



Promoting the Science of Ecology

---

Seedling Recruitment in Forests: Calibrating Models to Predict Patterns of Tree Seedling Dispersion

Author(s): Eric Ribbens, John A. Silander, Jr., Stephen W. Pacala

Source: *Ecology*, Vol. 75, No. 6 (Sep., 1994), pp. 1794-1806

Published by: Ecological Society of America

Stable URL: <http://www.jstor.org/stable/1939638>

Accessed: 21/08/2009 13:37

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/action/showPublisher?publisherCode=esa>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is a not-for-profit organization founded in 1995 to build trusted digital archives for scholarship. We work with the scholarly community to preserve their work and the materials they rely upon, and to build a common research platform that promotes the discovery and use of these resources. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).



Ecological Society of America is collaborating with JSTOR to digitize, preserve and extend access to *Ecology*.

<http://www.jstor.org>

## SEEDLING RECRUITMENT IN FORESTS: CALIBRATING MODELS TO PREDICT PATTERNS OF TREE SEEDLING DISPERSION<sup>1</sup>

ERIC RIBBENS, JOHN A. SILANDER, JR., AND STEPHEN W. PACALA<sup>2</sup>

*Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269-3042 USA*

**Abstract.** Recruitment, the addition of new individuals into a community, is an important factor that can substantially affect community composition and dynamics. We present a method for calibrating spatial models of plant recruitment that does not require identifying the specific parent of each recruit. This method calibrates seedling recruitment functions by comparing tree seedling distributions with adult distributions via a maximum likelihood analysis. The models obtained from this method can then be used to predict the spatial distributions of seedlings from adult distributions.

We calibrated recruitment functions for 10 tree species characteristic of transition oak–northern hardwood forests. Significant differences were found in recruit abundances and spatial distributions. Predicted seedling recruitment limitation for test stands varied substantially between species, with little recruitment limitation for some species and strong recruitment limitation for others. Recruitment was limited due to low overall recruit production or to restricted recruit dispersion. When these seedling recruitment parameters were incorporated into a spatial, individual-based model of forest dynamics, called SORTIE, alterations of recruitment parameters produced substantial changes in species abundance, providing additional support for the potential importance of seedling recruitment processes in community structure and dynamics.

**Key words:** dispersion; maximum likelihood statistics; oak–northern hardwood forest; seedling recruitment limitation; SORTIE.

### INTRODUCTION

Recruitment is the entry of new individuals into a population or community. Such entry has been considered to occur at stages ranging from entry into the seed bank to attaining a set diameter at breast height to entering the forest canopy. Any restriction on the entry into a new stage in the natural history of a species has the potential to alter community dynamics, but should be identified as recruitment for that specific stage (e.g., canopy recruitment, Canham 1990, Fulton 1991). We define a seedling recruit as a propagule that has germinated and is able to survive without maternal resources. This stage is frequently ignored, but, as we will show, is an important component of forest community dynamics.

Limited recruitment can exert dramatic effects on the composition and abundance of plant communities (Leak and Graber 1976), and such recruitment limitation may operate at different spatial and temporal scales. On a stand-level spatial scale, recruitment can be limited due to the low production of recruits (e.g.,

Graber and Leak 1992). Furthermore, even if there are numerous recruits present on a stand-level basis, recruitment limitation can still influence community dynamics if dispersal processes constrain the locations of recruits. Additionally, temporal fluctuations in plant seedling recruitment can occur due to year-to-year variability in propagule production (i.e., masting, see Godman and Mattson 1976, Graber and Leak 1992).

Several theoretical studies have examined the potential significance of recruitment limitation in plant communities. Spatial recruitment limitation has been theoretically demonstrated to be a mechanism promoting coexistence among competing plant species (e.g., Abrams 1984; G. C. Hurtt and S. W. Pacala, *unpublished manuscript*). Warner and Chesson (1985) proposed that temporal recruitment limitation could increase coexistence of competitors, and Ellner and Shmida (1981) suggested that temporal recruitment limitation may be a selective mechanism in desert plant populations. However, temporal variation is often overlooked, and too many ecological investigations still assume that random events dominate spatial processes in seedling locations, despite the implausibility of this assumption (Hamill and Wright 1986).

Two issues to be resolved are: what are the numbers of seedling recruits produced by an adult, and what are the spatial locations of these recruits? Despite the amount of attention that has been focused on com-

<sup>1</sup> Manuscript received 12 March 1993; revised 17 December 1993; accepted 20 December 1993; final version received 24 January 1994.

<sup>2</sup> Present address: Ecology and Evolutionary Biology, Princeton University, Princeton, New Jersey 08544 USA.

ponents of seed dispersal, rarely have attempts been made to quantify spatial seedling recruitment distributions or calculate seedling production as a function of adult size. Several studies have mapped seed rain or seedling distributions around isolated adults (e.g., Cremer 1966, Augspurger 1983, Manders 1986, Hoppes 1988, Johnson 1988), although none of these studies were performed in northern hardwood forests. Such isolated trees are difficult to find, especially in low-diversity forests, and these studies assume that the recruitment processes associated with isolated individuals are representative of the species. Furthermore, it must be assumed that even though the adult is isolated, its ability to produce recruits is the same as an individual in a larger population. However, isolated individuals will vary considerably in their ability to attract pollinators, seed predators, or dispersal agents, and isolated individuals may reflect the effects of an adverse abiotic environment.

Clearly seed dispersal patterns are a critical component of spatial variation in plant seedling recruitment. The importance of proximity to the parent in determining abundance and locations of seeds is well known (e.g., Schaal 1980, Hughes and Fahey 1988, Campbell et al. 1990). Secondary dispersal and post-dispersal seed predation (sensu Janzen 1970 and Connell 1971) can then substantially alter the shape of the primary seed dispersal profile (e.g., Howe et al. 1985, Schupp 1988), but often the result of seed predation is highly variable, and therefore is not easily predicted (Hamill and Wright 1986). Even with post-dispersal seed predation, the intensity of seedling recruits is usually highest adjacent to the parent and declines with increasing distance (Hubbell 1980).

We provide a framework for producing and testing field-calibrated models of recruitment which quantify the distribution of recruits around adults. Our technique can be used to analyze recruitment processes in forest communities and many other types of plant communities as well. Our approach is direct and requires only easily obtained field data. It does not require the identification of the specific mother of each recruit and does not require an a priori determination of the specific nature of offspring-parent spatial relationships. Therefore, we have avoided the need to collect data from isolated individuals. The heart of our technique is the use of maximum likelihood analysis of field data to identify parameter values for functions which describe recruitment distributions. In this paper, we present calibrated functions for 10 tree species derived from field data obtained in northwestern Connecticut and western Michigan. We show that seedling recruitment functions vary considerably between species and that the potential for seedling recruitment limitation is very real, even in low-diversity forests. Finally, we show that seedling recruitment limitation has an important impact on the structure and dynamics of the forests we examined.

## METHODS

### *Species and sites*

Most data used to calibrate our recruitment models were obtained from the Great Mountain Forest (GMF), a privately owned 2500 ha forest tract located in Norfolk and Canaan, Connecticut. This forest is a transition oak-northern hardwood forest. Additional data were collected from a forest stand with a similar species composition located north of Ludington, Michigan. Both sites are well-developed forests between 90 and 130 yr old.

Data were collected for 10 codominant or subdominant tree species, encompassing several modes of seed dispersal. The wind-dispersed species examined are red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), white ash (*Fraxinus americana* L.), white pine (*Pinus strobus* L.), and eastern hemlock (*Tsuga canadensis* (L.) Carr.). Black cherry (*Prunus serotina* Ehrh.) is primarily dispersed by birds. White oak (*Quercus alba* L.) and red oak (*Quercus rubra* L.) produce large seeds dispersed by a variety of small mammals and birds. Finally, American beech (*Fagus grandifolia* Ehrh.) also produces large edible seeds, but throughout much of its range it reproduces largely via root sprouts (Held 1983, Jones and Raynal 1986).

### *Field data*

Data were collected from belt transects running through mixed stands of adult trees. The transects were randomly oriented, were composed of successive 1-m<sup>2</sup> quadrats, and ranged in length from 80 to 400 m. The length of the transects was dictated by logistics of avoiding disturbances and unsuitable patches (such as bogs or logging roads) and ensuring that we encompassed spatial variation in adult abundances. Spatial coordinates and the number of recruits for each species were recorded for each successive 1-m<sup>2</sup> block along the transect. A total of 2047 quadrats were sampled, and >6000 recruits were recorded. For most species, we restricted our definition of a recruit to seedlings that had germinated during the current year and thus had not undergone a winter dormancy. Because we were not able to locate adequate numbers of seedlings for white oak and sugar maple, we expanded our definition of recruits for these species to include any individual <25 cm tall. We have obtained adequate samples of both beech seedlings and beech root sprouts, so we analyze beech recruitment separately for root sprouts and for seedlings.

The location and size of each adult potentially contributing to the seed pool in the vicinity of the transect was recorded by mapping every individual within 20 m of the transect that had a diameter at breast height (dbh; 1.4 m above ground) of 10 cm or more. Smaller individuals were presumed to produce few or no recruits. Mapping individuals beyond this distance from

the transect becomes increasingly difficult and time consuming, and for most species significant correlations were obtained when adults were mapped only to 20 m. Because white ash is a dioecious species (Burns and Honkala 1990), the sex of each individual white ash was determined, and males were excluded from the data analysis.

These data were collected in 1991–1993. From these data, we were able to construct recruitment models for all 10 species. Replicate data sets were obtained for hemlock, white oak, red oak, and red maple, providing a measure of stand-level variation in seedling recruitment.

#### DEVELOPMENT OF RECRUITMENT MODELS

##### *The recruitment function*

Our method joins a function that predicts seedling distributions with a maximum likelihood method that determines the probability that the predictions match the observed seedling numbers. The model parameters are then altered with an algorithm that converges on those values that best match observed with predicted distributions (i.e., maximizes the likelihood).

We predict recruitment (the number of seedling recruits per unit area) as following a Poisson distribution (commonly used for the distribution of counts), where the mean of the Poisson distribution is a function of the parental size (dbh) and distance from the parent, for all parents within a radius of 20 m. The function determining the mean of the Poisson consists of two components. The first component represents the total number of recruits produced by a single parent tree, and the second component determines the proportion of those recruits that are located in a given quadrat in the vicinity of the parent tree. The first component,

$$\text{STR} \cdot \left(\frac{\text{dbh}}{30}\right)^\beta, \quad (1)$$

determines the total number of recruits produced by a tree, where STR (standard total recruitment) is the number of recruits produced for a tree of a standardized dbh, and  $\beta$  modifies STR as a power function of the actual dbh observed.

The parameter STR estimates the reproductive success of a tree, and therefore incorporates both the production of seeds and the seed survivorship. We chose to scale STR relative to a 30 cm dbh tree, because 30 cm is approximately the average diameter of trees in the study areas. Moreover, this standardization enables direct comparisons of STR between species and sites.

The exponent  $\beta$  converts biomass of trees of other diameters into reproductive output, scaled relative to the 30 cm dbh tree. For example, a STR of 250 means that a tree with a 30 cm dbh produces a cohort of 250 recruits, and a  $\beta$  of 2 means that STR is altered as the square of the ratio between the tree and a 30 cm dbh tree. Varying STR will change the total area under the

curve of the resulting recruitment profile (Fig. 1A), and variations in  $\beta$  will change the total area under the curve of the profile for trees with different diameters (Fig. 1B).

The second portion of the equation,

$$\frac{1}{n} e^{-Dm^\theta}, \quad (2)$$

describes the mean density of recruits to be found in a 1-m<sup>2</sup> quadrat centered at a given distance of  $m$  (in meters) from the parent tree, assuming radial symmetry, where  $\theta$  determines the shape of the distribution,  $n$  is the normalizer (Eq. 3), and  $D$  determines the rapidity of the decline in recruit numbers as the distance from the parent increases. This is in effect an approximation to the integral of Eq. 2 when integrating between two points 1 m apart. Thus, a  $D$  very close to 0 means that the distribution of recruits is nearly constant for all locations around a parent tree. As  $D$  increases, the seedling recruitment shadow decays more rapidly for a given distance from the parent (Fig. 1C). Low values of  $\theta$  produce a recruit shadow with a flatter than normal distribution, and higher  $\theta$  values produce a distribution that is squarer than normal (Fig. 1D).

The normalizer ensures that the area under Eq. 2 is equal to 1 and takes the form:

$$n = \int_0^\infty 2\pi m [e^{-Dm^\theta}] dm. \quad (3)$$

The overall equation, combining Eq. 1 and Eq. 2 with the normalizer (Eq. 3) predicts the number of recruits  $P$  for a give location in the form:

$$P = \left[ (\text{STR}) \left( \frac{\text{dbh}}{30} \right)^\beta \right] \frac{1}{n} [e^{-Dm^\theta}]. \quad (4)$$

Initial data analysis showed that STR and  $\beta$  tended to trade off with each other, as did  $\theta$  and  $D$ . This is in part due to the similarity in the effects of these pairs of parameters (notice the similarities of Fig. 1A and B and C and D). Therefore, we performed a maximum likelihood analysis for a grid of values of  $\beta$  and  $\theta$ , using all integer combinations between 1 and 4, and found that  $\beta$  values of 2 and  $\theta$  values of 3 tended to produce models with the highest likelihood. Therefore, in this paper we set  $\beta$  to 2, we set  $\theta$  to 3, and estimate only STR and  $D$ . Each data set was thus analyzed using the reduced model:

$$P = \left[ (\text{STR}) \left( \frac{\text{dbh}}{30} \right)^2 \right] \frac{1}{n} [e^{-Dm^3}]. \quad (5)$$

For a particular set of function parameters, the expected number of recruits at any given location around a parent tree can be calculated. Similarly, the total expected number of recruits in a given location can be calculated by summing the numbers of expected recruits for all trees in the area. The number of recruits

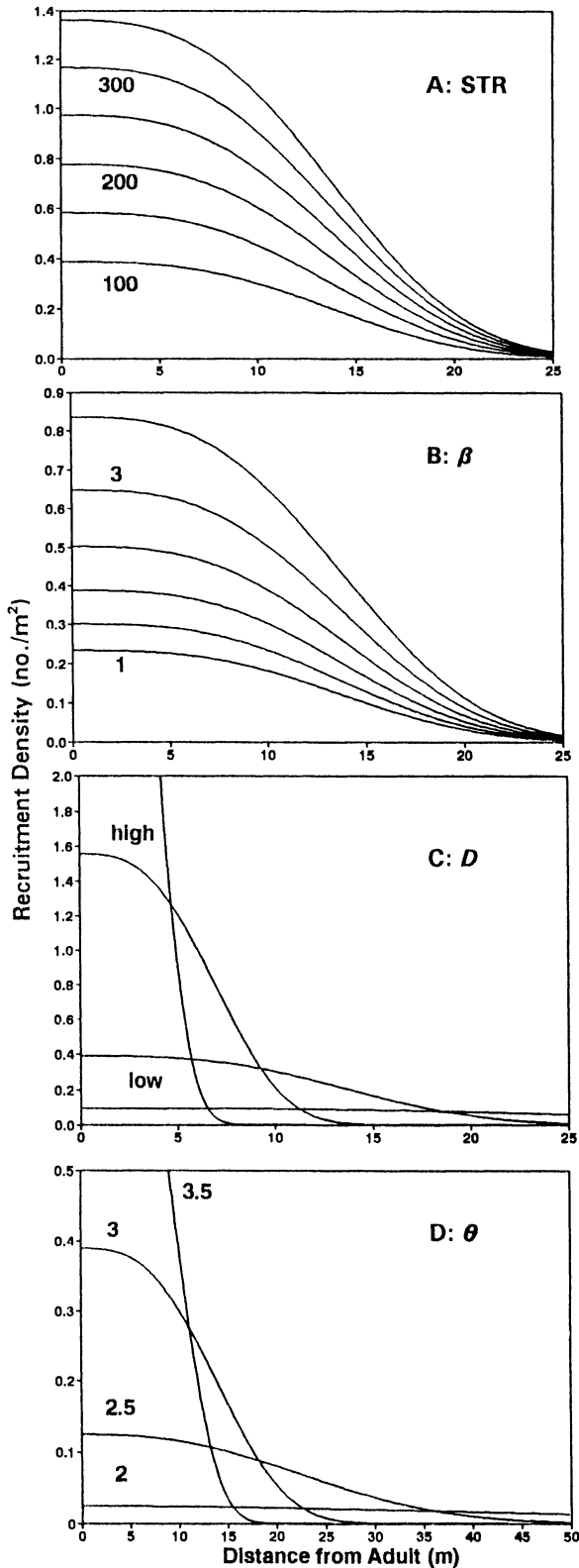


FIG. 1. Profiles of tree seedling recruitment models with only one parameter varying in each case. For each graph, the fixed parameter values were: STR = 100,  $\beta = 2$ ,  $D = 0.000025$  (MDD of 11.7 m), and  $\theta = 3$ , where STR = standard total

( $R$ ) predicted for quadrat  $i$  given  $T$  trees, using Eq. 5 is:

$$R_i = \sum_{j=1}^T (\text{STR}) \left( \frac{\text{dbh}_j}{30} \right)^2 \frac{1}{n} e^{-Dm_{ij}^3}, \quad (6)$$

where  $m_{ij}$  is the distance from the  $i^{\text{th}}$  quadrat to the  $j^{\text{th}}$  tree.

*The maximum likelihood evaluation*

A likelihood function gives the probability of obtaining a set of observations (Edwards 1972). The likelihood of observing  $O_i$  recruits when a mean of  $R_i$  recruits are expected under a Poisson distribution is:

$$\frac{e^{-R_i} R_i^{O_i}}{O_i!}, \quad (7)$$

and the likelihood for a set of  $Q$  quadrats is:

$$\prod_{i=1}^Q \frac{e^{-R_i} R_i^{O_i}}{O_i!}. \quad (8)$$

We have developed a computer package (RECRUITS) which calibrates parameters for the model we describe above. RECRUITS does so by searching the parameter space with the Metropolis algorithm (as in Szymura and Barton 1986), which converges on the combination of parameters that produce the maximum likelihood value. In so doing it brings into optimal congruence the spatial distribution of observed recruits and predicted distributions and identifies the most probable function parameter values.

STATISTICAL EVALUATIONS OF THE SEEDLING RECRUITMENT MODELS

Although the  $D$  parameter accurately determines the steepness of decay of the expected number of recruits with increasing distance from the parent tree, and therefore determines the spatial distributions of recruits, it is not a readily interpretable index. Therefore, we calculated the mean dispersal distance (MDD) by distributing expected recruits within a 100-m circle around a parent and determining the average distance from parent to recruit. Because MDD is a nonlinear function of the  $D$  parameter, it is possible to substitute MDD values for the  $D$  parameter and calculate confidence intervals for MDD. Approximate bivariate 95% confidence intervals were fitted for estimates of STR and MDD, using the inverse likelihood ratio test (Edwards 1972).

←  
recruitment, MDD = mean dispersal distance;  $D$  = a parameter that determines the rapidity of the decline in recruit density with distance from the parent tree. Each profile indicates the density of predicted recruitment for a 40-m transect originating at the parent. Profiles vary in depth, in the rapidity of drop-off, and in the total number of recruits predicted, depending upon the parameter values. The similarities between the STR and  $\beta$  graphs and the  $D$  and  $\theta$  graphs indicate the large degree of trade-offs between these parameters.

The likelihood statistic is a measure of the probability of obtaining the observed recruit values given the set of predicted means. Although it is useful for identifying the best predictors, comparisons of likelihoods among species or sites yield no meaningful information, due to heterogeneity in sample sizes. Therefore, we calculated product-moment correlation coefficients between the observed values and expected means for every species (Sokal and Rohlf 1981). The significance of product-moment correlation coefficients is normally evaluated using a *t* test with  $N - 2$  degrees of freedom. However, spatial autocorrelation increases the probability of Type I errors (Clifford et al. 1989). Therefore, all correlation significance tests were evaluated using the modification suggested by Clifford et al. (1989), which decreases the degrees of freedom in proportion to the degree of positive autocorrelation. The adjusted degrees of freedom are calculated using the equation

$$M = 1 + \frac{\sum_{k=1}^K N_k C_x(k) C_y(k)}{Q^2 S_x^2 S_y^2}, \quad (9)$$

where  $S_x^2$  is the sum of squares for the observed recruits,  $S_y^2$  is the sum of squares for the expected recruits,  $Q$  is the number of quadrats,  $N_k$  is the number of comparisons possible for the given lag amount,  $k$  is the amount of lag, and  $K$  is the number of possible lags in the spatial autocorrelation process. For the given lag  $k$ ,  $C_x(k)$  is calculated using

$$C_x(k) = \frac{\sum_{q=1}^{Q-k} (X_q - \bar{X})(X_{q+k} - \bar{X})}{N_k}, \quad (10)$$

and  $C_y(k)$  is calculated using

$$C_y(k) = \frac{\sum_{q=1}^{Q-k} (Y_q - \bar{Y})(Y_{q+k} - \bar{Y})}{N_k}, \quad (11)$$

where  $q$  is the current quadrat,  $X$  is the number of observed recruits,  $Y$  is the number of expected recruits, and  $\bar{X}$  and  $\bar{Y}$  are the means for the observed and expected numbers of recruits. This function adjusts the sample size by the amount of autocorrelation.

We performed several additional tests of the validity of our models. First, we compared the predicted parameters for those species for which we have replicate data sets. Second, we used parameters derived for one replicate data set to predict recruits for the other replicate and determined the extent of the correlation between the observed and independently derived predicted data sets. Third, we omitted every third quadrat in each data set, fitted models to the remaining quadrats, and then used these new models to predict recruitment for the omitted quadrats.

#### TESTING SEEDLING RECRUITMENT LIMITATION

We have described the development of models of recruitment. To analyze the potential for recruitment to influence community dynamics, we used three approaches.

##### *Seed augmentation*

To demonstrate that variation in seedling recruitment patterns are not solely determined by underlying environmental templates, we randomly selected 37 1-m<sup>2</sup> quadrats within a mixed stand stocked with both yellow birch and hemlock, divided each quadrat in half, and added  $\approx 300$  yellow birch seeds to one half and  $\approx 300$  hemlock seeds to the other half. During the following summer the numbers of seedlings in each of these quadrats plus 37 additional randomly selected control quadrats lacking seed augmentation were tallied.

##### *Stand recruitment limitation assessment*

To assess the potential for recruitment limitation at stand-level scales, we predicted seedling recruitment for each 5 × 5 m quadrat within test stands for each species, using the parameters calibrated in this paper. A 5 × 5 m quadrat was chosen as the appropriate scale to evaluate seedling recruitment limitation, because it approximates or exceeds the canopy size of most trees within our stands and therefore considers seedling recruitment processes at the scale of adult distributions. Quadrats for which fewer than one recruit was predicted were considered to be recruitment limited. This method of analysis can be applied to any stand (actual or theoretical) to predict recruitment limitation for entire forest communities.

We predicted seedling recruits using three test adult tree distributions for all 10 species. Each test data set consisted of 49 adults per hectare, with each adult 30 cm in dbh. The stands differed only in the distribution of the adults: one stand had a regular distribution, one a random distribution, and one a clumped distribution. Thus, this test assessed the potential for recruitment limitation for each species under three major categories of adult distribution patterns.

##### *SORTIE model simulation analysis*

To test the influence of seedling recruitment limitation on stand structure and dynamics over a longer time period, we modeled stand dynamics using a spatially explicit, individual-based model of forest dynamics (Pacala et al. 1993). SORTIE is driven by four species-specific submodels that predict growth, probability of survival, production of recruits, and local resource availability for each individual in the simulated stand. Growth predictors are based on local resource levels (Pacala et al. 1994), and mortality is predicted as a function of growth history (R. Kobe et al., *unpublished manuscript*). Spatial distributions of re-

cruits in SORTIE are predicted using the species-specific functions presented in this paper. Preliminary tests of the model indicated that it can accurately predict the species composition and dynamics of transition oak–northern hardwood forests (Pacala et al. 1993).

Because SORTIE explicitly incorporates spatial variation in seedling recruitment as a component of stand dynamics, the potential impact of recruitment limitation on population dynamics can be assessed by varying the seedling recruitment parameters and evaluating the community composition predicted by the simulator. SORTIE simulations modeling the dynamics of the two old-growth dominant species, hemlock and beech (as root sprouts), were compared to simulations in which hemlock or beech were permitted to disperse widely by increasing the MDD to 23 m, a dispersal distance somewhat greater than our calculated MDD for white pine. The amount of variation in basal areas between these three stands indicates the influence of seedling recruitment on stand dynamics. A second set of SORTIE simulations modeling the dynamics of yellow birch and hemlock were performed as well, comparing simulations using the field-calibrated dispersal parameters to simulations in which hemlock was permitted to disperse widely (as above), or in which yellow birch was restricted to a MDD of 9 m. Each simulated stand was 4 ha in size and modeled for 1500 yr.

## RESULTS

Strikingly different recruit dispersal profiles were revealed in the seedling recruitment models calibrated for all 10 species (Fig. 2). Four mean dispersal distance (MDD) categories can be distinguished (Table 1). Beech root sprouts and hemlock had very restricted dispersal distances (MDD values <6 m). Several species, including red oak, white oak, red maple, sugar maple, and black cherry, had moderate dispersal distances (MDD values between 6 and 12 m). White pine and white ash had long dispersal distances (MDD values between 15 and 20 m). Finally, yellow birch had extremely long dispersal distances (MDD values >60 m).

The standard total recruitment (STR) produced per parent exhibited substantial variation between species (Table 1). Some species clearly produced more recruits than other species. Red maple, white pine, yellow birch, and hemlock produced hundreds of seedlings per standardized (30 cm dbh) tree, red oaks produced 50–90 recruits per standardized tree, and white ash and black cherry produced 10–30 seedlings per standardized tree.

Recruits can be predicted for the transects along which the observed seedlings were recorded, using the model calibrated by the maximum likelihood analysis. Examples of predicted and observed seedling recruitment numbers are depicted for two species in Fig. 3. Correlations, which indicate the intensity of association between data sets (Sokal and Rohlf 1981), were calculated between these observed and predicted recruit numbers and ranged from <0.01 to 0.513 (Table 1).

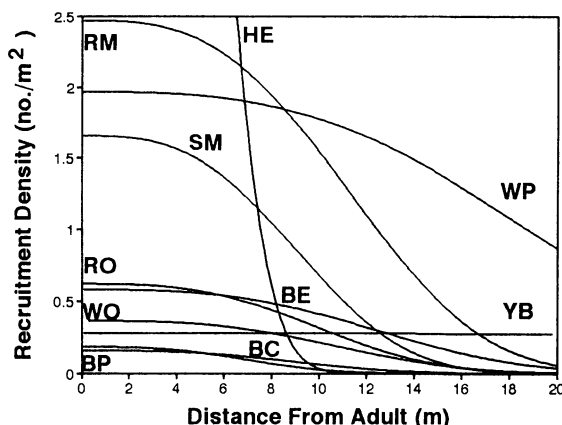


FIG. 2. Predicted recruitment profiles for nine transition oak–northern hardwood forest tree species. Each line shows the predicted density (seedlings/m<sup>2</sup>) of recruits around a 50 cm dbh tree, using the models calibrated for each species. Species displayed are hemlock (HE), red maple (RM), white pine (WP), sugar maple (SM), beech seedlings (BE), beech root sprouts (BP), black cherry (BC), white oak (WO), red oak (RO), and yellow birch (YB). Recruit densities for white ash never exceeded 0.06 seedlings/m<sup>2</sup> and are therefore not shown. The curve for hemlock is not displayed for values >2.5 seedlings/m<sup>2</sup> to avoid compression of other species curves; hemlock recruitment reached a maximum predicted density of 13 seedlings/m<sup>2</sup>.

All correlations were significant (using the adjusted *t* test described in Clifford et al. 1989 with  $\alpha = 0.05$ ), except for yellow birch. Although for yellow birch the maximum likelihood algorithm converged on a solution which indicated that yellow birch seedlings are widely distributed, the exact mean dispersal distances remain unknown, because our sampling methods do not handle long dispersal distances well. Thus, our yellow birch parameters are a qualitative estimate indicating that these seedlings are widely dispersed: we predict that >75% of yellow birch recruits are located >50 m from the parent. Because birches release their seeds throughout the winter, and Matlack (1989) notes that birch seeds are capable of secondary dispersal over several kilometres, the lack of correlation indicates that yellow birch should be examined over a larger spatial scale. In addition, yellow birch has also been shown to have exacting seedbed requirements (e.g., Tubbs 1969), and specific microsite conditions may need to be included before seedling recruitment can be accurately modeled for this species.

The confidence region for each species is unique, with the exception of some overlap between beech root sprouts and black cherry, and beech seedlings and red oak (Fig. 4). Confidence intervals for the species with long mean dispersal distances (white pine and white ash) are substantially broader than for the species with more restricted dispersal; this may reflect the uncertain effect of recruits derived from trees located outside the mapped area.

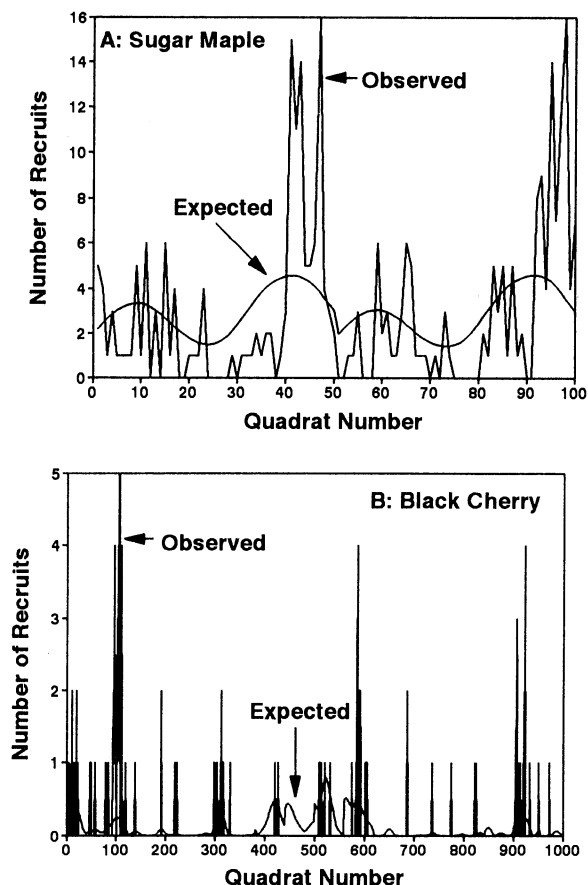


FIG. 3. Observed recruits and predicted seedling recruitment abundances in transition oak-northern hardwood forest. Actual recruits and predictions generated from the calibrated functions are shown for two species: sugar maple and black cherry.

For all species except white ash, white pine, and yellow birch, >50% of all recruits were predicted to be located within 10 m of the parent, and >95% of all recruits were predicted to be located within the 20 m mapping distance. Of the 10 species calibrated, only yellow birch had substantial numbers of recruits expected to be located >50 m from the parent, and only yellow birch, white ash, and white pine were expected to distribute >30% of their recruits farther than 20 m from the parent. Thus, mapping all adult trees within a 20 m radius of the quadrat is more than adequate to predict recruitment within that quadrat for all species except yellow birch, white pine, and white ash, and only for yellow birch would unmapped adults be expected to contribute >33% of the recruits.

#### Testing the recruitment functions

Comparisons of the replicate estimates for red maple, red oak, white oak, and hemlock (Table 1) indicate that MDD was more constant between replicates than were STR values. These variations do not affect the rank ordering by MDD of all species except red oak. This indicates that our models of seedling recruitment do reflect repeatable species-specific characteristics and suggests surprisingly small variation among sites. When we used the parameters calculated for one replicate to predict seedling recruitment distributions for the other replicate (Fig. 5), the correlations between the observed recruits and the independently derived predictions were significant for all species (Table 2). This confirms that our models are useful in predicting recruit distributions as well as in characterizing recruit distributions.

Because we did not have replicates for the remaining species, we used cross-validation to examine the predictive power of the remaining models by omitting every third quadrat, calculating new models, and then using the new models to predict recruitment for the

TABLE 1. Parameter values used in a model of tree seedling dispersion in transition oak-northern hardwood forest.†

Species	STR	MDD	<i>r</i>	Normalizer	<i>D</i> ‡
Hemlock, rep. 1§	468.67	4.480	0.556*	104.55	44.720410
Hemlock, rep. 2	350.82	3.512	0.422*	64.34	92.690773
Beech root sprouts	14.96	5.902	0.256*	181.32	19.572715
Black cherry	17.21	8.038	0.221*	336.14	7.751938
Sugar maple	182.42	8.150	0.513*	345.63	7.435026
White oak, rep. 1	55.31	8.545	0.352*	379.89	6.452054
White oak, rep. 2	50.28	8.754	0.231*	398.72	6.000372
Red oak, rep. 1	82.44	8.721	0.381*	395.74	6.068213
Red oak, rep. 2	51.72	5.584	0.442*	161.83	23.105629
Red maple, rep. 1	417.71	9.525	0.425*	472.03	4.658166
Beech seedlings	121.22	10.567	0.381*	580.84	3.412413
Red maple, rep. 2	219.33	11.591	0.239*	698.85	2.585597
White pine	916.66	15.769	0.342*	1293.26	1.027010
White ash	26.18	16.341	0.163*	1388.87	0.922805
Yellow birch	>2000	>66	<0.001	31415.8	0.000001

\* Significant at alpha = 0.05.

† STR = standard total recruitment, MDD = mean dispersal distance, observed - expected correlations, normalizer, and *D* values for all species, sorted by MDD. *D* = determinant of the rapidity with which recruit density declines with distance from the parent tree.

‡ *D* values shown equal  $D \times 10^5$ .

§ rep. = replicate.

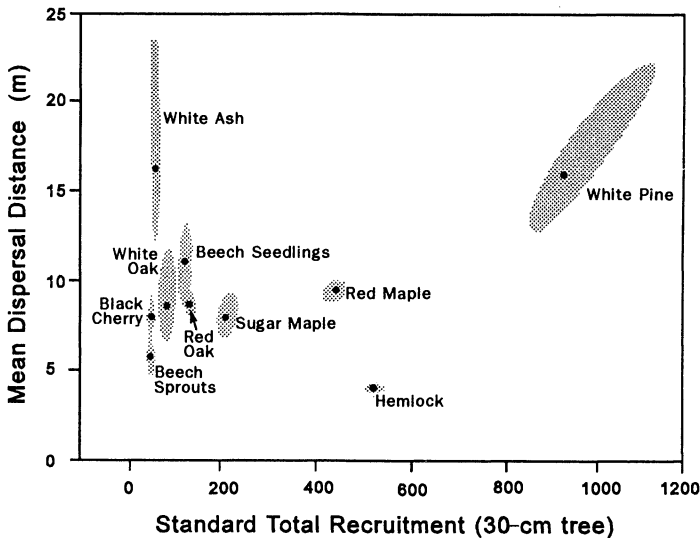


FIG. 4. Values and 95% confidence regions of recruitment parameters for nine transition oak–northern hardwood forest tree species. Each cloud of points represents values for mean dispersal distance (MDD) and standard total recruitment (STR) which produce likelihoods within a 95% confidence region. The unshaded circle within the cloud marks the position of the parameter values yielding the maximum likelihood. All species are shown except yellow birch, because the yellow birch correlation was not statistically significant.

quadrats omitted from the model development. When recruits were predicted for the omitted quadrats, correlations between predictions and observed seedling recruit distributions were all significant (Table 3).

Finally, several previous studies provide support for our findings. First, our prediction of a MDD for hemlock of  $<5$  m corresponds to Burns and Honkala's (1990) note that generally hemlock seeds fall beneath the parent's canopy. Second, Hoppes (1988) showed that black cherry seed dispersal was tightly clustered around artificial displays of black cherry fruit, and we calculated a MDD of 2.6 m from his data. This is the only study of which we know that described seed dispersal profiles for any of these species, and he used artificial fruit displays; however, the tight clustering of seeds confirms our MDD estimate that black cherry recruits are not widely dispersed. Third, Johnson (1988) mapped sugar maple seedlings around an isolated adult and found a monotonically declining distribution centered on the parent. Although this study was done in an old field, with very different wind and microsite conditions, it supports our assumptions of a monotonically declining dispersion profile.

#### *Tests of recruitment limitation*

When yellow birch and hemlock seeds were added to quadrats, significantly higher recruit numbers of both species were found in quadrats with seeds added (Fig. 6). If no additional recruits were found, this test would not have conclusively demonstrated that seedling recruitment is limited due to microsite conditions, because the absence of additional seedlings may be due to seed predation, dormancy, or placement techniques. However, the presence of additional seedlings when seeds are added confirms that seedling recruitment is not determined solely by microsite quality and that recruitment may be limited due to the scarcity of propagules.

The distribution of seedling recruits was predicted for  $5 \times 5$  m quadrats in three test stands to determine the frequency of quadrats within which fewer than one seedling recruit would be predicted. In these test stands, we predicted wide variation in recruitment limitation among species and among tree distributions (Fig. 7). The regular distribution produced no expected recruitment limitation and little variation in predicted seedling recruitment patterns among species. However, the clumped and random stands produced substantial areas of predicted recruitment limitation for some species. Within the clumped stand, yellow birch and white pine were not recruitment limited, and white ash and red maple showed little predicted seedling recruitment limitation. Beech root sprout recruits were expected in  $<60\%$  of the quadrats, and hemlock and black cherry failed to recruit into  $>30\%$  of the quadrats. Furthermore, fewer than five seedling recruits were predicted for  $>75\%$  of the quadrats for white ash, white oak, and beech. Of the species with substantial recruitment limitation, some (e.g., white ash) were due to low STR values, while other species (e.g., beech root sprouts and hemlock) were limited in their recruitment as a result of short mean dispersal distances.

TABLE 2. Correlations between observed recruits and recruits predicted from parameters calculated for the replicate data set.

Species	Correlation
Hemlock, replicate 1	0.428*
Hemlock, replicate 2	0.533*
Red maple, replicate 1	0.419*
Red maple, replicate 2	0.238*
Red oak, replicate 1	0.405*
Red oak, replicate 2	0.410*
White oak, replicate 1	0.356*
White oak, replicate 2	0.227*

\* Significant at  $\alpha = 0.05$ .

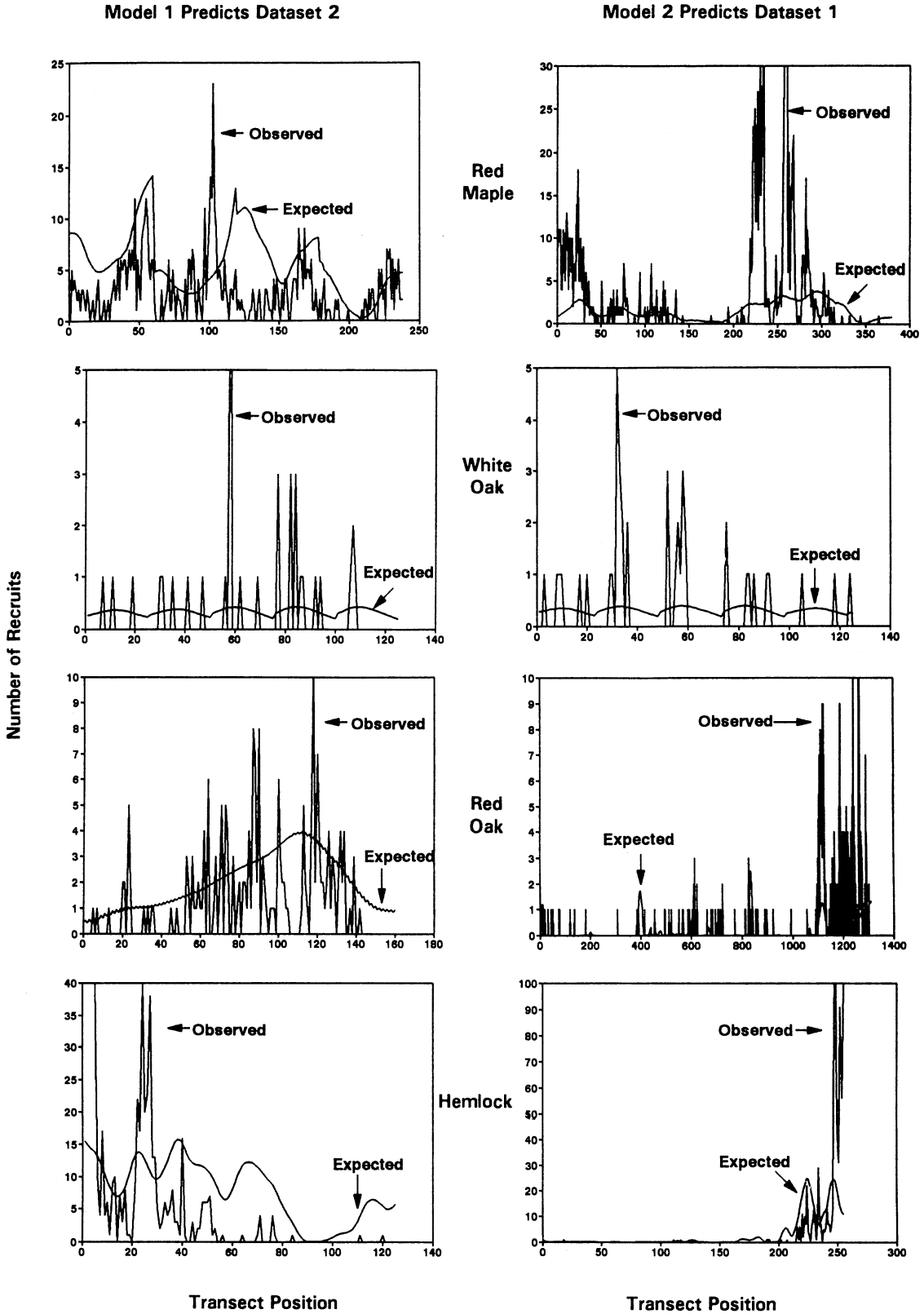


FIG. 5. Observed tree seedling recruits and recruitment abundances predicted from replicate transects. Actual recruits and predictions generated from functions calibrated on a replicate data set are shown for the four species for which replicates were obtained: hemlock, red maple, red oak, and white oak.

**Seed Augmentation**

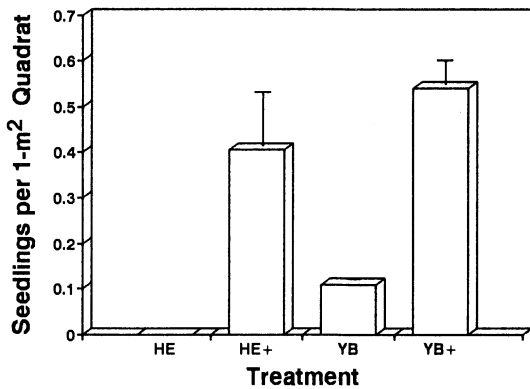


FIG. 6. Effects of seed augmentation. When seeds were added to quadrats, significant increases (at alpha = 0.05, 36 df, YB  $t = 1.88$ , HE  $t = 1.17$ ) were observed in seedling abundances. Each bar represents the number of seedlings found in 37 1-m<sup>2</sup> quadrats. Species are hemlock (HE) and yellow birch (YB).

This analysis demonstrated that recruitment limitation can be evaluated at a stand level, that some species can be expected to be recruitment limited to a much higher degree than other species, and that seedling recruitment processes, even within a 1-ha stand, are far from uniform. Additionally, it demonstrated that the magnitude of the recruitment limitation for many species reflects the distribution patterns of adults within the stand. Finally, it indicated that seedling recruitment can be limited due to low MDD and STR parameters in our models.

*SORTIE simulations*

To evaluate recruitment effects for stands over longer time periods and larger spatial scales, SORTIE simulations of beech and hemlock, two old-growth dominant species with restricted dispersal, and simulations of hemlock and yellow birch, two coexisting species with different dispersal abilities, were generated. Each pair was modeled with the field-calibrated dispersal parameters and with modified dispersal parameters to determine the effect of the dispersal component of seedling recruitment on stand dynamics.

TABLE 3. Cross-validation correlations between observed recruits in one of every three quadrats and expected recruits derived from models calibrated using the remaining quadrats.

Species	Correlation
Sugar maple	0.465*
White pine	0.170*
Beech seedlings	0.307*
Beech root sprouts	0.210*
Black cherry	0.217*
White ash	0.182*

\* Significant at alpha = 0.05.

The outcomes of both types of simulations were influenced by dispersal. In the hemlock-beech simulations, the field-calibrated parameters produced a predicted stand with substantial amounts of both beech

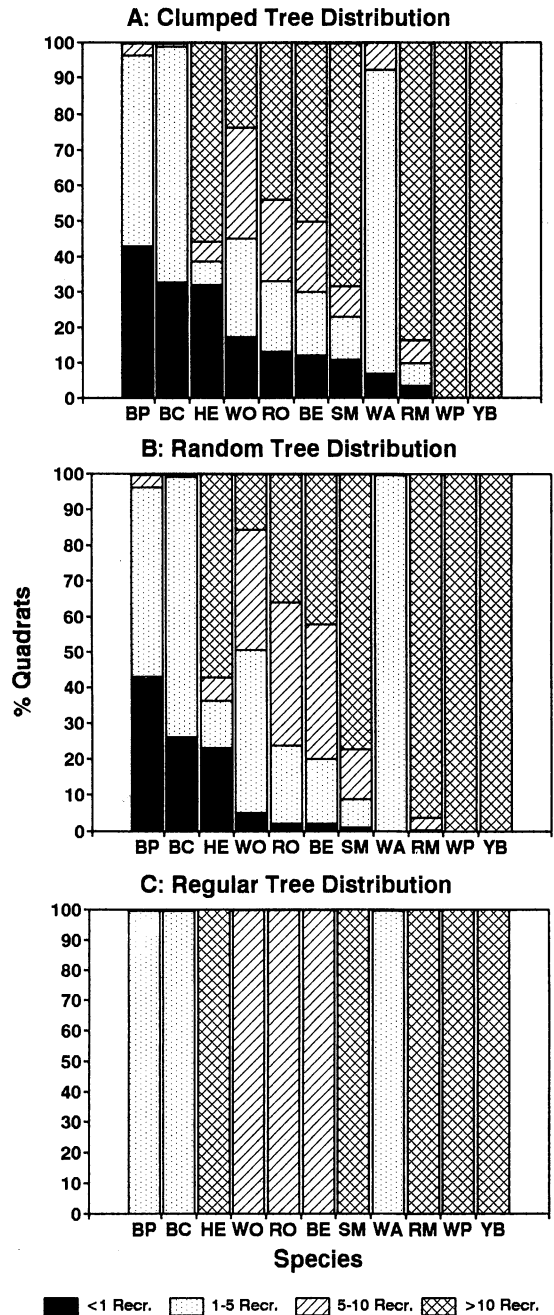


FIG. 7. Predicted stand recruitment limitation. Each bar represents a species within the sample stand for which recruitment within 5 × 5 m quadrats was predicted. Bars are sorted from left to right by decreasing predicted recruitment limitation. Species are beech seedlings (BE), beech root sprouts (BP), black cherry (BC), hemlock (HE), white ash (WA), white oak (WO), red oak (RO), sugar maple (SM), red maple (RM), white pine (WP), and yellow birch (YB).

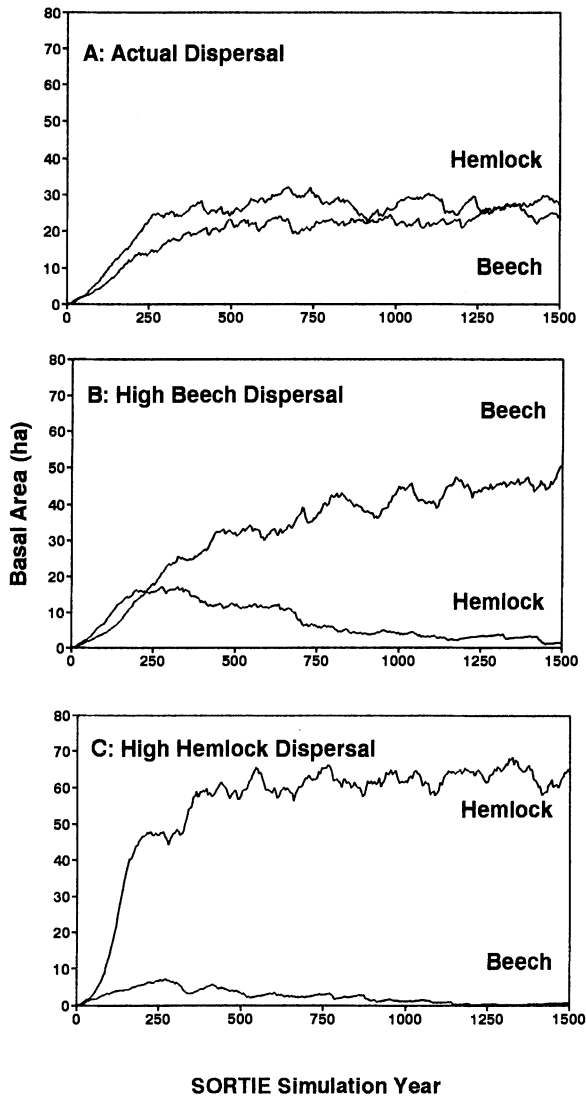


FIG. 8. Results of SORTIE simulations of beech-hemlock forest dynamics. Each graph shows basal area over time for a SORTIE simulation comprised of beech and hemlock. (A) Calculated mean dispersal distance (MDD) values (beech MDD = 5.9 m, hemlock MDD = 4.5 m; Table 1). (B) High dispersal (MDD = 23.3 m) for hemlock. (C) High dispersal (MDD = 23.3 m) for beech.

and hemlock. However, when either hemlock or beech is modeled with a higher MDD, and thus disperses recruits more widely (Fig. 8), that species eventually dominates, due to an increased ability to colonize sites not immediately adjacent to adults. For yellow birch-hemlock simulations (Fig. 9), the field-calibrated recruitment parameters produced a stand with yellow birch somewhat more abundant than hemlock. However, when either hemlock MDD is increased or yellow birch MDD is decreased, hemlock becomes much more abundant than yellow birch. Thus, within SORTIE simulations, recruitment affects stand composition and dynamics, and alternative recruitment functions can

produce substantial changes. Analysis of SORTIE (Pacala et al. 1993) has determined that species coexist in the model due to a series of trade-offs: as high-light growth rate increases, low-light survivorship decreases, mean dispersal distance increases, and the shade cast by an individual tree decreases. These trade-offs may influence the type of recruitment limitation most likely to be experienced by a given species.

#### DISCUSSION

We have developed a method for predicting the locations of recruited seedlings in relation to adults. Although other researchers have compared juvenile spatial patterns with adult patterns (e.g., Hamill and Wright

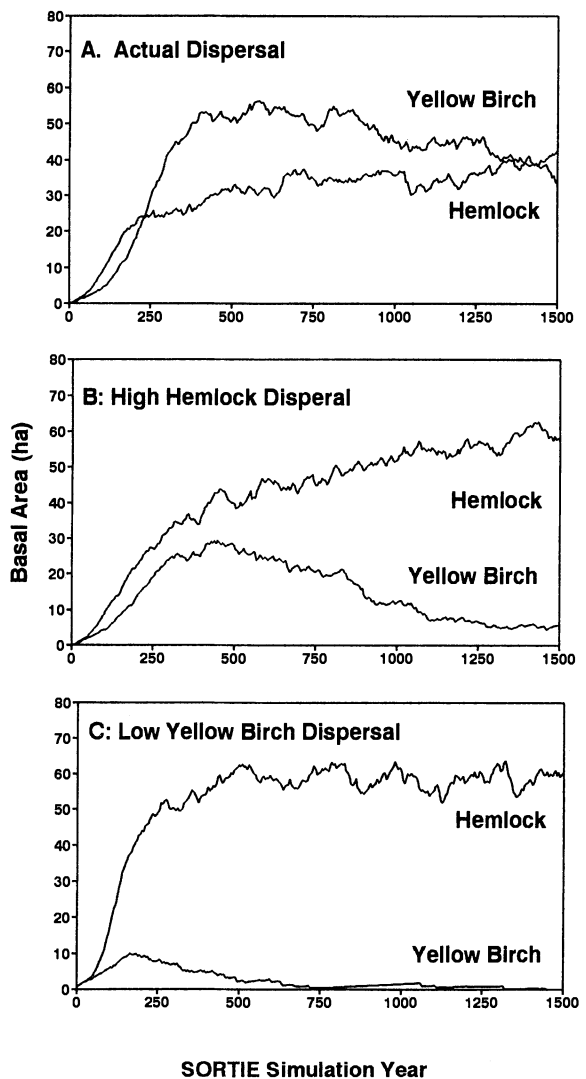


FIG. 9. Results of SORTIE simulations of yellow birch-hemlock forest dynamics. Each graph shows basal area over time for a SORTIE simulation comprised of yellow birch and hemlock. (A) Calculated mean dispersal distance (MDD) values (yellow birch MDD = 66 m, hemlock MDD = 4.5 m; Table 1). (B) High dispersal (MDD = 23.3 m) for hemlock. (C) Low dispersal (MDD = 9.3 m) for yellow birch.

1986), those approaches were designed to determine whether juveniles were randomly distributed or clumped relative to the adults. Until now techniques have not been available to predict spatial seedling recruitment patterns from adult tree distributions; indeed, it has not been clear that such patterns could be identified without mapping seedling distributions around isolated adults. Our approach eliminates many of the assumptions required for work with isolated adults, uses easily obtained data, and produces simple, flexible models that generate predictions that significantly correlate with observed recruit distributions.

This study is the first to characterize seedling recruitment for an entire forest community, and the first study to use the same general model to predict seedling recruitment for different species. We know of one study of black cherry seed dispersal (Hoppes 1988) and one study of recruit distributions around isolated sugar maple adults (Johnson 1988), but aside from these, direct comparisons of our values to other studies are not possible.

How stable do we expect these estimates to be? Temporal variation in reproductive effort can undoubtedly be large; mast years occur in many northern hardwood species, with enormous variability in seed production (e.g., Godman and Mattson 1976, Houle and Payette 1990, Sork et al. 1993). Therefore, we expect that standard total recruitment (STR) values can vary widely, due to temporal variation in seed production, disturbance events, or pre-establishment survival (e.g., Vose and White 1987, Yamamoto 1988). However, these variations should only affect the intercept, not the slope, of a seedling dispersal profile, and thus STR is the parameter most likely to be affected. Temporal variation in mean dispersal distance (MDD) values are less likely, because MDD reflects the physics of seedfall and secondary seed dispersal. Significant MDD shifts would be most likely in species with animal seed dispersal vectors or with seed predators that consume much of the crop. For these species, fluctuations in the abundances of the animals with which they interact may alter MDD values. However, the five wind-dispersed species (red maple, sugar maple, yellow birch, white pine, and hemlock) should demonstrate little variation in MDD, and we found little variation in the species for which we have replicates.

In most forest stand simulation models (e.g., JABOWA, Botkin et al. 1972, FORET, Shugart 1984), recruitment is not quantitatively linked to the adults present in the model. Rather, these models draw recruits from a fixed species distribution that is independent of the adult distributions and abundances. Thus, these are open population models that avoid explicit descriptions of dispersal, treat recruitment as a "black box," and do not contain any direct link between current adult abundance and recruitment. Rather, recruits are either chosen randomly, or the species pool from which recruits are drawn is reduced in an

attempt to reflect conditions that favor germination or establishment of certain species (Shugart 1984). Not only do these models fail to connect current adult abundance and recruits, but typically the number of recruits permitted to enter is fixed (e.g., seven per modeled unit), and no attempt is made to disperse recruits in a nonrandom manner. Some more recent models (e.g., Smith and Urban 1988) have a mix of open and closed recruitment, but the methods for calibrating these models are not clear, and the validity of these recruitment submodels remains problematical.

Thus, in many current models of forest dynamics, recruitment is assumed to be (1) a simple stochastic process, (2) globally distributed (e.g., Davis and Botkin 1985), (3) determined by site conditions rather than the availability of parents (e.g., Phipps 1979, Kienast and Kuhn 1989), and (4) not linked to the actual presence of parents (e.g., Kienast 1991). In contrast, we have shown that recruitment is not globally dispersed, that seedling recruitment is significantly correlated with the distribution of parents, and that recruitment is severely limited or totally absent when parents are not present. The methods presented in this paper will allow the development of computer simulation models of forest dynamics with more realistic recruitment submodels.

Our approach does not consider or attempt to evaluate long-distance dispersal events. As Silvertown (1991) points out, statistical approaches such as the one we employed are not suitable for detecting and evaluating rare events. Furthermore, the dispersal distances that we predict are not directly applicable to clearcuts, which are subject to different weather and wind dynamics.

The models we have generated for each species, when used to predict recruitment for a stand, clearly indicate that some species are much more recruitment limited than others, and that for more than half of the species in a transition oak-northern hardwood forest, recruitment limitation can be common at a stand-level spatial scale. Recruitment limitation can have substantial and long-lasting effects on community composition and dynamics, as demonstrated by SORTIE simulations. We have also distinguished between two types of seedling recruitment limitation: recruitment limitation can be due to low numbers of recruits as a result of low STR values, or it can be due to a poor dispersal of recruits as a result of low MDD values.

#### ACKNOWLEDGMENTS

This research was funded by grants from the National Science Foundation (BSR-8918616), the Department of Energy (DE-FG02-90ER60933), and the National Aeronautics and Space Administration. Adrien Finzi, Jim Hill, Richard Kobe, and Barbara Ribbens assisted in data collection. The constructive criticism of Charles Canham, Robin Chazdon, Christopher Dunn, David Greene, Jim Hill, Richard Kobe, Carl Schlichting, and two anonymous reviewers was invaluable. Marie-Josée Fortin and Don MacQueen provided valu-

able statistical advice, and Edward C. Childs generously granted permission to conduct research on his property.

## LITERATURE CITED

- Abrams, P. A. 1984. Recruitment, lotteries, and coexistence in coral reef fish. *American Naturalist* **123**:44–55.
- Augspurger, C. K. 1983. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* **40**: 189–196.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Rationale, limitations, and assumptions of a northeastern forest growth simulator. *IBM Journal of Research and Development* **16**: 101–116.
- Burns, R. M., and B. H. Honkala, technical coordinators. 1990. *Silvics of North America: 1. Conifers. 2. Hardwoods*. USDA Forest Service Agricultural Handbook **654**.
- Campbell, B. M., T. Lynam, and J. C. Hatton. 1990. Small-scale patterning in the recruitment of forest species during succession in tropical dry forest, Mozambique. *Vegetatio* **87**:51–57.
- Canham, C. D. 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bulletin of the Torrey Botanical Club* **117**:1–7.
- Clifford, P., S. Richardson, and D. Hémon. 1989. Assessing the significance of the correlation between two spatial processes. *Biometrics* **45**:123–134.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 in B. J. den Boer and G. R. Gradwell, editors. *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Cremer, K. W. 1966. Dissemination of seed from *Eucalyptus regnans*. *Australian Forestry* **30**:33–37.
- Davis, M. B., and D. B. Botkin. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperature change. *Quaternary Research* **23**:327–340.
- Edwards, A. W. F. 1972. *Likelihood*. Cambridge University Press, Cambridge, England.
- Ellner, S., and A. Shmida. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* **51**:133–144.
- Fulton, M. R. 1991. Adult recruitment as a function of juvenile growth rate in size-structured plant populations. *Oikos* **62**:102–105.
- Godman, R. M., and G. A. Mattson. 1976. Seed crops and regeneration problems of nineteen species in northeastern Wisconsin. USDA Forest Service Research Paper NC-123.
- Graber, F. E., and W. B. Leak. 1992. Seed fall in an old-growth northern hardwood forest. USDA Forest Service Research Paper NE-663.
- Hamill, D. N., and S. J. Wright. 1986. Testing the dispersion of juveniles relative to adults: a new analytic method. *Ecology* **67**:952–957.
- Held, M. E. 1983. Pattern of beech regeneration in the east-central United States. *Bulletin of the Torrey Botanical Club* **110**:55–62.
- Hoppes, W. G. 1988. Seedfall pattern of several species of bird-dispersed plants in an Illinois woodland. *Ecology* **69**: 320–329.
- Houle, G., and S. Payette. 1990. Seed dynamics of *Betula alleghaniensis* in a deciduous forest of northeastern North America. *Journal of Ecology* **78**:677–690.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* **66**:781–791.
- Hubbell, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* **35**:214–229.
- Hughes, J. W., and T. J. Fahey. 1988. Seed dispersal and colonization in a disturbed northern hardwood forest. *Bulletin of the Torrey Botanical Club* **115**:89–99.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* **104**:501–528.
- Johnson, W. C. 1988. Estimating dispersibility of *Acer*, *Fraxinus*, and *Tilia* in fragmented landscapes from patterns of seedling establishment. *Landscape Ecology* **1**:175–187.
- Jones, R. H., and D. J. Raynal. 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). *American Journal of Botany* **73**:1723–1731.
- Kienast, F. 1991. Simulated effects of increasing atmospheric CO<sub>2</sub> and changing climate on the successional characteristics of Alpine forest ecosystems. *Landscape Ecology* **5**: 225–238.
- Kienast, F., and N. Kuhn. 1989. Simulating forest succession along ecological gradients in southern central Europe. *Vegetatio* **79**:7–20.
- Leak, W. B., and R. E. Graber. 1976. Seedling input, death and growth in uneven-aged northern hardwoods. *Canadian Journal of Forest Research* **6**:368–374.
- Manders, P. T. 1986. Seed dispersal and seedling recruitment in *Protea laurifolia*. *South African Journal of Botany* **52**:421–424.
- Matlack, G. R. 1989. Secondary dispersal of seed across snow in *Betula lenta*, a gap-colonizing tree species. *Journal of Ecology* **77**:853–869.
- Pacala, S. W., C. D. Canham, and J. A. Silander, Jr. 1993. Forest models defined by field measurements. 1. The design of a northeastern forest simulator. *Canadian Journal of Forest Research* **23**:1980–1988.
- Pacala, S. W., C. D. Canham, J. A. Silander, Jr., and R. K. Kobe. 1994. Sapling growth as a function of resources in a northern temperate forest. *Canadian Journal of Forest Research*, *in press*.
- Phipps, R. L. 1979. Simulation of wetlands forest vegetation dynamics. *Ecological Modelling* **7**:257–288.
- Schaal, B. A. 1980. Measurement of gene flow in *Lupinus texensis*. *Nature* **284**:450–451.
- Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* **51**:71–78.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer-Verlag, New York, New York, USA.
- Silvertown, J. W. 1991. Dorothy's dilemma and the unification of plant population biology. *Trends in Ecology and Evolution* **6**:346–348.
- Smith, T. M., and D. L. Urban. 1988. Scale and resolution of forest structural pattern. *Vegetatio* **74**:143–150.
- Sokal, R. R., and J. F. Rohlf. 1981. *Biometry*. Freeman, New York, New York, USA.
- Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast fruiting in three species of North American deciduous oaks. *Ecology* **74**:528–541.
- Szymura, J. M., and N. H. Barton. 1986. Genetic analysis of a hybrid zone between the fire-bellied toads near Cracow in southern Poland. *Evolution* **40**:1141–1159.
- Tubbs, C. H. 1969. The influence of light, moisture, and seedbed on yellow birch regeneration. USDA Forest Service Research Paper NC-27.
- Vose, J. M., and A. S. White. 1987. Processes of understory seedling recruitment one year after prescribed fire in an Arizona ponderosa pine community. *Canadian Journal of Botany* **65**:2280–2290.
- Warner, R. R., and P. L. Chesson. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. *American Naturalist* **125**:769–787.
- Yamamoto, S.-I. 1988. Seedling recruitment of *Chamaecyparis obtusa* and *Sciadopitys verticillata* in different microenvironments in an old growth *Sciadopitys verticillata* forest. *Botanical Magazine of Tokyo* **101**:61–71.