion of adults, (B) adult fecundities, and (C) dispersal distances of seed. These three constraints on seed arrival are here termed: (A) source-density, (B) source-strength, and (C) dispersal limitations, respectively (Fig. 1). A fourth limitation on recruitment we examine here, (D) establishment limitation, depends on seed survival and germination and seedling survival. We refer to “establishment” as the time from seed arrival at the soil surface (estimated by seed traps) to the time seedlings are censused during the first year of growth. Each

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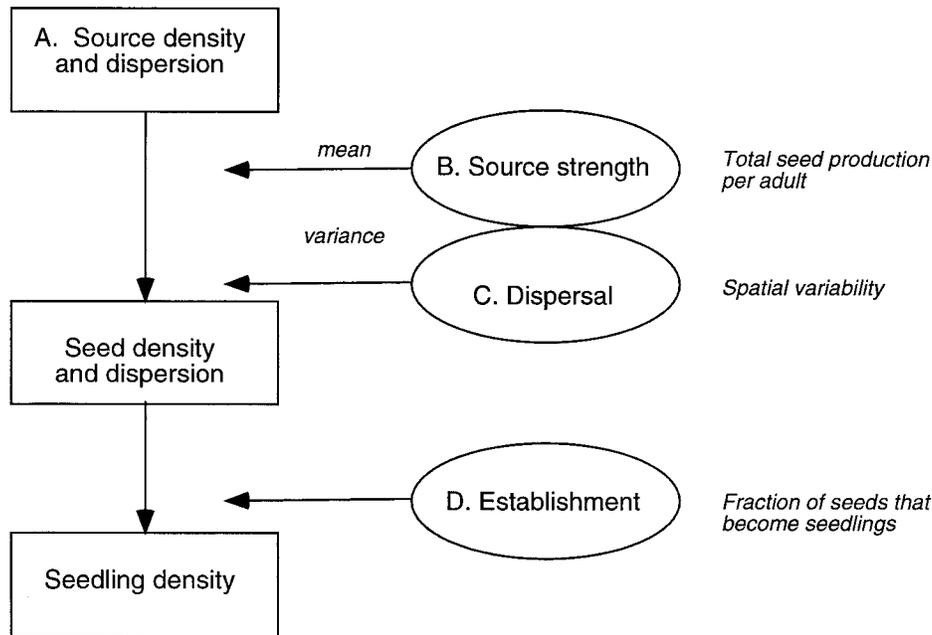


FIG. 1. The four limitations on recruitment analyzed here (labeled A–D) that link adults to seedlings.

stage may depend on processes operative at several spatial scales (Schupp 1993, Nakashizuka et al. 1995). At the broadest scale, the distribution of a species along geographic or environmental gradients sets limits on the presence of reproductive individuals (A, source density). Fine spatial scales describe local densities and crown areas of seed-bearing trees (A, source density) and dispersal distances (C), which, in turn, determine identities of neighboring plants and interaction intensities. Seedling establishment (D) depends on physical (e.g., light, water, and nutrients) and biotic (e.g., litter depth, seed and seedling predators, pathogens, and competitors) factors that vary at several spatial scales, both “within” and “among” stands (Godman and Mattson 1976, Beatty 1984, Streng et al. 1989, Peterson and Pickett 1990, Alvarez-Buylla and García-Barrios 1991, Houle 1992a).

Unfortunately, appreciation that recruitment limitation can occur does not remove the obstacle that caused many to ignore it in the first place: lack of characterization methods. Most efforts to quantify seed production and dispersal are highly indirect. Seed arrival at the forest floor is sometimes estimated from seedling distributions, a method requiring establishment success, i.e., that seeds become seedlings. Does absence of seedlings mean seeds did not arrive or that seeds arrived, but did not germinate? If microrelief or biotic interactions influence germination success (Godman and Mattson 1976, Beatty 1984), there may be little (or even a negative) relationship between seed rain and seedlings (Augspurger 1986, Augspurger and Franson 1988, Houle 1992a, Nakashizuka et al. 1995, Shibata

and Nakashizuka 1995). Any spatial bias imposed by post-dispersal processing of seed (e.g., secondary dispersal by wind (Matlack 1989) or animals (Abbott and Quink 1970, Schupp 1988, Willson and Whelan 1990, Whelan et al. 1991, Willson 1993) alters the relationship between seed arrival and seedlings. Moreover, distributions and abundances of seedlings do not necessarily give much insight into seed production (fecundity) (Willson 1993). Because of these problems parameterizing seed production and dispersal, we are aware of no studies showing how recruitment limitations compare among species that co-occur in closed stands.

A way forward is available through models that associate offspring with the spatial pattern and sizes of potential parents. Ribbens et al. (1994) used the relationship between seedlings and conspecific trees to estimate seedling production and dispersal. Their model predicts seedling density as the summed contribution of seedlings from all trees on a sample plot. The approach is a significant advance over simple seedling counts, because it estimates fecundity and dispersal distance (of seedlings, rather than seeds) based on the summed contributions of potential parent trees. A next step is the analysis of seed rain to estimate factors affecting seed arrival (limitations A, B, and C) vs. establishment (D).

Our objectives are (1) to develop a model to estimate seed production and dispersal under closed forest canopies, (2) to introduce methods for evaluation of the approach, and (3) to determine contributions of seed arrival vs. seedling establishment to the distributions

TABLE 1. Stand characteristics and basal areas (m²/ha).

	Stand 1	Stand 2	Stand 3	Stand 4	Stand 5
Elevation (m)	786	802	866	1085	1387
Setting	xeric ridge	mesic cove	slope	slope	slope
<i>Acer</i>	1.96	4.83	4.69	6.58	3.86
<i>A. pensylvanicum</i>	0.01	0.07	0.02	1.13	1.15
<i>A. rubrum</i>	1.86	4.50	5.71	5.45	0.31
<i>A. saccharum</i>	0.00	0.26	0.00	0.00	2.37
<i>A. spicatum</i>	0.00	0.00	0.00	0.00	0.06
<i>Amelanchier arborea</i>	0.47	0.03	0.00	0.02	0.18
<i>Betula</i>	0.03	2.55	0.70	0.02	12.76
<i>B. alleghaniensis</i>	0.00	0.09	0.11	0.00	8.25
<i>B. lenta</i>	0.03	2.46	0.59	0.02	4.52
<i>Carya glabra</i>	1.33	3.55	3.86	1.35	0.34
<i>Castanea dentata</i>	0.10	0.00	0.04	0.31	0.00
<i>Cornus florida</i>	0.17	0.61	0.22	0.16	0.02
<i>Fagus grandifolia</i>	0.01	0.00	0.00	0.00	0.59
<i>Fraxinus americana</i>	0.00	0.00	0.00	1.23	1.80
<i>Hamamelis virginiana</i>	0.03	0.06	0.00	0.00	0.21
<i>Liriodendron tulipifera</i>	0.03	9.97	0.71	0.03	0.00
<i>Magnolia</i>	0.13	0.02	0.00	0.40	0.00
<i>M. acuminata</i>	0.01	0.00	0.00	0.02	0.00
<i>M. fraseri</i>	0.12	0.02	0.00	0.38	0.00
<i>Nyssa sylvatica</i>	0.69	0.33	2.97	2.03	0.00
<i>Oxydendrum arboreum</i>	1.62	0.15	3.13	2.88	0.00
<i>Pinus rigida</i>	6.35	0.00	0.00	0.00	0.00
<i>Quercus</i>	8.65	6.92	13.51	15.40	8.71
<i>Q. alba</i>	0.83	0.00	0.00	0.00	0.37
<i>Q. coccinea</i>	3.56	0.00	0.00	0.95	0.00
<i>Q. marilandica</i>	0.40	0.00	0.00	0.00	0.00
<i>Q. prinus</i>	2.74	3.35	10.30	9.83	0.00
<i>Q. rubra</i>	0.10	1.65	2.70	4.12	8.33
<i>Q. velutina</i>	1.01	1.92	0.46	0.00	0.00
<i>Q. sp.</i>	0.00	0.00	0.05	0.51	0.00
<i>Robinia pseudo-acacia</i>	0.77	0.64	0.51	0.32	0.00
<i>Sassafras albidum</i>	0.57	0.00	0.09	0.00	0.00
<i>Tilia americana</i>	0.00	0.59	0.00	0.00	4.42
<i>Tsuga canadensis</i>	0.00	0.19	0.04	0.52	0.00

Note: Rounding results in discrepancies for some totals.

of first-year seedlings in five of the principal stand types of southern Appalachian forests. We use spatial distributions of mature trees, seed arrival, and seedling establishment to quantify recruitment limitations at two scales. Model results produce a simple "colonization index," the average fraction of 1-m² plots of soil surface expected to receive some seed in any given year. We use the relationship between seed rain and seedling distributions as the basis for identifying arrival vs. establishment limitations on recruitment at the stand and at the square-meter scales. Because we expected the relative contributions of seed arrival vs. establishment limitation to vary among species and across environmental gradients, we analyzed 14 species across five stands that span gradients in elevation and moisture.

THE STUDY AREA

The study area consists of five stands along an elevation gradient at Coweeta Hydrologic Laboratory in the southern Appalachians (35°03' N, 83°27' W). The watershed is characterized by high and topographically variable precipitation (177–222 cm/yr). The two principal vegetation gradients are those discussed by Whitaker (1956), elevation and moisture. Our five stands

are located to sample these gradients (Table 1). Mesic sites include Cove hardwoods at mid elevation (stand 2) and Northern hardwoods at high elevation (stand 5)(Table 1). A Pine/oak ridge (stand 1) is the most xeric stand. Intermediate in elevation and moisture status are oak-dominated stands (3 and 4). Species restricted to high elevation and/or high moisture stands include *Acer pensylvanicum*, *A. saccharum*, *Betula alleghaniensis*, *Fraxinus americana*, and *Tsuga canadensis*. Cove hardwoods additionally include *Liriodendron tulipifera*. Oak stands (3 and 4) are centers of abundance for *Acer rubrum*, *Nyssa sylvatica*, *Quercus prinus*, and *Q. rubra*. Xeric stand 1 is dominated by *Pinus rigida*, *Q. alba*, *Q. coccinea*, *Q. marilandica*, *Q. velutina*, and *Sassafras albidum*.

METHODS

Data collection was designed to characterize recruitment limitations at four stages (Fig. 1) and two spatial scales. Our nested sampling design allowed modeling of seed production and dispersal at the local (within-stand) scale and comparisons of average seed rain among stands. Within-stand sampling allowed us to estimate fecundity and dispersal of seed by modeling

spatial pattern in seed rain relative to locations and sizes of adult trees. Stand differences in parent tree abundance, seed rain, and seedling establishment demonstrated how recruitment limitation varied with canopy composition across the principal environmental gradients. The first limitation, (A) source abundance (Fig. 1), was assessed from basal areas. Source strength (B) was estimated (1) at the local scale, from modeled seed rain within stands, and (2) as a stand average, from average seed rain and basal areas. Regressions between stand basal area and seed rain determined whether differences in seed rain among stands (i.e., across environmental gradients) were explained by average basal area of adults. Limitations due to source density and distribution (A), source strength (B), and seed dispersal (C) were collectively estimated from the fraction of ground surface expected to receive some seed in a given year, based on modeled seed rain within stands. Establishment limitation (D) was assessed at both scales. Comparisons of seedling distributions within stands with predicted seed rain permitted estimation of establishment success at fine spatial scales. Differences in stand averages of seed rain vs. seedling establishment were used to identify how establishment success varied across vegetation types. Together these results were used to interpret how different species may be limited at different stages by factors operating at local scales (dispersion of adult trees, dispersal of seed, and microrelief) and at broader scales (gradients in elevation and moisture).

Tree, seed, and seedling data

From each of five stands we (1) mapped all trees greater than 1 m tall on 60×60 m (0.36 ha) plots, (2) collected seed in twenty 0.42×0.42 m seed traps, and (3) took a census of seedlings along a 1×60 m belt transect. Trees were identified, located using a Topcon electronic Total Station, and diameters measured at a height of 1.3 m.

Twenty seed traps were established within each of the five stands at 5-m intervals along two transects spaced 20 m apart. We tested several seed trap designs. The design used consists of a plastic basket frame supported 1.5 m above the ground by PVC pipes. The basket has drain holes, but seeds falling in the trap remain elevated above the bottom of the basket by 1 mm mosquito netting. Elevation of the trap above the ground and a layer of wire mesh covering the trap minimized removal of *Quercus* and *Carya* seed by squirrels and other vertebrate seed predators. Concerns that the wire mesh might cause some seeds to bounce out of traps led us to conduct efficiency trials. We released seeds from sufficient heights to insure terminal velocities were reached at the trap opening and recorded numbers of successful trap entries. Trap efficiencies were generally high; clear differences among taxa could be attributed to size and tendency to bounce. Small *Betula* seeds never bounced off the covering

mesh. Lowest efficiencies were for *Carya* (0.86 ± 0.05) and *Quercus* (0.88 ± 0.03), but even these taxa entered traps with high probability. Intermediate were *Liriodendron* (0.98 ± 0.02), *Pinus* (0.95 ± 0.04), and *Acer* (0.94 ± 0.04).

Traps were deployed in the field September 1991 and emptied at 2–4 mo intervals through July 1996. Because few species released seed during summer months, annual averages are based on seed collections between July of each year. All debris in traps was removed at collection dates and sorted with the aid of sieves. Seeds were identified to the lowest taxonomic unit possible (Table 2). All seeds collected over the course of the study are archived according to trap and collection date at the Duke University Phytotron.

Seedling transects were established within each of the five stands in June 1992 along the lower portion of sample stands, with location differing somewhat among stands to avoid areas disturbed by foot traffic. Annual censuses of newly emerged seedlings were completed in July of 1992, 1993, 1994, 1995, and 1996 to match the period for seed rain collection. Newly emerged seedlings were readily distinguished from older seedlings for all species that occurred within our stands.

Seed dispersal vectors and taxonomic resolution

Not all seeds and seedlings could be resolved to species in our study. To permit comparisons among seeds, seedlings, and trees, we used the lowest common taxonomic group for analysis (Table 2). For example, all *Acer* seed is treated as a single taxon. Although many could be confidently identified to species, others (particularly damaged seeds) could not. Because *Acer saccharum* trees are abundant only in stand 5, and *Acer pensylvanicum* shrubs are short and not close to traps, most seeds on the remaining four plots were probably *Acer rubrum*. Acorns were separated as “red” vs. “white,” and several were identified to species. However, because many could not be separated, and because acorns were few, we lumped all *Quercus*. *Carya* nuts could not be confidently identified to species, but trees within our stands were principally *Carya glabra*. For remaining taxa, either seed could be identified to species or only a single species representative of the taxon occurred in the study area. Genders of dioecious species *Nyssa sylvatica* and, sometimes, *Fraxinus americana*, were not determined, so all individuals were included in the analysis. We did identify seed bearing individuals of *Acer rubrum*, so only those individuals were used to estimate fecundity and dispersal. The minute seeds of *Oxydendrum arboreum* were not recovered in our traps, but we did quantify the dehiscent capsules.

Seeds analyzed include species principally dispersed by wind and animals (Table 2). Our elevated traps characterize primarily wind dispersal; seeds “scatterhoarded” by birds and mammals or dispersed secondarily by wind (e.g., *Betula*, Matlack 1989, Houle and Payette 1990) are not expected to enter traps.

TABLE 2. Resolution of taxa analyzed in this study and their probable dispersal vectors.

Taxon	Trees	Seed	Ist-yr seedlings	Dispersal vector
<i>Acer</i>	<i>A. pensylvanicum</i>	<i>A. pensylvanicum</i>	<i>A. pensylvanicum</i>	wind
	<i>A. rubrum</i>	<i>A. rubrum</i>	<i>A. rubrum</i>	
	<i>A. saccharum</i>	<i>A. saccharum</i>	<i>A. saccharum</i>	
	<i>A. spicatum</i>	<i>Acer</i> sp.	<i>Acer</i> sp.	
<i>Amelanchier</i>	<i>A. arborea</i>	<i>Amelanchier</i> sp.	<i>A. arborea</i>	birds
<i>Betula</i>	<i>B. alleghaniensis</i>	<i>Betula</i> sp.	<i>Betula</i> sp.	wind
	<i>B. lenta</i>			
<i>Carya</i>	<i>C. glabra</i>	<i>Carya</i> sp.	none	mammals
<i>Cornus</i>	<i>C. florida</i>	<i>C. florida</i>	<i>C. florida</i>	birds
<i>Fraxinus</i>	<i>F. americana</i>	<i>Fraxinus</i> sp.	none	wind
<i>Liriodendron</i>	<i>L. tulipifera</i>	<i>L. tulipifera</i>	<i>L. tulipifera</i>	wind
<i>Nyssa</i>	<i>N. sylvatica</i>	<i>N. sylvatica</i>	none	birds
<i>Oxydendrum</i>	<i>O. arboreum</i>	<i>O. arboreum</i> capsules	none	wind
<i>Pinus</i>	<i>P. rigida</i>	<i>Pinus</i> sp.	none	wind
<i>Quercus</i>	<i>Q. alba</i>	<i>Q. rubra</i>	<i>Q. prinus</i>	mammals
	<i>Q. coccinea</i>	<i>Q. velutina</i>	<i>Q. rubra</i>	
	<i>Q. marilandica</i>	Red oak	<i>Q. velutina</i>	
	<i>Q. prinus</i>	White oak	Red oak	
	<i>Q. rubra</i>			
	<i>Q. velutina</i>			
<i>Robinia</i>	<i>R. pseudo-acacia</i>	<i>R. pseudo-acacia</i>	none	wind
<i>Tilia</i>	<i>T. americana</i>	<i>T. americana</i>	none	wind
<i>Tsuga</i>	<i>T. canadensis</i>	<i>T. canadensis</i>	none	wind

Seed production estimation at the stand scale

Fecundity parameters (β) were estimated at two spatial scales. An estimate of β among stands is obtained as the slope of the regression of seed rain against basal area:

$$s_{jk} = \beta \bar{b}_k \tag{1a}$$

where \bar{b}_k is the basal area of the k th stand, and s_{jk} is seed arrival at the j th seed trap in the k th stand. To evaluate constancy of fecundity among stands we also estimated β for each stand separately as the ratio of average seed rain and stand basal area:

$$\beta_k = \frac{\bar{s}_k}{\bar{b}_k} \tag{1b}$$

The following section (*Seed production and dispersal modeling*) describes a third estimate of β based on spatial patterns of trees and seed rain within stands.

Seed production and dispersal modeling

Our summed seed shadow (SSS) model predicts seed arrival at a location as the summed contribution of seed dispersed from all conspecific trees in the sample area. The method assumes that each tree's contribution to seed rain at a location depends on its size (basal area) and distance. Functions describing how seed rain depends on fecundity, tree basal area, and distance are parameterized from an array of seed input data (e.g., seed traps) and a map of tree locations and sizes (basal areas). The model allows estimation of the seed contributions of individual trees. Our SSS model shares some attributes of that used by Ribbens et al. (1994) to estimate seedling distributions and by Kuuluvainen et al. (1993) to model spatial effects of adult trees.

Clumped distribution of seed.—Distributions of seed arrivals in our stands were “clumped,” having higher variance than a Poisson process. This clumped distribution was described by a negative binomial distribution, generally appropriate for mixtures of random sources (e.g., Johnson and Kotz 1969). Consider m seed traps located at various distances from a seed source (a tree). Our likelihood function is based on negative binomial seed arrival:

$$L(\mathbf{S} | \mathbf{p}, \theta) = \prod_{j=1}^m \frac{\Gamma(s_j + \theta)}{\Gamma(s_j + 1)\Gamma(\theta)} \frac{\hat{s}^{s_j}(b, x_j; \mathbf{p})\theta^\theta}{(\hat{s}(b, x_j; \mathbf{p}) + \theta)^{s_j + \theta}} \tag{2}$$

where $\Gamma(\cdot)$ is the gamma function, s_j is the observed rate of seed arrival to a given seed trap j , \mathbf{S} is the data set containing m seed traps (the collection of s_j 's), $\hat{s}(b, x_j; \mathbf{p})$ is the “expected” seed abundance at trap j , and θ is a dimensionless “clumping parameter.” The expected seed arrival at trap j is a function $\hat{s}(b, x_j; \mathbf{p})$ that depends on distance x_j from a seed source and the size (basal area) b of that source, with fitted parameters \mathbf{p} (see *Fitting the model*, below). The degree of clumping is determined by the data (θ is a fitted parameter). Values of $\theta < 1$ imply highly contagious distributions (overdispersed), whereas large values ($\theta \gg 1$) tend to a Poisson process.

The uneven distribution of seed sources.—Now consider a stand of many trees, each producing seeds with a source strength that depends on basal area and dispersing seed some distance. The expectation of the negative binomial distribution at a given location depends on the sizes and distances to all trees in the stand. Here we derive this expectation as the sum of seed shadows of individual trees. Tree i 's contribution to total seed

arrival at location j is the product of its source strength $Q(b_i)$, a function of its basal area b_i :

$$Q(b_i) = \beta b_i \tag{3}$$

with fitted parameter β (seeds per basal area), and (a density function of) seeds dispersed to a trap located x_{ij} meters away, $f(x_{ij})$. The proportion of a tree's $Q(b_i)$ seeds arriving on the area subtended by a trap of diameter dx and arc angle $d\varphi$ is

proportion of seeds falling on the area $(x, x + dx, \varphi)$

$$= \int_x^{x+dx} \oint_{\varphi} f(x', \varphi') d\varphi' dx' \approx \varphi x f(x) dx.$$

We fitted dispersal functions $f(x, \varphi)$ of varying forms and numbers of parameters, including ones that allow for the ‘‘skip’’ distance that can be associated with dispersion from an elevated source (Sutton 1953, Okubo and Levin 1989, Andersen 1991), ones with varying degrees of kurtosis, and mixed models. Models with a skip distance did not fit the data, because crowns are too broad to be regarded as point sources (a boundary condition assumed in most solutions of Gaussian plume models having an elevated source [Okubo and Levin 1989]); seeds are broadly dispersed under individual crowns and then fall off with distance. Models with large kurtosis did not fit our data, yielding unstable fecundity estimates. We were unable to obtain convergence of mixed models that had some proportion of seed allocated to a widely dispersed tail due to parameter redundancy.

The density used is isotropic, i.e., there is no directional bias in the dissemination of seed. It has a mode at the source and adjustable kurtosis:

$$f(x_{ij}) = \frac{1}{N} \exp\left[-\left(\frac{x_{ij}}{\alpha}\right)^c\right]$$

where α is a dispersion parameter in metres, c is a dimensionless shape parameter, and N is a normalization constant obtained by integrating arc-wise and with distance:

$$\begin{aligned} N &= \int_0^\infty \oint_{2\pi} \exp\left[-\left(\frac{x}{\alpha}\right)^c\right] d\varphi' dx \\ &= 2\pi \int_0^\infty x \exp\left[-\left(\frac{x}{\alpha}\right)^c\right] dx = \frac{2\pi\alpha^2\Gamma(2/c)}{c}. \end{aligned}$$

The proper form of N is required to obtain unbiased parameter estimates (see *Fitting the model*, below). The m th moment of this density is

$$\mu_m = \int_0^\infty \oint_{2\pi} (x')^m f(x', \varphi') d\varphi' dx' = \frac{\alpha^m \Gamma\left(\frac{m+2}{c}\right)}{\Gamma(2/c)}$$

giving mean dispersal distance

$$\mu_1 = \frac{\alpha\Gamma(3/c)}{\Gamma(2/c)} \tag{4}$$

and kurtosis that depends only on the shape parameter

$$\frac{\Gamma(6/c)\Gamma(2/c)}{\Gamma^2(4/c)}.$$

This flexible density includes some familiar ones as special cases. Exponential densities have $c = 1$ (Johnson 1988, Willson 1993). Our model is Gaussian, having $c = 2$. Kurtosis of this arc-wise Gaussian density (i.e., two) is lower than that of a one-dimensional Gaussian density (kurtosis = 3). Ribbens et al. (1994) used a third special case with $c = 3$ and a lower kurtosis. Our density then is

$$f(x_{ij}; c = 2) = \frac{1}{\pi\alpha^2} \exp\left[-\left(\frac{x_{ij}}{\alpha}\right)^2\right] \tag{5}$$

with mean displacement from Eq. 4:

$$\mu_1 = \frac{\alpha\sqrt{\pi}}{2} = 0.886\alpha.$$

Arc-wise integration gives the fraction of seed that travels distance x in all directions, which yields the Weibull density:

$$F_0(x; c = 2) = \frac{2x}{\alpha^2} \exp\left[-\left(\frac{x}{\alpha}\right)^2\right].$$

The product of source strength (Eq. 3) and density of seed arrivals (Eq. 5) is termed the ‘‘seed shadow’’ of a tree i :

$$\hat{s}(b_i, x_{ij}; \mathbf{p}) = Q(b_i)f(x_{ij}).$$

Note that for global dispersal the average seed arrival reduces to Eq. 1b.

Fitting the model.—Assume each tree i disperses seed to trap j . Seed arrival at trap j is the cumulative contribution of n conspecific sample trees, each tree having source strength and seed shadow described by Eqs. 3 and 5, respectively:

$$\begin{aligned} \hat{s}_j(\mathbf{b}, \mathbf{x}; \mathbf{p}) &= \sum_{i=1}^{n \text{ trees}} Q(b_i)f(x_{ij}) \\ &= \frac{\beta}{\pi\alpha^2} \sum_{i=1}^{n \text{ trees}} b_i \exp\left[-\left(\frac{x_{ij}}{\alpha}\right)^2\right] \end{aligned} \tag{6}$$

where \mathbf{p} is a vector of fitted parameters $[\alpha, \beta]$ that maximize the likelihood given in Eq. 2, \mathbf{b} is a length- n vector of tree basal areas b_i , and \mathbf{x} is the $n \times m$ matrix of distances between trees and traps x_{ij} . We simultaneously fit θ ; the degree of clumping in the data is estimated together with the seed shadows, $\hat{s}(b_i, x_{ij}; \mathbf{p})$, around individual trees. Bias corrected and accelerated (BC_a) confidence intervals for α , β , and θ were obtained by 1000 bootstrapped maximum likelihood (ML) estimates (Efron and Tibshirani 1993). The BC_a interval differs from the standard percentiles in two ways. First, it corrects for the median bias (the difference between

median and mean) in the parameter estimate obtained from the set of bootstrap estimates. Second, it corrects for the fact that the standard error of the estimate can depend on the parameter value. This correction is accomplished through an acceleration quantity that estimates the rate of change in the standard error relative to the true parameter value. We compared BC_a confidence intervals with those obtained from standard percentiles and from a minimum volume ellipse for all parameter estimates. Although BC_a endpoints are more accurate than those obtained by other methods (Efron and Tibshirani 1993), we found differences to be small at the 95% level, the level reported here.

Parameter correlations were determined from the bootstrapped data set, and scatter plots of parameter estimates were examined. Negative correlations in α and β estimates obtained from a simplified version of the model demonstrated need for a proper normalization constant. The normalization constant assures that negative correlation between parameters does not dominate the fit, an instability we observed for an unnormalized version of the model that permits a large source strength parameter β to offset a small dispersion parameter α . The normalized model fitted here, however, can have the opposite tendency. Positive correlation occurs when large dispersion flattens the curve and can be compensated by large source strength. We obtained positive correlations only in a few cases where fits were poor.

Parameter estimation and evaluation was accomplished for each species in four steps: (1) estimation of the best (ML) dispersal parameter value α incorporating information obtained from all five stands; (2) assessment of consistency of dispersal parameters from stand to stand; (3) comparison of model performance against a null model of nonlocal dispersal; and (4) examination of potential for bias in parameter estimates resulting from finite area of mapped stands. One obvious source of variance in dispersal among stands is that associated with different arrangements of trees relative to seed traps. Because there are no conventional hypothesis tests for such models, we developed several. Our first two steps involve a hypothesis test that dispersal parameters differ among stands. We compute two likelihoods of the data. The first likelihood provides parameter estimates that incorporate information from all q (≤ 5) stands having sufficient trees to obtain a fit, yielding the ML of the data for the model with a species-specific α parameter:

$$L(\mathbf{S}_q | \mathbf{p}_{q+1}, \theta) = \prod_{k=1}^{q \text{ stands}} L(\mathbf{S}_k | \mathbf{p}_k, \theta) \quad (7)$$

where the parameter set for stand k is $\mathbf{p}_k = [\alpha, \beta_k]$, and $\mathbf{p}_{q+1} = [\alpha, \beta_1, \dots, \beta_q]$ includes separate fecundity estimates for each stand and a single dispersal parameter α that best predicts seed rain across all stands. The number of stands q included in the likelihood function

varied with species, because trees of all species did not occur on all plots. In some cases trees did occur, but numbers were too low to obtain fits. The $q + 1$ degrees of freedom for this model are the $q + 1$ parameters in \mathbf{p}_{q+1} , plus one for the clumping parameter θ , minus one. By simultaneously taking advantage of data from all available stands, this model provides the best estimate of dispersal distance.

Step 2 requires a ML for the model in which each stand has a separate α_k in order to test whether stand-specific dispersal parameters substantially improve the likelihood of the data, so much so that we conclude that dispersal distance may differ among stands. This likelihood has parameter set $\mathbf{p}_{2q} = [\alpha_1, \dots, \alpha_q, \beta_1, \dots, \beta_q]$ with $2q$ degrees of freedom. The likelihood ratio statistic, or deviance

$$D = -2 \ln \left[\frac{L(\mathbf{S}_q | \mathbf{p}_{2q}, \theta)}{L(\mathbf{S}_q | \mathbf{p}_{q+1}, \theta)} \right] \quad (8)$$

is asymptotically distributed as χ^2 with $q - 1$ degrees of freedom, the difference in degrees of freedom (number of parameters) of the individual models. Large deviance means that dispersal distance differs across stands.

For step 3, we viewed an appropriate null model for testing our results to be one where seed arrival is independent of tree locations, i.e., nonlocal dispersal. This null model is analogous to the conventional regression null model of a slope parameter equal to zero, i.e., no relation between variables. Our likelihood ratio test compares the likelihood obtained with $q + 2$ ML parameter estimates with the likelihood under the (null) hypothesis that all traps receive, on average, the mean seed rain. The null model has fixed expectation \bar{s}_k in Eq. 2 and a single fitted parameter θ . The deviance for this model,

$$D = -2 \ln \left[\frac{L_{\text{ML}}(\mathbf{S}_q | \mathbf{p}_{q+1}, \theta)}{L_{\text{null}}(\mathbf{S}_q | \theta)} \right] \quad (9)$$

has q degrees of freedom, $q + 1$ parameters from the ML model, minus one parameter for the null model. To safeguard against the event that D was not distributed as χ^2 we also conducted permutation tests that involved generating a distribution of deviances from permuted data sets, where \mathbf{S}_q in Eq. 9 was replaced with $\mathbf{S}_{q,k}$, the k th random permutation of the data. The probability of D calculated from the original data was determined from this distribution of D_k 's.

The fourth step of model evaluation was a test for bias in parameter estimates that might arise from finite size of mapped stands. Contributions of seed from trees outside the mapped plot might bias fecundity estimates upward, because the model implicitly assumes that all seeds derive from trees in the plot. Dispersal parameters might also be sensitive to plot sizes. We fitted the model beginning at a minimal map area that included the central 20×40 m to progressively larger map areas out to the full 60×60 m.

There is no simple estimate of the variance explained by the model, but we provide a rough index. The Pearson correlation coefficient between model and data has been used for such comparisons, but it characterizes the level of agreement to a best-fitting linear regression to the model. Thus, high correlations can result even when model predictions are biased (i.e., good fit to a linear model of slope $\neq 1$). We used instead the correlation describing the level of agreement between model and data, i.e., the scatter about the line of slope = 1:

$$r^2 = 1 - \frac{\sum_{k=1}^{q \text{ stands}} \sum_{j=1}^{20 \text{ traps}} (s_{jk} - \hat{s}_{jk}(\mathbf{x}, \mathbf{b}; \mathbf{p}))^2}{\sum_{k=1}^{q \text{ stands}} \sum_{j=1}^{20 \text{ traps}} (s_{jk} - \bar{s}_k)^2} \quad (10)$$

where s_{jk} is the observed seed rain at trap j in stand k , and \bar{s}_k is the mean seed rain for stand k . When data are highly skewed (i.e., $\theta \ll 1$), and the fit weak, this index has the limitation that it can be negative (i.e., the mean better accounts for seed rain than does the model). It is a conservative index of variance in the data explained by the model.

Seed limitation index

Seed limitation at the local scale (1 m²) was estimated as the probability that no seed would arrive in a given 1-m² patch. The 1-m² scale was chosen for this index, because microsites typically analyzed for recruitment success are of this order. We considered two sources of limitation: (1) source limitation, the influence of source density, distribution, and fecundity; and (2) dispersal limitation, the influence of the local and clumped nature of seed dispersal. We estimated these limitations from probabilities calculated using the annual predicted seed rain density at each 1 m² in the central 20 × 40 m rectangle of each stand using the tree census maps and parameterized seed dispersal models.

Our index of source limitation consists of a comparison of seed arrival predicted from the fitted model with that expected if seed rain was not influenced by limited dispersal. Assuming uniform distribution of seed and independent (unclumped) arrivals, the probability of any 1-m² patch j receiving at least some seed in a given year is

$$C(\bar{s}) = \Pr\{\hat{s}_j > 0 | \text{Poisson}(\bar{s})\} = 1 - e^{-\bar{s}} \quad (11)$$

where

$$\bar{s} = \frac{1}{m} \sum_{j=1}^m \hat{s}_j$$

is the average seed rain density, and \hat{s}_j is the expected seed rain to patch j from Eq. 6. Low values of $C(\bar{s})$ occur if the total production of seed is low (i.e., inadequate source density, fecundity, or both), yielding

$$\text{Source limitation} = 1 - C(\bar{s}). \quad (12)$$

Limited dispersal and clumping of seed reduce the actual colonization rate below that which would occur if dispersal were global, as estimated by $C(\bar{s})$. Our estimate of dispersal limitation makes use of the probability that any given 1-m² patch j receives some seed given the best estimates of local dispersal and clumping:

$$C(\hat{s}_j) = \Pr\{\hat{s}_j > 0 | \text{Negative Binomial}(\hat{s}_j, \hat{\theta})\} \\ = 1 - \left(\frac{\hat{\theta}}{\hat{s}_j + \hat{\theta}} \right)^{\hat{\theta}}$$

The average of these estimates across the $m = 800$ central 1-m² patches in each sample stand is the colonization index:

$$\bar{C} = \frac{1}{m} \sum_{j=1}^m C(\hat{s}_j) \quad (13)$$

the expected fraction of patches (at the 1-m² scale) receiving some seed in a given year. The contribution of dispersal limitation to the colonization index is estimated as the relative difference between the colonization index that includes only source limitations, $C(\bar{s})$, and the colonization index that incorporates dispersal and clumping \bar{C} :

$$\text{Dispersal limitation} = 1 - \frac{\bar{C}}{C(\bar{s})}. \quad (14)$$

Predicted seed rain and observed seedlings

“Establishment limitation,” the stage between seed dispersal and establishment as a 1st-yr seedling (Fig. 1), was assessed by comparing 1st-yr seedlings with seed rain at stand and local (1-m²) scales. The fraction of seed that produces 1st-yr seedlings was estimated at the stand scale by comparing average annual seed rain estimated from the 20 traps with average density of 1st-yr seedlings from the belt transects over 5 yr,

$$\text{Establishment fraction} \\ = \frac{1}{5} \sum_{y=1}^5 \frac{\text{1st-yr seedling density}_y}{\text{seed density}_y}$$

To test for establishment limitation at the 1-m² scale, we compared predicted seed rain to observed 1st-yr seedling density along the belt transects. Parameterized models were used together with the mapped tree distributions to predict seed rain densities at each 1-m² quadrat of the belt transects in each stand. The spatial scale of coherence between predicted seed rain and annual average 1st-yr seedling densities was assessed by cross-correlation. Significance levels included correction for the autocorrelation within each series by adjusting degrees of freedom according to Clifford et al. (1989).

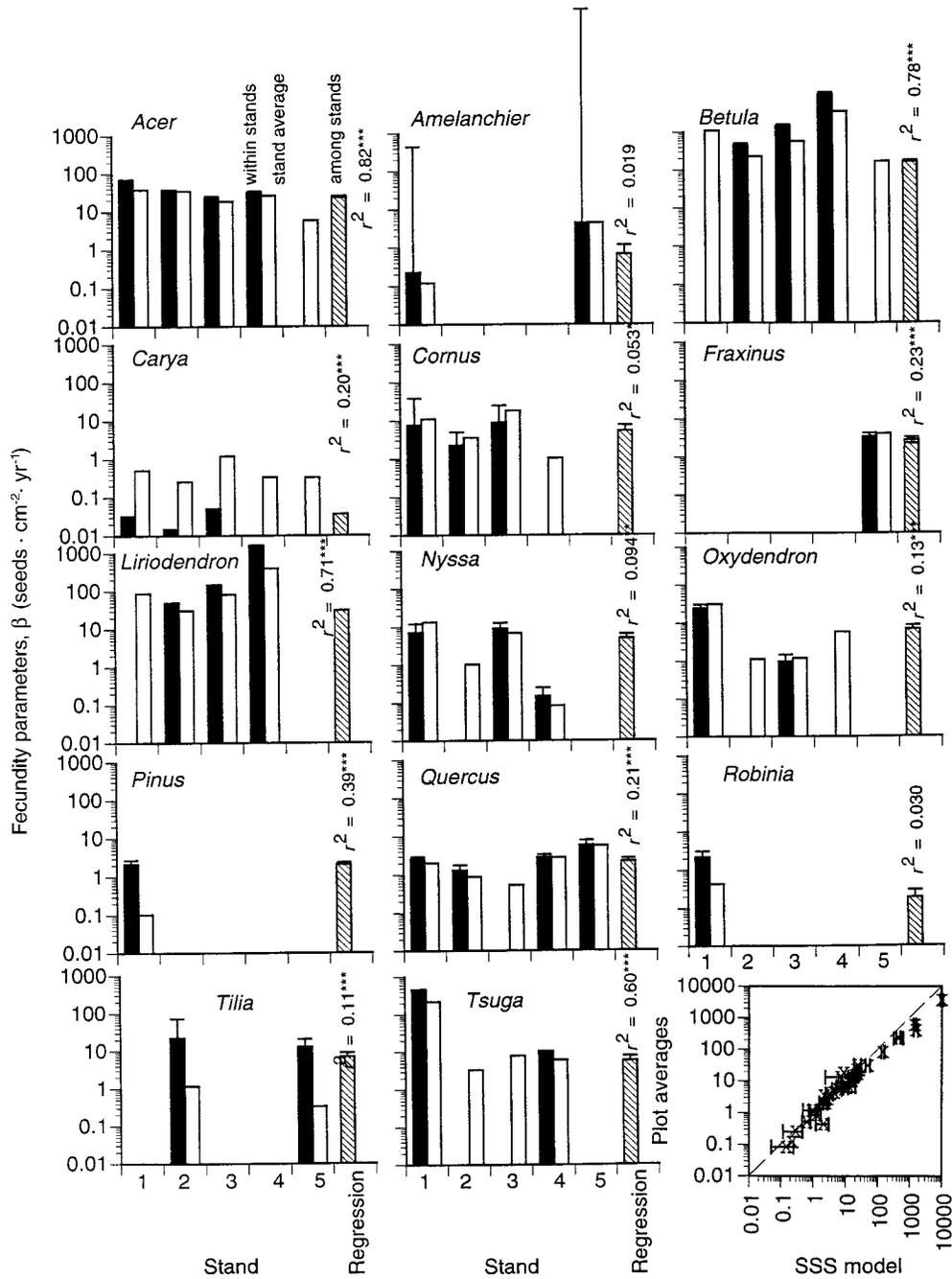


FIG. 2. Three estimates of the fecundity parameter β : (1) "within stands," the value fitted by the Summed Seed Shadow model, incorporating locations of seed traps relative to individual trees (solid bars); (2) the "stand average," obtained by dividing average seed rain of 20 traps by stand basal area (unshaded bars) (Eq. 1b); and (3) "among stands," obtained by regressing seed rain against basal area across all five stands (hatched bars) (Eq. 1a). The lower right panel indicates that the different methods show close agreement. For taxa showing poorest agreement, the Summed Seed Shadow model fits appear to be overestimates. Standard errors are bootstrapped (SSS parameter estimates) or from regression.

RESULTS

Density of sources

The most fundamental limitation on recruitment is absence of parent trees. Some taxa were abundant across most or all sites (e.g., *Acer rubrum*, *Carya*,

Quercus prinus, *Q. rubra*), whereas others were confined to specific stand types (*Acer saccharum*, *Betula alleghaniensis*, *B. lenta*, *Fraxinus*, *Liriodendron*, *Pinus*, *Tilia*, Table 1). Several taxa were present in most stands, but were nowhere abundant (*Cornus*, *Nyssa*,

TABLE 3. Summed seed shadow model parameter estimates, goodness-of-fit, and hypothesis tests.

Taxon	Stand q^\dagger	Distance $\alpha \pm 1 \text{ SE (m)}$	Fecundity ‡ $\beta_k \pm 1 \text{ SE (cm}^{-2}\cdot\text{yr}^{-1}\text{)}$	Clumping $\theta \pm 1 \text{ SE}$	Explained variance §
<i>Acer</i>	4 (1, 2, 3, 4)	25.2 \pm 2.39	$\beta_1 = 69.2 \pm 6.82$ $\beta_3 = 37.7 \pm 4.00$ $\beta_3 = 23.4 \pm 2.58(c)$ $\beta_4 = 32.2 \pm 2.84(c)$	10.8 \pm 1.95	0.714***
<i>Amelanchier</i>	2 (1, 5)	16.9 \pm 185	$\beta_1 = 0.231 \pm 450$ $\beta_5 = 4.44 \pm 522$	0.165 \pm 3500	0.125
<i>Betula</i>	3 (2, 3, 4)	37.1 \pm 2.87	$\beta_2 = 448 \pm 62.7(c)$ $\beta_3 = 1470 \pm 141$ $\beta_4 = 10200 \pm 1040$	5.83 \pm 1.22	0.681***
<i>Carya</i>	3 (1, 2, 3)	10.8 \pm 2.06	$\beta_1 = 0.657 \pm 0.196$ $\beta_2 = 0.296 \pm 0.179$ $\beta_3 = 1.02 \pm 0.267$	0.670 \pm 1.16	0.529***
<i>Cornus</i>	3 (1, 2, 3)	3.65 \pm 1.52	$\beta_1 = 7.68 \pm 30.7$ $\beta_2 = 2.28 \pm 2.73$ $\beta_3 = 8.87 \pm 15.9$	0.447 \pm 1.15	0.566***
<i>Fraxinus</i>	1 (5)	19.3 \pm 5.84	$\beta_5 = 3.40 \pm 0.847$	0.632 \pm 0.757	0.379**
<i>Liriodendron</i>	3 (2, 3, 4)	33.9 \pm 2.56	$\beta_2 = 49.8 \pm 7.89(c)$ $\beta_3 = 147 \pm 15.2(c)$ $\beta_4 = 1590 \pm 254$	5.76 \pm 1.21	0.707***
<i>Nyssa</i>	3 (1, 3, 4)	6.02 \pm 4.48	$\beta_1 = 7.30 \pm 4.87$ $\beta_3 = 9.12 \pm 3.68$ $\beta_4 = 0.151 \pm 0.101$	0.528 \pm 1.12	0.554***
<i>Oxydendrum</i>	2 (1, 3)	9.23 \pm 2.86	$\beta_1 = 24.5 \pm 6.26$ $\beta_3 = 0.975 \pm 0.484$	0.472 \pm 0.254	0.593***
<i>Pinus</i>	1 (1)	15.1 \pm 3.27	$\beta_1 = 2.16 \pm 0.558$	2.01 \pm 88.1	0.364**
<i>Quercus</i>	4 (1, 2, 4, 5)	11.8 \pm 1.32	$\beta_1 = 2.52 \pm 0.383$ $\beta_2 = 1.31 \pm 0.468$ $\beta_4 = 2.85 \pm 0.488$ $\beta_5 = 5.84 \pm 1.99$	1.30 \pm 0.282	0.270***
<i>Robinia</i>	1 (1)	14.8 \pm 1.33	$\beta_1 = 9.57 \pm 0.454$	65.6 \pm 20.6	0
<i>Tilia</i>	2 (2, 5)	13.0 \pm 2.95	$\beta_2 = 22.3 \pm 50.5$ $\beta_5 = 12.9 \pm 7.57$	0.485 \pm 0.374	0.114
<i>Tsuga</i>	2 (1, 4)	19.7 \pm 5.04	$\beta_1 = 503 \pm 170(c)$ $\beta_4 = 10.6 \pm 2.24(c)$	>100	0.523***

Note: Maximum likelihood estimates for parameters α and β include bootstrapped standard errors. BC_a confidence intervals are included in Fig. 4. Likelihood-ratio statistics (D) and associated r^2 values include probability estimates for null models described in text.

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$.

† The number of stands having sufficient seeds and trees to obtain fits followed by the list of stands in parentheses.

‡ Estimates with the designation (c) indicate correlations between α and β_k exceed 0.60, where k is stand designation.

§ The r^2 for agreement between data and model (Eq. 10).

\parallel Deviance for the hypothesis test that seed dispersal is nonlocal (Eq. 9) with $df = q$. Probabilities are from permutation tests, but χ^2 probabilities did not differ at the levels in footnotes *, **, or ***.

∇ Deviance for the hypothesis test that dispersion parameters α_k are the same across stands (Eq. 8) with $df = q - 1$. Blank cells are for $q = 1$ and, thus, no degrees of freedom.

Robinia). Unless seed production and dispersal are great, recruitment limitation is likely for many taxa simply on the basis of parent tree abundance.

Seed rain at the stand scale

Spatial variability in seed rain affected our ability to estimate fecundity differences among stands. Regressions of seed rain against basal areas of the five stands (Eq. 1a) provide β (seeds per basal area) estimates based on varying abundances across the landscape ("among stands" in Fig. 2). Significant β values were obtained for *Acer*, *Betula*, *Carya*, *Cornus*, *Fraxinus*, *Liriodendron*, *Nyssa*, *Oxydendrum*, *Pinus*, *Quercus*, *Tilia*, and *Tsuga* (Fig. 2). Best fits ($r^2 > 0.5$) were obtained for taxa having adults distributed rather evenly across plots, intermediate to large dispersal distances,

and low levels of clumping, including *Acer*, *Betula*, *Liriodendron*, and *Tsuga*. These factors insure that seeds are evenly spread at the stand scale and, thus, reflect average tree abundance. Seed rain of taxa with low dispersal distances, clumped distributions, or highly uneven distributions of adults, including *Amelanchier*, *Carya*, *Cornus*, *Nyssa*, *Oxydendrum*, *Quercus*, *Robinia*, and *Tilia*, was not well-predicted from basal area at the stand scale (r^2 values < 0.25). Intermediate levels of explained variance were obtained for *Fraxinus* and *Pinus*, both of which were abundant in single stands and had intermediate dispersal distances.

Fecundity parameters β estimated from within individual plots varied among stands for some taxa (Fig. 2). *Betula* consistently had the highest fecundities, with lowest values obtained in stand 5, the only stand having

TABLE 3. Extended.

H_0 : nonlocal dispersal		H_0 : consistent dispersal	
D	P	D	P
70.4	<0.001	9.55	0.023
3.49	0.077	0.0464	0.829
68.4	<0.001	27.7	0
31.0	<0.001	0.822	0.663
79.8	<0.001	3.25	0.197
7.16	0.016
40.7	<0.001	17.5	0.000157
41.6	0.002	2.19	0.334
11.7	0.003	3.47	0.0626
23.0	<0.001
69.6	<0.001	5.47	0.140
4.34	0.11
22.3	<0.001	2.74	0.0981
4.72	0.053	0.190	0.663

substantial *B. alleghaniensis* (Table 1). Fecundities of *Acer* and *Liriodendron* were consistently high. *Acer* fecundity was high and especially uniform across stands 1–4. Seed came from three species. *Acer rubrum* accounted for most seeds in stands 1–4. The few *A. rubrum* trees in stand 5 were not reproductive. *A. saccharum* is dominant at stand 5 (Table 1) and had substantially lower fecundity than *A. rubrum*. *Acer pennsylvanicum* likely contributed some seed in stands 4 and 5. *Carya* and *Quercus* showed consistently low values across all stands, despite differences in species composition for *Quercus*. Other taxa with low fecundity parameters were *Fraxinus americana* and *Pinus rigida*.

Amelanchier, *Nyssa*, *Oxydendrum*, *Tilia*, and *Tsuga* had variable fecundity estimates. The anomalously high fecundity for *Tsuga* in stand 1 is explained by the fact that much seed probably derived from trees outside the sample plot. Stand 1 had only two small *Tsuga* trees. Variable fecundity estimates of *Amelanchier*, *Nyssa*, and *Oxydendrum* are probably due to limited dispersal.

Several taxa had seed rain on stands where trees were absent. Some *Pinus* seed in the higher elevation stands (i.e., other than stand 1) likely derived from nearby

watersheds dominated by *Pinus strobus*. Likewise, *Tsuga* seed was encountered in stand 5. Seed of several tree taxa was rare or absent, including *Amelanchier arborea*, *Robinia pseudo-acacia* (Fig. 2), and *Sassafras albidum* (no seed encountered).

Local seed rain

The summed seed shadow (SSS) model provided consistently good fits for all but a few taxa having especially rare seed, few adults, or both. Likelihood ratio tests led to the rejection of the null hypothesis of uniform dispersal for all but three taxa, two that were rare in the data set (*Amelanchier*: $P = 0.077$, *Robinia*: $P = 0.11$) and one with the most broadly dispersed seed (*Tsuga*: $P = 0.053$). The r^2 values from Table 3 give a rough guide to the proportion of variance explained by the model. These were >0.35 and highly significant for all but *Amelanchier*, *Robinia*, and *Tilia*. Thus, the model leaves much unexplained in the pattern of *Tilia* seed rain, yet it provides a significantly better explanation of the pattern than does uniform seed distribution.

Taxa for which good fits were obtained have well-resolved parameter estimates. Standard errors around dispersion parameters α are generally within 20% of ML estimates for those taxa having significant likelihood ratio tests (Table 3). Standard errors on fecundity parameters β are also within this range for wind-dispersed taxa having large dispersion parameters ($\alpha > 15$ m), with the exception of *Tilia* and *Tsuga*, for which model fits are less good. Poorly dispersed types ($\alpha < 10$ m) are those dispersed by animals. These types have low fecundities, large standard errors on fecundity parameters, and high degrees of clumping ($\theta < 1$). Model fits for several wind-dispersed types (*Acer* in stands 3 and 4; *Betula* in stand 2; *Liriodendron* in stands 2 and 3; and *Tsuga* in stands 1 and 4) have correlations between α and β that exceed 0.6. *Tsuga* is ill-fitted by the model due to rare, well-dispersed seed that occurred sporadically in several stands lacking nearby trees. Although well-described by the model, overlapping seed shadows for *Acer*, *Betula*, and *Liriodendron* mean that parameters tended to compensate in some stands (parameter correlation in Table 3). Low taxonomic resolution may weaken fits for *Quercus*.

Parameter estimates are generally consistent among stands and for different methods. There is variability among stands in β estimates for the same species, but differences among species exceed variability within species. An exception is *Oxydendrum*, which has large differences in β between stands 1 and 3; these differences also apply to plot-average estimates (Fig. 2). β estimates fitted by the SSS model are in good agreement with those obtained from stand average seed rain (Fig. 2, lower right panel). SSS models tend to predict higher β values than do stand averages for the wind-dispersed types, with highest dispersal parameters (α

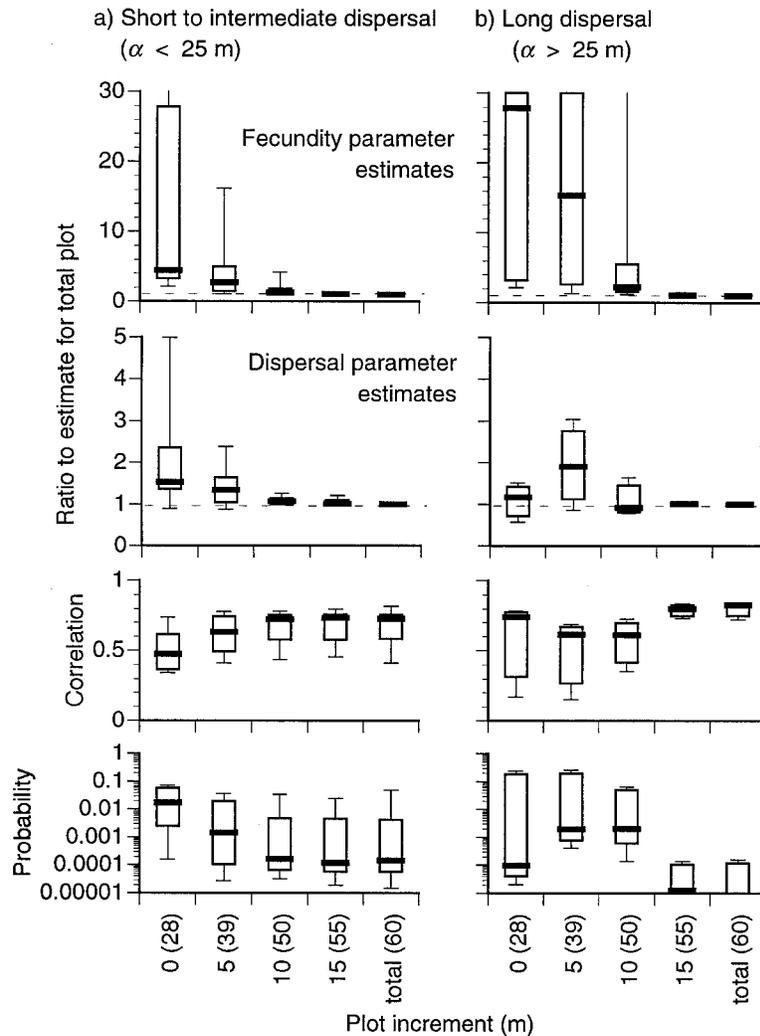


FIG. 3. Effect of increasing sample plot area on bias in parameter estimates. Smallest plot area ("0 m") includes in the parameter estimation only those trees that occur within the central 20×40 m of each stand. Plot-increment labels are followed by geometric mean plot diameters in parentheses. Progressively larger plot areas (up to "total" with geometric mean diameter of 60 m) show the effect of adding trees that occupy increasing dimensions around this inner 20×40 m area. Box plots show median values (thick lines) for all taxa with low (a) and high (b) dispersal estimates, upper and lower quartiles (75% box edges) and deciles (90% whiskers). Upper panels show the ratio of parameter estimates in reduced plot areas to the ML estimate obtained for the total plot. The ratio of 1.0 (i.e., convergence) is indicated by a dashed line. Lower panels are correlations (Eq. 10) and correlation probabilities.

> 15 m) and lowest clumping ($\theta \gg 1$), for *Acer*, *Betula*, *Liriodendron*, and *Tsuga* (Fig. 2).

We failed to reject the null hypothesis of consistent dispersal estimates among stands (i.e., uniform α) for all but three taxa with the highest dispersal estimates and tendency for parameter correlation: *Acer*, *Betula*, and *Liriodendron* (Table 3). In the case of *Acer* and *Liriodendron*, anomalous estimates come from stands with such high densities of trees that seed shadows of individual trees cannot be readily discriminated, a problem most acute for seed that tends to be well-dispersed, but also evident for *Quercus* in stand 3. An anomalously high estimate for *Betula* in stand 4 comes

from a single tree. Consistent estimates from remaining taxa and straightforward interpretations for anomalous fits for these few well-dispersed taxa indicate that dispersal is generally consistent from stand to stand.

By changing the area of mapped plots we found that parameter estimates converged to stable values at plot dimensions smaller than those used in this study (Fig. 3). Fecundity parameters are consistently overestimated when sample plot areas are inadequate, because the model assumes all seed is contributed by mapped trees. Dispersal parameters are also overestimated for undersized plots, because poor fits inevitably tend to converge on broad (nonlocal) dispersal; the model is un-

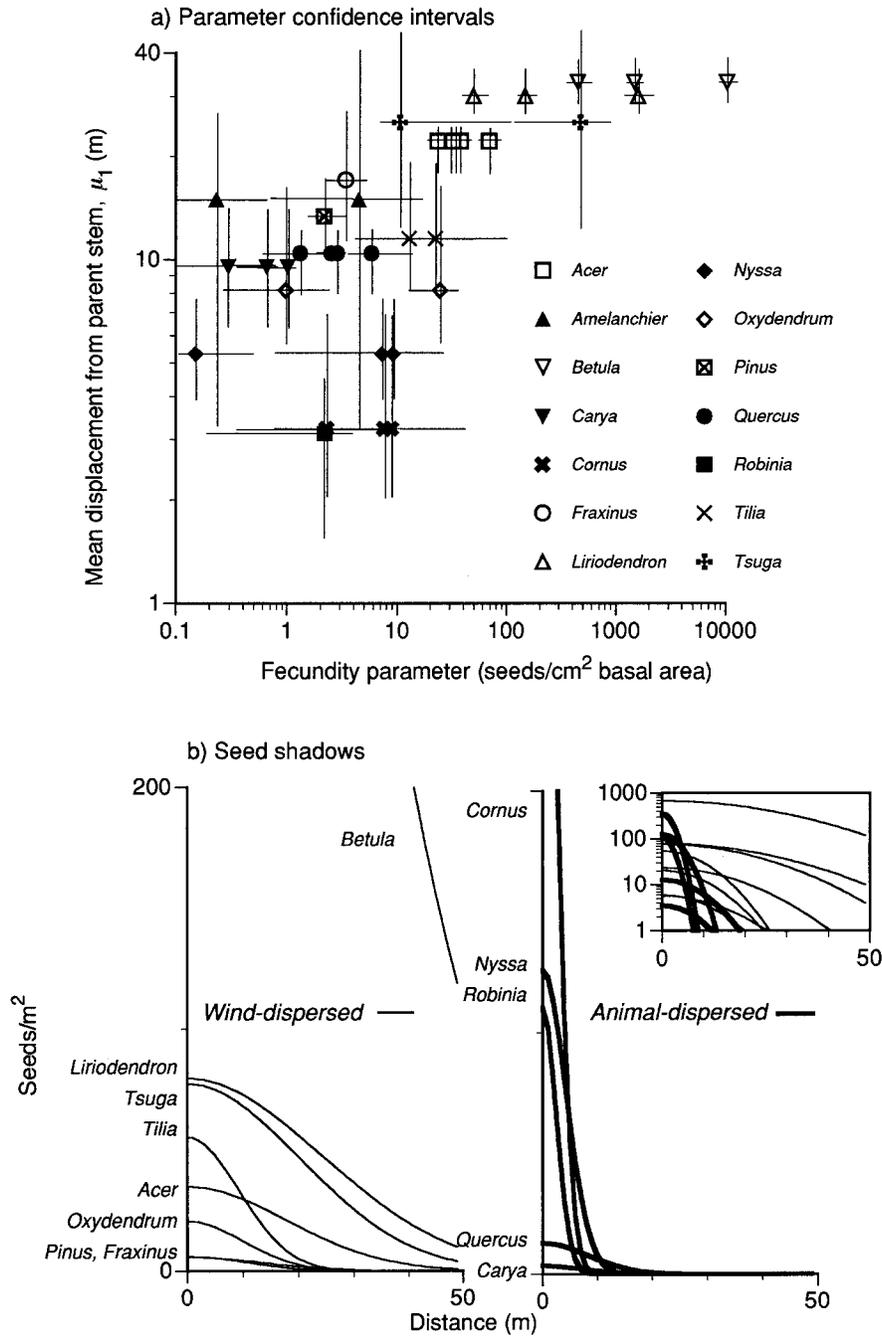


FIG. 4. (a) BC_a 95% confidence intervals for fecundity parameter β and mean displacement of seed from the parent tree μ_1 derived from dispersal parameter α (Eq. 4). The fitted model is Eq. 7, having q estimates of β and a species-specific α estimate. (b) Fitted seed shadows are for a 50 cm diameter tree. Note that animal-dispersed taxa (shaded symbols) have low fecundity and dispersal estimates (a), which results in localized seed dispersal (b) (see log-scale insert).

able to identify the pattern of seed rain based on trees within the map. Fortunately, biases in parameter estimates associated with undersized plots are not hidden; they are flagged by poor model fits. The biased parameter estimates of small plot areas are attended by low correlation between data and model and unacceptably high P values (Fig. 3a, b). The stabilization of param-

eter estimates that is achieved with increasing plot area occurs as median correlations rise to >0.6 and median P values fall to <0.001 . Overcoming parameter bias requires larger mapped plots for better dispersed seed types (Fig. 3b). Parameter estimates for short to intermediate dispersed types converged to stable values within 10 m of the of the interior 20×40 m plot (Fig.

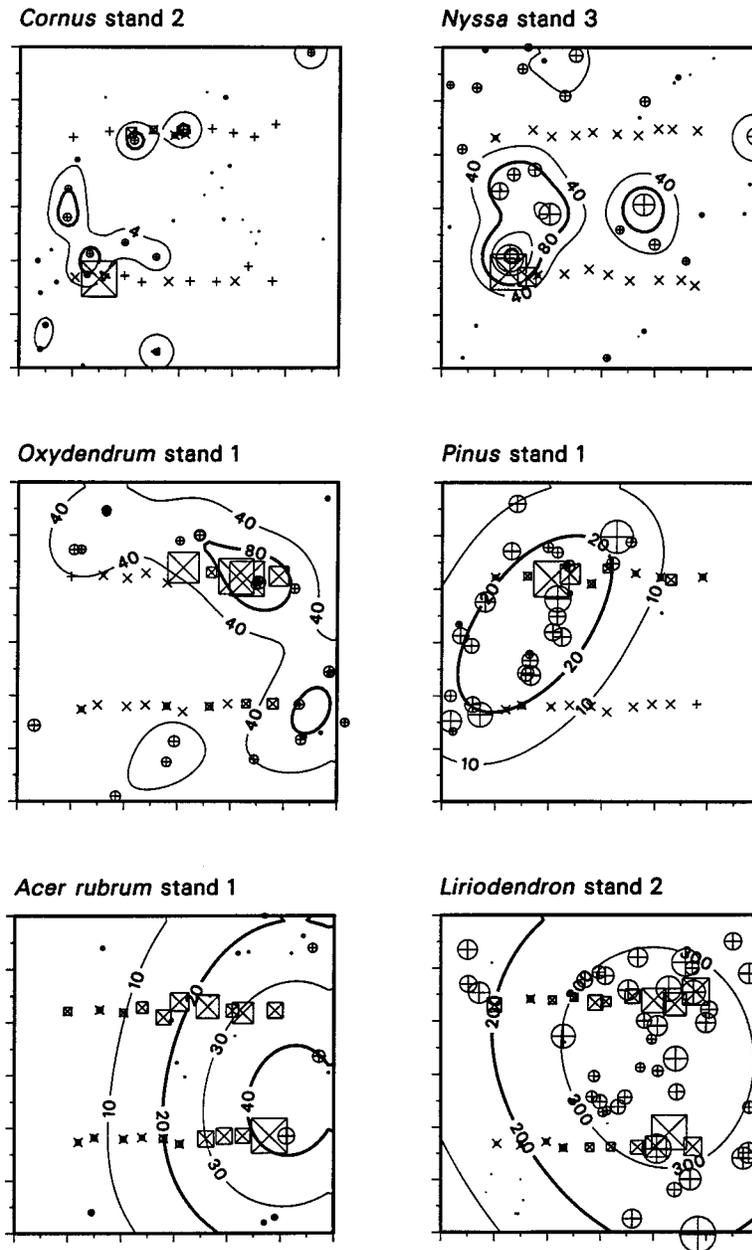


FIG. 5. Maps of trees, seed rain, and fitted seed shadows in mapped stands. Trees are indicated by \oplus scaled to indicate relative sizes of trees. Seed traps that received no seed are indicated by $+$. Seed traps receiving at least one seed over the sample interval are indicated by \times within a box, the size of which is proportionally scaled to seed density. Contour intervals indicate seed rain ($\text{m}^{-2}\cdot\text{yr}^{-1}$) predicted by the model for fitted parameters in Table 3. Taxa are arranged from poorly dispersed (upper left) to well dispersed (lower right).

3a). Plots this size have geometric mean diameters of 50 m, well above the mean seed displacement distances of taxa having $\alpha < 25$ m. Well-dispersed types (*Betula*, *Liriodendron*, *Tsuga*), however, require at least 15 m (Fig. 3b), and these types are still not well-fitted by the model in all stands.

Seed rain modeling revealed large interspecific differences in fecundities and dispersal distances (Fig. 4a) and, thus, in seed-shadow shapes (Fig. 4b). The most

obvious differences are among taxa having different dispersal modes. High fecundity/well-dispersed taxa (*Betula*, *Liriodendron*, and *Tsuga*), contrast with low fecundity/poorly-dispersed taxa (*Amelanchier*, *Carya*, *Cornus*, *Nyssa*, *Quercus*, and *Robinia*) that mostly rely on animal vectors for dispersal. Wind-dispersed taxa with intermediate fecundities (*Acer*, *Fraxinus*, *Pinus*, and *Tilia*) also have intermediate dispersal distances. The dehiscent capsules of *Oxydendrum* have restricted

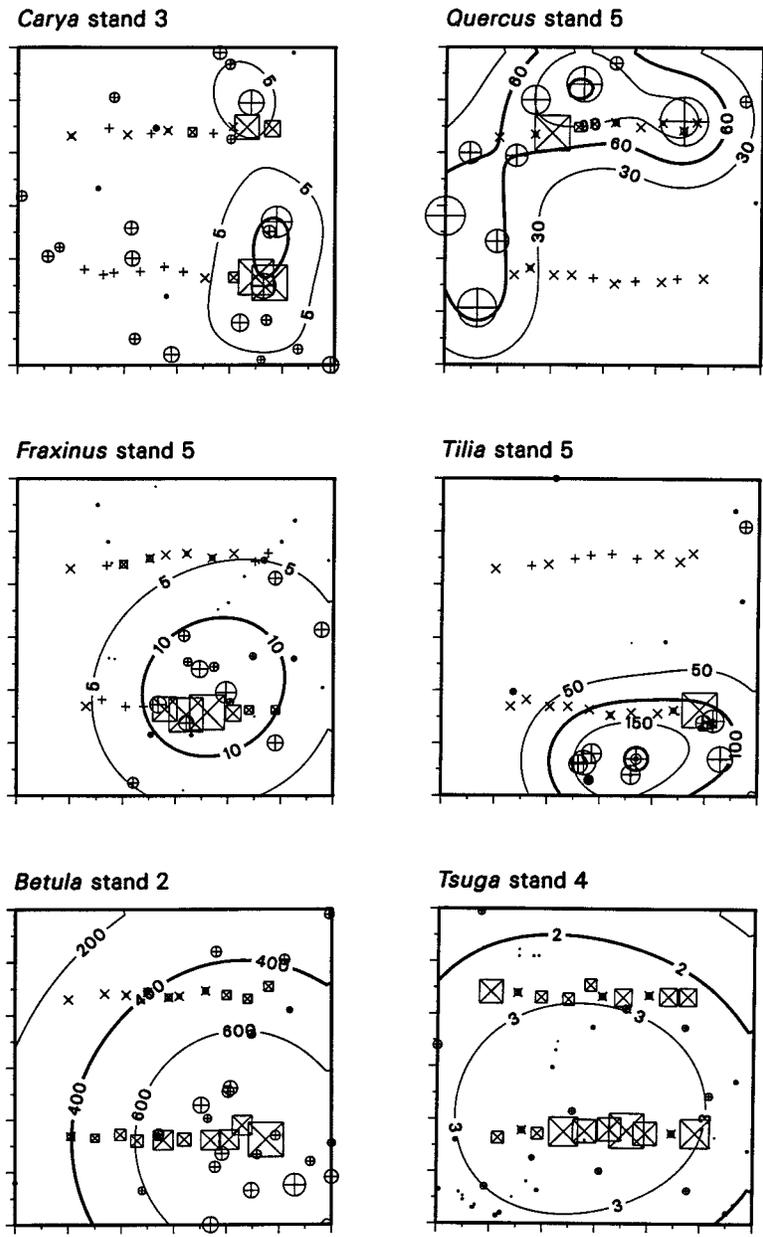


FIG 5. Continued.

dispersal, likely because they lack specialized dispersal structures.

Comparisons of parameterized SSS models with observed seed rain (Fig. 5) demonstrate how nonuniform distributions of trees and restricted dispersal limit seed arrival. Highly restricted dispersal for taxa having mean displacement distance $\mu_1 < 10$ m (e.g., *Cornus*, *Nyssa*, *Carya*, and *Quercus*) leaves much of the ground surface uncolonized by seed, despite abundant adult trees. Thus, seed recovered from these typically animal-dispersed taxa was largely restricted to below the crown area. This restricted dispersal exaggerates dif-

ferences in seed rain among nearby traps. Although not animal-dispersed, *Oxydendrum* capsules also remain close to adult trees. Intermediate dispersal distances were observed for *Pinus*, *Fraxinus*, *Tilia*, and *Acer* (Fig. 5). High seed production of *Acer rubrum* in stand 1 contributed to well-resolved patterns in seed rain.

Maps for *Liriodendron*, *Tsuga*, and *Betula* illustrate potential problems resolving individual seed shadows for well-dispersed taxa (Fig. 5). When seed is evenly dispersed over broad areas, the likelihood surface (Eq. 2) flattens, and parameter resolution is difficult. Despite these limitations, good fits were obtained for both *Lir-*

iodendron and *Betula* on plots where adults were not too dense (Table 3). Maps show that the ground surface becomes saturated with seed in these stands. Although *Tsuga* has relatively high fecundity, our stands contained only small individuals, and seed rain was low and sporadic. We did not capture cones in our traps.

Additional sources of spatial variability in seed rain that are weakly related or unrelated to distributions of adults and dispersal distances cause clumping, described by parameter θ . Clumping is greatest for animal dispersed taxa ($\theta < 1$) (Table 3). Once the variability in seed rain contributed by tree location and dispersal distance is taken into account, the residual variation in well-dispersed types is indistinguishable from a Poisson process ($\theta \gg 1$). There remains, however, much unexplained variation in animal-dispersed seed distributions.

Sources of variability in colonization

The sources of variation that determine the probability of leaving sites unoccupied included densities and fecundities of trees (A and B in Fig. 1), arrangement of trees in stands (A in Fig. 1), dispersal distances (summarized by α), and clumping (summarized by θ), i.e., the dispersion of seed about the mean seed shadow (C in Fig. 1). In the absence of variability conferred by dispersal, differences among stands in colonization indices $C(\bar{s})$ (the odds of at least some seed arrival given that the mean seed arrival \bar{s} is everywhere the same) would depend only on densities and fecundities of adults. $C(\bar{s})$ thus serves as a baseline against which we evaluate colonization limitation that results from restricted dispersal. The dispersal limitation index (Eq. 14) contrasts the odds of seed arrival given the true arrangement of trees and estimated seed shadows \bar{C} (Eq. 13) against that predicted for uniform seed arrival $C(\bar{s})$. This ratio is near unity if seeds blanket much of the ground surface (neither source limitation nor dispersal limitation) or if seeds are well-dispersed but everywhere rare (source limitation only).

The effect of dispersal on colonization in our stands is illustrated with two distributions. The contribution of the mean seed shadow (the contours in Fig. 5) is extracted in Fig. 6 to show how the spread about this mean seed shadow controls \bar{C} . The seed shadows for *Acer*, *Cornus*, and *Tsuga* are each the means of (negative binomial) distributions \hat{s} that decrease with distance (right-hand side of Fig. 6). In the absence of any spread about the mean, the distribution of seed arrivals across the stand would be $g(\hat{s})$ (thick line on left-hand side of Fig. 6). The spread about \hat{s} in Fig. 6 contributes variance to seed arrivals, described by a probability distribution of seeds:

$$p(s) = \sum_{\hat{s}=0}^{\infty} p(s|\hat{s}, \hat{\theta})g(\hat{s}) \quad (15)$$

where $p(s|\hat{s}, \hat{\theta})$ is a negative binomial distribution describing the conditional probability of s seeds given

expectation \hat{s} and clumping $\hat{\theta}$. Note that $\bar{C} = 1 - p(0)$. Thus, in the case of *Acer* (Figs. 5, 6a, all 1-m² patches in stand 1 are predicted to receive, on average, >1 seed-m⁻²·yr⁻¹ (distribution $g(\hat{s})$), yet the additional variability about mean seed shadows (Fig. 6a) means substantial probability for seed densities lower than this value ($p(s)$). Two other examples in Fig. 6 include contrasting dispersal types *Cornus* (Fig. 6b) and *Tsuga* (Fig. 6c). Poor dispersal for *Cornus* means that most 1-m² patches receive, on average, no seed, and high clumping serves to further reduce colonization (i.e., it increases $p(0)$). *Tsuga* is relatively rare in stand 4, yet so well-dispersed, that all patches are expected to receive two to three seeds each year ($g(\hat{s})$ in Fig. 6c). Despite minimal clumping, however ($\theta \gg 1$ in Table 3), the spread about the mean seed shadow is still enough to yield measurable probability of no seed arrival $p(0)$.

Dispersal and source limitations (Fig. 7) are correlated with dispersal distance and fecundity, and they depend on spatial pattern of trees. The odds of 1-m² patches receiving at least some seed are high for fecund and well-dispersed *Acer*, *Betula*, *Liriodendron*, and *Tsuga* in all stands where trees are present, and, thus, colonization is as successful as it would be with unlimited dispersal (dispersal limitation near zero in Fig. 7). *Tsuga* is the only well-dispersed taxon having consistently low colonization indices (Fig. 7), due to few adults. Colonization indices are high for some poorly dispersed taxa *Quercus*, *Nyssa*, and *Oxydendrum* in stands where parent trees were abundant. Restricted dispersal especially limits poorly dispersed and less abundant *Amelanchier*, *Carya*, *Cornus*, and *Robinia* (Fig. 7). Restricted and clumped dispersal explain low *Carya* and *Cornus* indices, while source limitation (rather than restricted dispersal) is the primary cause for low colonization indices in other taxa in particular stands, including *Nyssa*, *Quercus*, *Tilia*, and well-dispersed *Tsuga*.

Establishment relative to other limitations at the stand scale

Over the five years of seedling censuses, total seedlings and, especially, newly emerged seedlings were rare. 1st-yr seedlings were sufficiently rare that we were able to estimate establishment fractions (1st-yr seedlings divided by seed rain) for a limited subset of species present in the overstory. Establishment fractions were highest for *Acer*, ranging from 0.019 (stand 4) to 0.87 in stand 2 (Fig. 8a). Seedlings in stand 5 were mostly *Acer pensylvanicum*, and they were abundant in only one of the five sample years.

Limitations on *Acer rubrum* recruitment vary across the five stands. Seedling recruitment appears limited by source density (basal area) on low elevation stands 1 and 2; seed rain is proportional to basal area (Fig. 2), implying that increased basal area would result in increased seed density. Establishment does not limit

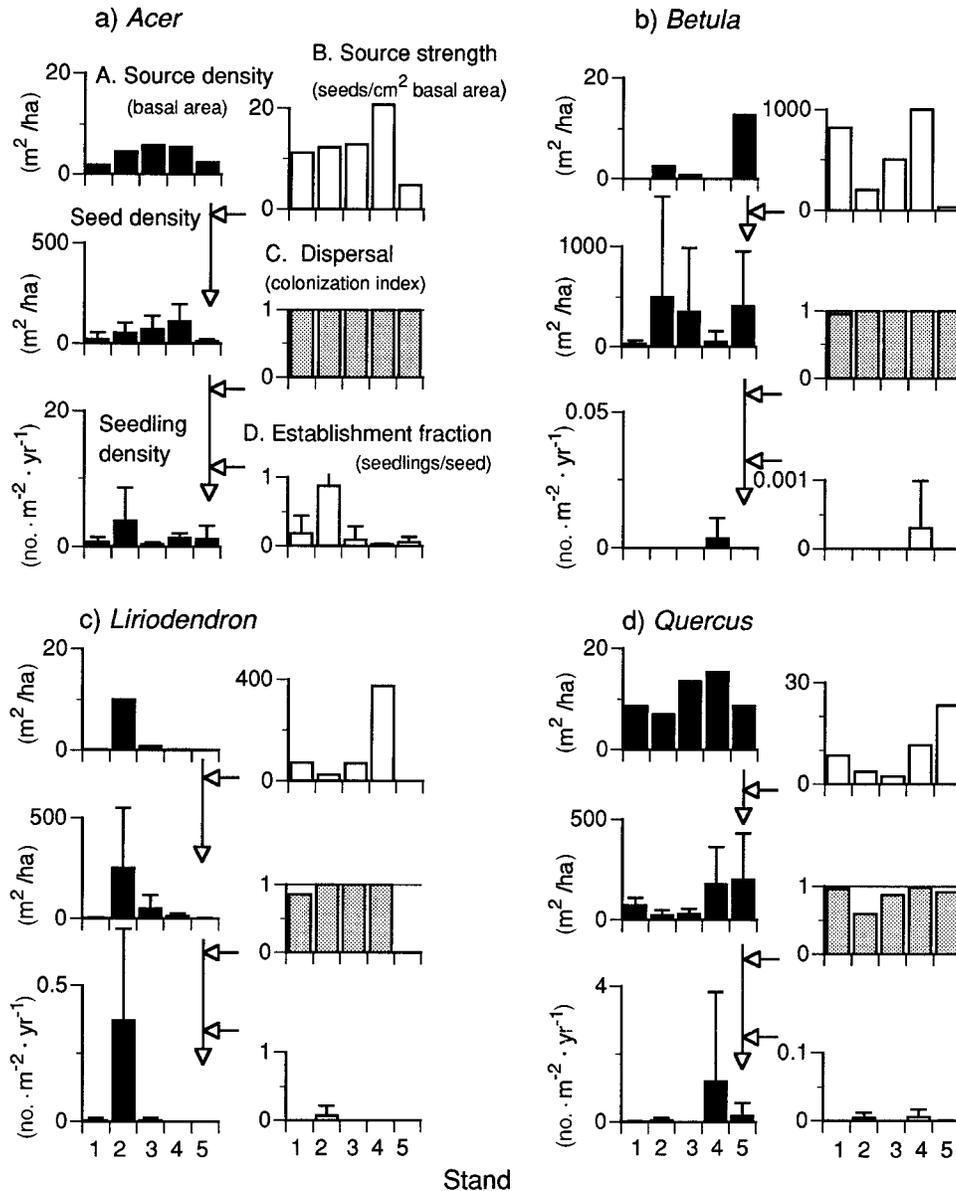


FIG. 8. The four limitations on recruitment summarized in Fig. 1 for four taxa having at least some seedlings across the five stands. Solid bars indicate densities of individuals at three stages (adults, seeds, and seedlings). Unshaded bars indicate three limitations that determine transition rates from one stage to the next.

recruitment in the cove hardwoods stand 2, where >80% of seeds become 1st-yr seedlings, but establishment is a strong limitation on all other stands, especially at higher elevations (stands 3, 4, and 5). *Acer saccharum* has a source of seed only at stand 5. Limitations in seed production and in establishment both appear important here.

Betula is limited in all stands by establishment success (Fig. 8b). High fecundity and long dispersal blanket all stands with seed. Even stand 1, which includes only three small trees, has higher *Betula* seed rain than of most other taxa. First-year seedlings are absent from

all stands but 4, and their establishment fractions are less than one seedling in 1000 seeds.

Liriodendron limitation varies substantially among stands. Source trees and establishment are important limitations in xeric (stand 1) and upper elevation (stands 4 and 5) stands (Fig. 8c). Both source density and establishment fraction are high in the cove hardwood stand 2, indicating conditions amenable for *Liriodendron* seedlings and adults. The low colonization index in stand 1 results from lack of source trees, rather than short dispersal.

Establishment and dispersal are principal limitations

on *Quercus* recruitment. Adult trees are everywhere abundant, insuring moderate seed rain across all stands. Poor dispersal of that seed, however, means that much of the stand area receives little or no seed. Establishment fraction is highest in stand 4 (0.0054) and nearly nonexistent elsewhere. The 5-yr average fraction used here yields low fecundity estimates that belie high seed production in most years (years one and five of this analysis).

Despite lack of seedlings, colonization indices for other taxa permit interpretation of how density of source trees, dispersal, and clumping contribute to recruitment limitation. Low colonization indices for *Amelanchier*, *Carya*, *Cornus*, *Nyssa*, *Oxydendrum*, and *Robinia* suggest that even if suitable microsites were available, these taxa would fail to colonize due to lack of seed.

Establishment limitation at the local scale

Analysis of the relationship between seed rain and seedling recruitment at the local scale was hindered by the low density of seedlings found at our site. Only *Acer* seedlings were sufficiently abundant to permit comparisons between predicted seed rain and 1st-yr seedling density at the 1-m² scale. For this genus, no consistent relationship is apparent between seed rain and seedlings, with cross correlations between seeds and seedlings at lags <10 m being weak or absent in all stands (Fig. 9). With the high fecundity and intermediate dispersal of *Acer*, few safe sites would likely be left uncolonized (Fig. 7). If 1st-yr seedling pattern merely reflects the distribution of safe sites, little relationship between seed rain and 1st-yr seedling density would be expected.

Local regression (Cleveland and Devlin 1988) between predicted seed rain and 1st-yr seedlings taken across all stands suggests a weak positive association between seeds and seedlings at low seed density (Fig. 10). This suggests that colonization of safe sites is proportional to seed density when the flux of seeds is low, but that density-dependent seed predation or seedling mortality may limit 1st-yr recruitment when seed density is high and/or seeds and seedlings are close to conspecific adults.

DISCUSSION

In contrast with the growing tendency to treat tree population dynamics as though seeds are always available, we found that all tree populations in our study area face substantial recruitment limitation. The stage(s) at which limitation occurs varies considerably. We found that limitations from source density, source strength, dispersal, and establishment vary among species, within species across environmental gradients, and across different scales of measurement. Few of the tree populations in our study area are capable of saturating the forest floor with seed. Only a small fraction of that seed germinates and survives to be censused in

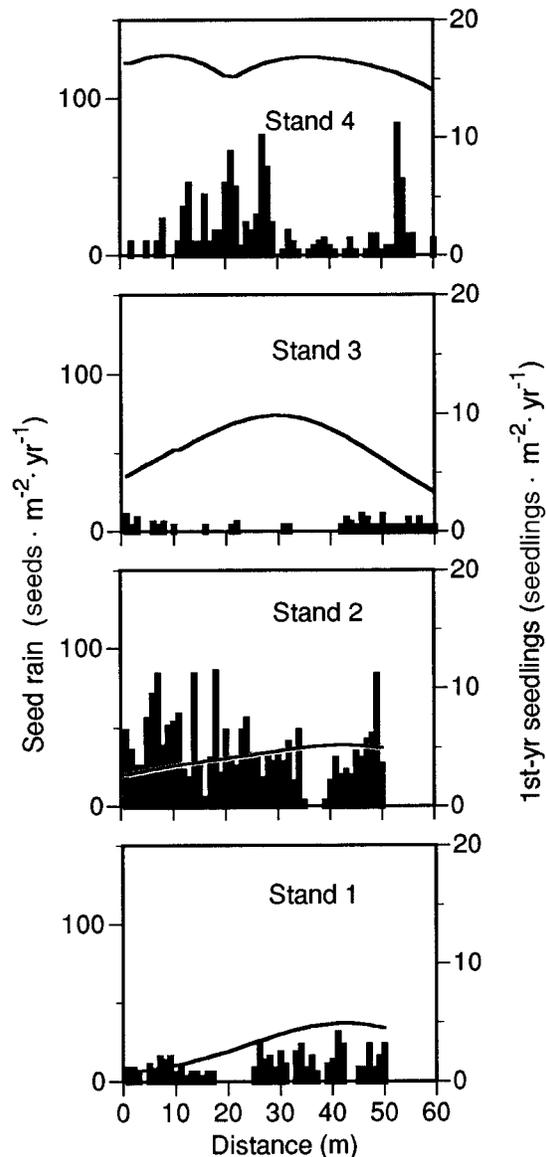


FIG. 9. The relationship between *Acer* seed rain predicted by the parameterized model and seedlings across the four stands (smooth curve) compared with seedlings in 1-m² contiguous census plots (bars).

the first year. Distributions of seedlings in our study site provided little indication of which stages were responsible for poor recruitment. Before considering the magnitudes of these limitations, we first discuss the advantages and limitations of this method for identifying stages that limit reproduction in tree populations.

How to fit seed shadows in closed stands

Tracking dispersal of falling seeds as the basis for interpreting how seed arrival controls recruitment involves several obstacles. The statistical estimation of fecundities and dispersal from trees having overlapping crowns is complicated by high temporal and spatial

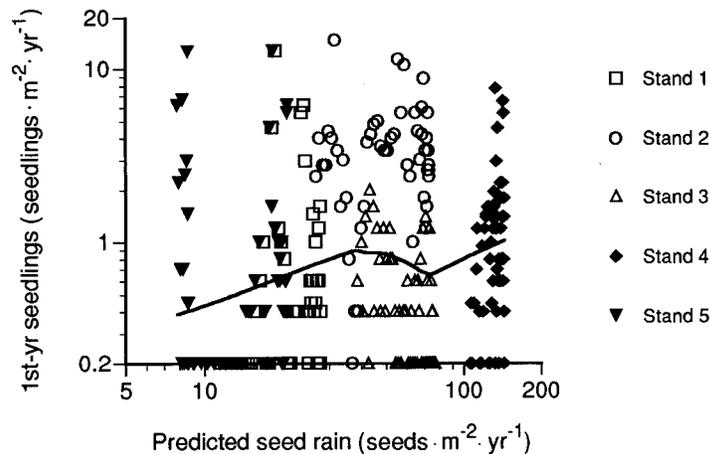


FIG. 10. Locally weighted (LOWESS) regression for combined data in Fig. 9.

variability contributed by factors other than dispersal. Our results provide some guidance for handling statistical challenges pertaining to sampling and analysis. Lack of conventional models for parameter estimation and hypothesis testing led us to introduce evaluation procedures for bias in estimates, comparison with alternative models, and parameter consistency that should simplify recruitment analysis in future studies.

The data: how much and where to sample?—Equipped with little more than vague notions of seed production and dispersal distances and with knowledge that seed shadows must strongly overlap, the first problem we encountered concerned sampling, i.e., numbers of seed traps and how to distribute them within and among stands. Intervals of 5 m between traps distributed over areas of 10^3 m² worked reasonably well, giving good parameter estimates for both poor- and well-dispersed taxa. Mapped plot areas of trees with mean diameters twice as large as the mean seed-displacement distances may be a rule-of-thumb minimal plot area (Fig. 3). This limit is approached by our best dispersed taxa; they are the only taxa tending toward parameter correlation and inconsistent dispersal estimates (Table 3). The inclusion of multiple stands proved invaluable for our model parameterization, for it afforded different densities and arrangements of trees. Multiple stands were the basis for both of the hypothesis tests.

What sort of a spatial process is seed dispersal?—Inability of a Poisson model to describe the clumped pattern of seed arrival led us to implement (and, now, recommend) a negative binomial (Eq. 2). A model including the many sources of variation responsible for clumping would require a far greater number of parameters than could be fitted with realistic data sets. We simply acknowledged that many sources are probably operative, which led us to the negative binomial. We obtained much lower error on fecundity and dispersal parameters using the negative binomial (Fig. 4) than with alternative distributions. The model also permitted comparison of clumping differences among taxa

(Table 3). For animal dispersed taxa clumping has a large influence on colonization rates.

How to sort out the overlapping crowns?—The solution to the overlapping crown problem, independently derived by Ribbens et al. (1994), is to add them together (Eq. 6). By estimating contributions of individual trees to any location on the forest floor, the method is, thus far, the sole broadly applicable approach for analyzing the link between recruitment and the population of adults responsible for producing those recruits. Dispersion patterns of seeds or seedlings around isolated adults provide valuable insights (Sharpe and Fields 1982, Johnson 1988, Guevara and Laborde 1993), but dispersal distances in open fields differ from those in closed canopies (Willson 1993), and the approach cannot be applied where seed shadows of conspecific trees overlap. Nevertheless, the conceptual simplicity of the model and small number of parameters belie some statistical challenges.

Model evaluation: defining some conventions.—Because conventional methods provide little guide to model evaluation, our approach was to stay close to convention by way of analogy. The r^2 between model and data (Table 3) is a rough guide to explained variation. Tests of hypotheses that local dispersal better explains pattern than does evenly distributed seed, and that dispersion parameters are consistent among sites, provide a basis for model evaluation. These tests contributed to our conclusion that sample plots were near the minimum size needed to parameterize seed shadows of the best dispersed taxa. For example, *Betula* showed excellent agreement between model and data ($r^2 = 0.68^{***}$), was clearly identified as local dispersal ($P < 0.001$), yet produced inconsistent dispersal parameter estimates across sites ($P = 0$). Together, these results suggest the fit might be improved with larger mapped plots for *Betula*. *Tilia* was not well-described by the model ($r^2 = 0.11$, NS), yet the model was clearly a better description of seed rain than was the alternative that seed rain is independent of trees ($P < 0.001$), and

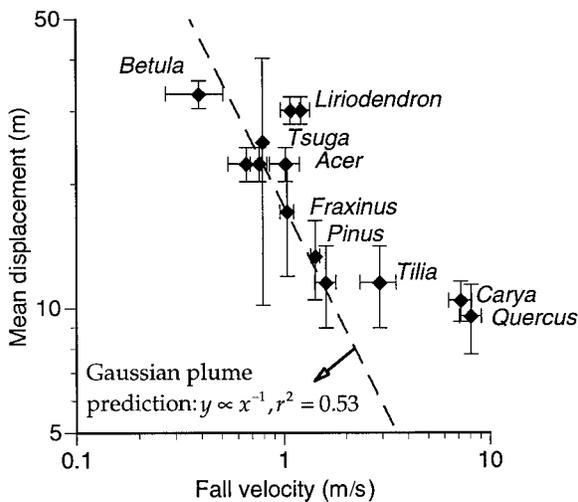


FIG. 11. Mean displacement of wind-dispersed seed taxa and fall velocities measured in studies cited in text and (for *Carya* and *Quercus*) from J. HilleRisLambers (personal communication). A Gaussian plume model predicts that modal dispersal distance is roughly proportional to the inverse of fall velocity (Okubo and Levin 1989).

dispersal estimates were consistent among stands ($P = 0.0981$). These results suggest the fit for *Tilia* would be improved with a larger data set, e.g., more traps and/or longer collection period. In remaining cases, the agreement between indices (acceptable explained variance, local dispersal, and consistent dispersal estimates) indicate that the model provides a good description of seed shadows.

How good are the estimates?—Although parameters were well-resolved by the model and generally consistent across stands (α 's in Table 3) and scales (β 's in Fig. 2), we find further support from evidence external to our data sets. Our dispersion estimates generally agree with measured fall velocities from other studies, and they match the prediction of Gaussian plume models that modal distance is roughly proportional to the inverse of fall velocity (Fig. 11). Rolling samaras of *Fraxinus* have higher fall velocities than nonrolling *Acer* (Green 1980), in agreement with the relationship we found between α values. Heavy *Tilia* clusters attached to large bracts have higher fall velocities than *Acer* (Matlack 1987), consistent with estimated low α values for *Tilia*. High dispersal for *Betula* agrees with its low measured fall velocities. Our low-dispersal estimates for animal-dispersal taxa (Fig. 4) are consistent with lack of specialized structures for wind dispersal. The high-dispersal estimates we obtained for *Liriodendron* contrast with relatively rapid descent for these rolling samaras (Green 1980). *Liriodendron* trees tended to be taller than other species of similar diameter. Dispersal distance is expected to increase with release height (Okubo and Levin 1989, Willson 1993). Because models like ours consider only diameter, and not height, long dispersal for *Liriodendron* might reflect allometry.

What limits recruitment?

Summed seed shadow models demonstrated substantial differences among species within different stands in limitations due to source density (parent tree abundance), source strength (fecundity), dispersal, and establishment limitation.

Source density: number, sizes, and dispersion of adults.—Absence of parent trees was a limitation on seed arrival for the many taxa that are rare in our stands (Table 1). The importance of a nearby source obviously depends on dispersal distance (Figs. 4, 5). Because adults were often clumped within stands, source density limited seed availability not only for poorly dispersed taxa, but also for some taxa with well-developed structures for wind dispersal. Low adult density, clumping of adults, or both, meant that seed did not reach much of the ground surface for *Carya*, *Cornus*, *Fraxinus*, *Liriodendron*, *Nyssa*, *Quercus*, *Pinus*, *Tilia*, and *Tsuga* in some or all stands (Figs. 5, 7); only *Acer* and *Betula* seed consistently blanketed the forest floor in sufficient density to insure high colonization indices (Fig. 7). The parameterized model demonstrates that the abundance and contagion of adults combined with local dispersal is the cause of this limitation.

Source strength: rates of seed production.—Orders of magnitude differences among taxa in their fecundities tended to compound limitations produced by limited dispersal. Correlation between fecundity and dispersal (Fig. 4) means that taxa producing few seeds dispersed seed short distances. Little tendency for positive parameter correlations (Table 3) means that such correlation is not by chance. And the agreement between fecundity estimates at two scales (Fig. 2) suggests that the correlation is not spurious but results from a tendency for seed number to trade off with seed size (Smith and Fretwell 1974, Salisbury 1976, Geritz 1995). This is a likely explanation for the differences between animal- and wind-dispersed taxa. Although empirical evidence for this relationship within these two dispersal modes is not strong (Greene and Johnson 1986, Primack 1987), there is a clear tendency for the wind-dispersed taxa with low dispersal to also have lower seed production in our study (Fig. 4). We did not estimate seed viability, but low viabilities of many taxa would reduce fecundity estimates. These can be less than 5% for *Acer rubrum* and *Tsuga canadensis* in New Hampshire (Graber and Leak 1992) and *Tilia americana* in Wisconsin (Godman and Mattson 1976) and range from 5–70% for *Acer pensylvanicum*, *A. saccharum*, and *Betula alleghaniensis* (Houle and Payette 1990, Graber and Leak 1992, Houle 1992b). Animal-dispersed seed can also have low germination rates (Smith 1975).

Dispersal.—Dispersal limitation was taxon-specific and explained by seed morphologies that increase drag and (for spinning samaras) generate lift (Green 1980, Augspurger 1986, Matlack 1987) or that attract animal

vectors (Howe and Smallwood 1982, Willson et al. 1990, Martínez-Ramos and Soto-Castro 1993). Our results imply that recruitment of *Carya*, *Cornus*, *Nyssa*, and *Quercus* is limited by dispersal throughout our study area. High frequency of adult trees did not result in seed arrival to much of the forest floor (Fig. 8d). Animal vectors are the sole means for moving seed outside the perimeters of tree crowns for some taxa. Like Masaki et al. (1994), we found the bulk of seed directly below crowns and scattered arrivals elsewhere.

Establishment.—Establishment limitation is among the strongest filters on recruitment for many taxa on different parts of the Coweeta watershed. Few taxa had 1st-yr seedlings achieving densities as high as 5 seedlings/m² (Fig. 8). The only one that did so consistently (*Acer rubrum*) (Fig. 8a) had seedlings poorly correlated with seed shadows (Fig. 9b,c). Environmental gradients appear to have governed establishment limitations at several scales. Fine-scale variability within sample plots appears responsible for altering seedling distributions after seed arrival (Fig. 9). This difference between seed rain and seedling distributions is expected if germination (for 1st-yr seedlings) or seedling survival (for older seedlings) depends on suitable microsites that are poorly correlated with the distribution of parent trees (e.g., Nakashizuka 1989, Houle and Payette 1990, Houle 1992a, Shibata and Nakashizuka 1995). Even for late-successional *Acer saccharum* and *Betula alleghaniensis*, our germination percentages were far lower than viabilities estimated in New Hampshire (Graber and Leak 1992). Although we only considered here 1st-yr seedlings, survival rates of these seedlings were low for a combination of reasons now under investigation.

Implications for forest communities

Our analysis supports the argument that conventional assumptions concerning recruitment limitation (or lack thereof) in forests are overly simplistic (Clark 1993, Pacala and Hurtt 1993, Schupp 1993). Factors controlling seed arrival, including distribution and abundances of adults, fecundities, and dispersal distances, all vary substantially among species. While previous studies demonstrate large species-specific differences for primarily animal-dispersed taxa in tropical forests, we show this also to be the case in temperate forests containing mostly wind-dispersed taxa having overlapping crowns. The relatively high densities of canopy individuals in relatively low-diversity forests (compared to the tropics) does not necessarily mean that seed reaches much of the soil surface. Establishment limitation varied considerably among species, and the relative importance of all limitations varied across environmental gradients. These differences mean that the limitations imposed by the recruitment process are likely to be an important factor affecting diversity in forests, patterns of species composition within stands, and distributions of species across environmental gradients.

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