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APP

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INTERPRETING RECRUITMENT LIMITATION IN FORESTS[1]

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Studies of tree recruitment are many, but they provide few general insights into the role of recruitment limitation for population dynamics. That role depends on the vital rates (transitions) from seed production to sapling stages and on overall population growth. To determine the state of our understanding of recruitment limitation we examined how well we can estimate parameters corresponding to these vital rates. Our two-part analysis consists of (1) a survey of published literature to determine the spatial and temporal scale of sampling that is basis for parameter estimates, and (2) an analysis of extensive data sets to evaluate sampling intensity found in the literature. We find that published studies focus on fine spatial scales, emphasizing large numbers of small samples within a single stand, and tend not to sample multiple stands or variability across landscapes. Where multiple stands are sampled, sampling is often inconsistent. Sampling of seed rain, seed banks, and seedlings typically span <1 yr and rarely last 5 yr. Most studies of seeding establishment and growth consider effects of a single variable and a single life history stage. By examining how parameter estimates are affected by the spatial and temporal extent of sampling we find that few published studies are sufficiently extensive to capture the variability in recruitment stages. Early recruitment stages are especially variable and require samples across multiple years and multiple stands. Ironically, the longest duration data sets are used to estimate mortality rates, which are less variable (in time) than are early life history stages. Because variables that affect recruitment rates interact, studies of these interactions are needed to assess their full impacts. We conclude that greater attention to spatially extensive and longer duration sampling for early life history stages is needed to assess the role of recruitment limitation in forests.

Key words: dispersal; establishment; fecundity; forest dynamics; mortality; population growth; seed rain.

There are two views concerning the role of recruitment for forest dynamics. The first view is that populations are "recruitment limited," with low and uncertain seed supply or seedling establishment being among the causes for absence or rarity. Lack of local seed sources or failure of seed crops combined with restricted dispersal have lasting impacts on population dynamics (Downs and McQuilkin, 1944; Fleming and Heithaus, 1981; Augspurger and Franson, 1988; Hughes and Fahey, 1988; Streng, Glitzenstein, and Harcombe, 1989; Schupp, 1990; Houle, 1992a; Ribbens, Silander, and Pacala, 1994; Clark, Macklin, and Wood, 1998). These transitions are represented by arrows labeled "Fecundity" and "Dispersal" in Fig. 1a. Foresters have long appreciated the need for adequate seed supply for stand regeneration on logged sites (Hartig, 1889; Hagner, 1965; Alexander, 1969). Theorists have been especially interested in how fecundity and dispersal can affect plant community dynamics (Shmida and Ellner, 1984; Pacala and Tilman, 1994; Clark and Ji, 1995; Hurtt and Pacala, 1995).

The second view ascribes a more limited role in the dynamics of forests to seed supply and seedling establishment. Here the focus shifts to distributions and quality of microsites (Duncan, 1954; Beatty, 1984; Webb, 1988; Nakashizuka, 1989; Peterson and Pickett, 1990; Cho and Boerner, 1991; Houle, 1992b) and factors affecting growth and mortality in seed banks and seedling stages (Burton and Bazzaz, 1991; Choinski and Tuohy, 1991; Reader and Buck, 1991). Empirical analyses tend to emphasize demography of early life history stages and the spatial and temporal pattern of "safe sites" that provide the right mix of conditions for seedling establishment, growth, and survival. Gap simulations of forest dynamics formalize the overwhelming importance of factors other than seed availability and seedling establishment. These models assume a "sapling rain," where recruitment does not depend on trees (there is no transition from "Canopy trees" to "Saplings" in Fig. 1b). Downplaying the importance of seed production and dispersal can be attributed to two factors, (1) seeds are hard to count and track in closed forests and (2) vast amounts of seed are "wasted," appearing to be produced well in excess of that needed for successful recruitment.

There can be reasons to adopt either of the views in Fig. 1. Gauging the relative contribution of seed availability to recruitment requires estimates of transitions across stages in Fig. 1a (Smith, 1975; Clark and Clark, 1984; Schupp, 1990; Nakashizuka et al., 1995). A transition probability substantially lower than others represents a limiting life history stage. Recruitment limitation may involve more than one stage, and relative importances may vary in time and space, depending on climate fluctuation and the appearances of canopy gaps, nurse logs, and so forth. If the important limitations include fecundity, dispersal, or both, then the details in Fig. 1a matter. Alternatively, if transition probabilities involving

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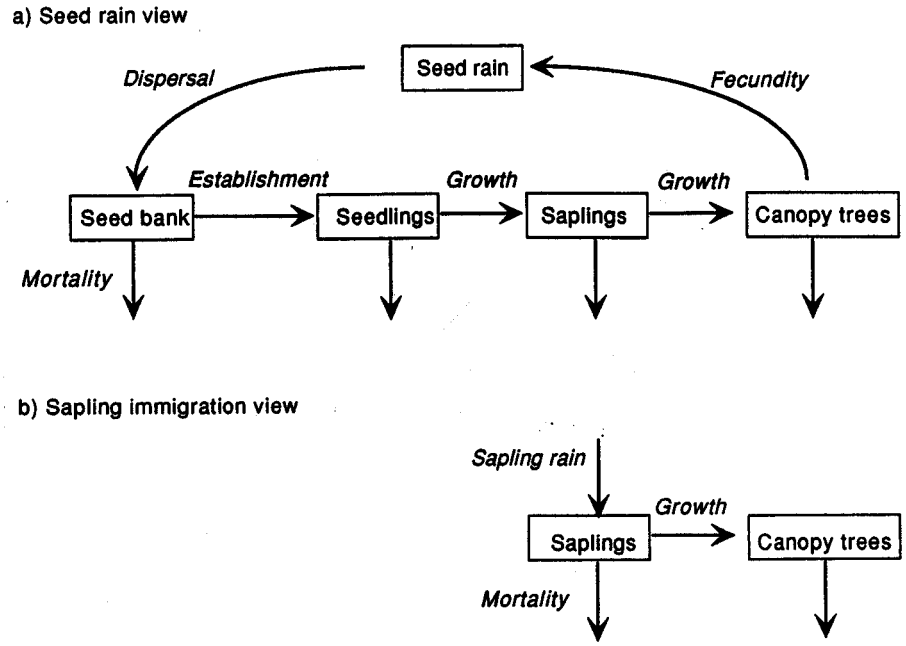

Fig. 1. Two views on the role of recruitment limitation in forests guide collection of field data and development of models of forest dynamics.

seed production, dispersal, and seedling establishment are high, and they are compensated by subsequent density-dependent mortality, then recruitment might be simplified to the model outlined in Fig. 1b. Limited benefit is gained from detailed empirical or modeling analysis of stages that have little consequence.

In light of the number of studies devoted to forest dynamics, there is surprisingly little guidance from the literature as to which view represents the most efficient path to understanding recruitment limitation. Because spatial and temporal variability is critical for recruitment, and trees are long lived, the data needed to estimate these transitions can be extensive. A review over a decade ago (Canham and Marks, 1985) suggests that few quantitative generalities could be made at that time concerning the relative importances of recruitment stages. Although there have been several more recent efforts to quantify the relative importances of transitions in Fig. 1a (Streng, Glitzenstein, and Harcombe, 1989; Alvarez-Buylla and Garcia-Barrios, 1991; Drake, 1992; Graber and Leak, 1992; Houle, 1992a; Schupp and Fuentes, 1994; Herrera et al., 1994; Shibata and Nakashizuka, 1995; Clark, Macklin, and Wood, 1998), most studies focus on a limited subset of Fig. 1a or on a few variables (e.g., resources) that affect recruitment, precluding comprehensive comparisons.

Our goals are twofold. First, we ask whether the data are sufficient to permit some general conclusions concerning the importance of recruitment limitation and the stages at which it operates. We survey published literature to quantify the spatial and temporal extent of observations and experiments on transitions that constitute recruitment. Second, we ask what we can infer regarding recruitment limitation from data of the extent available in the literature. Rather than attempt a general overview of the sort available from previous literature reviews, we ask instead how data affect our understanding of transitions illustrated in Fig. 1. Our strategy here involves comparisons of results from data sets of the extent available in published literature with those from data sets that are both extensive and long term. Together, these two sets of results are used to assess where we stand with respect to the question of what stages limit recruitment.

HOW RECRUITMENT IS SAMPLED

Sampling variability—Both theory and field observation tell us that recruitment variability is a requirement for high diversity and a common feature of all forests. Recruitment variability at fine spatial scales (within a forest stand) can promote diversity by limiting interspecific competition. Species-specific differences in seed production, dispersal, resource use, apparancy to predators and pathogens, phenology, and potential growth rates provide basis for niche differentiation (e.g., Streng, Glitzenstein, and Harcombe, 1989). Together with environmental variation, species-specific responses can produce wide fluctuations in seed production, dispersal, seed bank mortality, predation, germination, and seedling growth and survival. Variation in recruitment along environmental gradients affects composition pattern across landscapes.

The foregoing is common knowledge (Grubb, 1977; Canham and Marks, 1985), but the magnitudes of vital rates in Fig. 1 are not. In our literature survey and data analyses, we examined how recruitment stages in Fig. 1a are studied at several scales. For our literature survey we attempted to extract common indices related to sampling effort. To examine consequences of local variability for stand composition, we examined the intensity of sampling within stands. To explore how recruitment contributes to composition variability across landscapes, we examined sampling among stands. To assess the degree and importance of temporal variability, we examined sample duration and frequency. Our data analyses were then completed for the same set of indices used to evaluate literature sampling. Here we define the indices in the context of our literature survey.

We quantified extensive sampling across landscapes as "number of stands." Because many recruitment studies are conducted on old fields or clear-cuts, the term "stand" need not imply a forested landscape. We judged a sampling procedure to include multiple stands if the authors describe samples taken at different locations, containing different com-

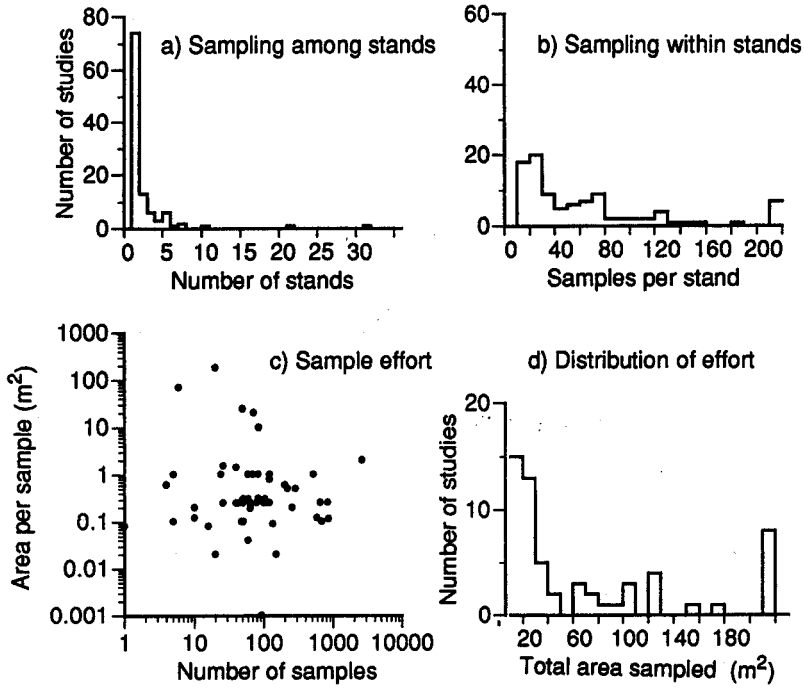

Fig. 2. Sampling of seed production and dispersal from the survey of literature, including number of stands (a), samples per stand (b), the relationship between sample number and area per sample (c), and total area of ground surface sampled.

positions, or both. Clear-cut areas and old fields were each designated as a separate "stand."

We summarized sampling effort within stands by numbers of samples within each stand and by the area per sample. For cases where "sample plots" were arranged contiguously along transects, the total number of plots per stand was calculated as the number of plots per transect times the number of transects. In a few cases, transects or sample plots were nested within treatments in a single stand (e.g., the "gap"/"non-gap" sampling of Augspurger and Franson, 1988).

We recorded the duration and the sample frequency of each study, and we examined the relationship between sampling interval (length of time between data collections) and the duration of the study. Studies designated as <1 yr in duration were those for which sampling encompassed a single fruiting or growing season.

Search strategy—We used different strategies to summarize recruitment literature depending on life history stage. The survey reflects our research interests, being dominated by recruitment studies in forested ecosystems and being biased toward studies of temperate deciduous and boreal forest. For seed fecundity, dispersal, and seed banks we attempted comprehensive reviews. We included all studies we encountered that contained at least some estimate of seed production or dispersal. For seed banks we noted whether each study quantified densities in soil cores as opposed to seed mortality in burial experiments. We further noted whether seed inputs to the seed bank were measured simultaneously.

We did not attempt comprehensive analysis of seedling establishment, growth, and survival studies, because the literature is large. Instead, we sampled papers listed in *Biological Abstracts* since 1969, with emphasis on *American Midland Naturalist, Canadian Journal of Forest Research, Ecology, Ecological Monographs, Journal of Ecology, Oecologia,* and *Oikos*. "Establishment" studies consider germination and first-year survival. "Growth and survival" studies consider dynamics of seedlings older than 1 yr. For each published study we determined the number of factors studied, including microsites, seedling competition, canopy gaps, predation, pathogens, and resources. For each "factor" we determined the number of "factor types." Thus, "microsites" (Harper, Williams, and Sagar, 1965) represents one factor that can include a number of microsite types, such as nurse logs, pits, and mounds. "Canopy gaps" is a factor that includes gap types that might be defined by different sizes or modes of origin. The factor "predation" includes different types of seed or seedling predators, sometimes represented by selective exclosures. Resources types included moisture, nitrogen, phosphorus, light, and carbon dioxide. We did not define as separate "types" different levels of manipulation of a single resource.

For sapling growth and survival we included papers listed in *Biological Abstracts* since 1985, supplemented by commonly cited papers published before 1985. In addition, we included the USDA Forest Service Forest Inventory Analysis (FIA) data sets and related publications listed on their web sites. We noted spatial and temporal sampling patterns and whether each study examined effects of environmental variables on growth or mortality.

Results from the literature—We reviewed >100 studies each on seed rain, seedling growth, and seedling establishment, 90 on seed banks, and 53 on sapling and tree growth and mortality.

Fecundity and dispersal—Seed rain studies in ecological journals tended to examine seed transport by wind or animals, whereas forestry journals were more apt to examine supply of seed to recently logged areas, especially for commercial softwood species. Sampling for seed production and dispersal varied widely, often within a single study. Estimates come from small sample plots, typically from seed traps or counts of seedlings in plots placed either at random within stands, in clear-cuts, and in open fields or oriented with respect to potential source trees. Nonrandom placement of samples was sometimes on a regular grid, along transects, along radii, or along hedgerows.

Most replication was concentrated "within stands" (Fig. 2b); most data concerned variability at scales relevant to local seed dispersal and few concerned differences that result from variability in stand structure or composition. Studies that sampled widely tended not to sample in a manner that provided replication. The vast majority of studies are taken

from a single stand, and studies that include more than five stands are rare (Fig. 2a). Even among studies including multiple stands, the numbers and locations of samples within each stand were often unique and rarely conceived with the intent of quantifying variability among stands or stand types. Estimation was not the goal of most studies. Indeed, some of the studies reporting the most intensive sampling efforts calculated only mean values (e.g., Fowells and Schubert, 1956; Alexander, 1969).

Because of the idiosyncratic nature of sampling, there was no relationship among studies between sample number and area per sample (Fig. 2c). We might expect such a relationship if acquisition of large numbers of samples limits the sizes of individual samples. Seed traps or sample plots typically range from 0.2 to 1.0 m^2 (Fig. 2c). Total area sampled for seed rain (number of stands × samples per stand × area per sample) also varied widely (Fig. 2d). Although most studies (including those involving seed traps) sampled <50 m^2 of soil surface, there were many that sampled large areas. Studies having large sample areas in Fig. 2d involved searching the ground surface for seeds or seedlings.

Interpretation of seed rain data usually entails assumptions concerning the source of seed recovered in samples. The knowledge of seed source studies varied widely. Precise knowledge is available for studies that test mechanistic models (Green, 1980; Augspurger and Franson, 1987; Matlack, 1987; Greene and Johnson, 1989), where direct observation of dispersal distance or settling time is related to drag, release height, a wind field, or some combination thereof. A coarser estimate of source applies to studies of seed rain near forest edges or around isolated trees studied in open fields or under closed canopies (Johnson, 1988). Here, seed density depends on the integrated production across a distributed source, represented by the nearby stand or by the canopy projection of an isolated individual. Still less knowledge is provided from seed rain studies under closed canopies where seed shadows of conspecific adults overlap. In these cases, inverse modeling permits statistical estimates of seed shadows (Ribbens, Silander, and Pacala, 1994; Clark, Macklin, and Wood, 1998; Clark et al., 1999).

Seed banks—Seed bank studies were of two types. The more common type (80%) involved the extraction or germination of buried seed from soil cores to estimate densities (Fig. 3a). The less common type (20%) involved seed burial experiments to determine the term of viability. Whereas soil core studies generally focused on the entire seed bank or on that for a group of species (e.g., herbaceous taxa), burial experiments typically assayed for one or a few species.

Sampling effort for seed banks indicates a trade-off between sample number and area per sample such that total area sampled (median = 0.9 m^2) deviates little across studies relative to differences in sample number and area per sample. The scatter of points in Fig. 3b does not deviate far from −1, which describes the case where investigators tend to expend similar sampling efforts (similar total areas), compensating for larger numbers of samples with proportionate reduction in area of individual samples. Thus, while a few studies sampled as much as 5 m^2 of the forest floor (Fig. 3c), the studies that used large sample areas did so at the cost of low replication. Nearly all studies having >100 samples per plot had individual samples <0.01 m^2 (Fig. 3b). Soil cores and other samples used in seed bank studies are, on average, an order of magnitude smaller in area than samples of seed rain (compare Figs. 2d and 3c).

Seed banks in forests are often dominated by herbaceous taxa, fostering a notion that seed banks are unimportant for woody species. Thirty-four of the 50 studies that used soil cores to examine the diversity of seed banks (as opposed to the seed bank of one or a few taxa) concluded that seeds of woody plants were too rare to have much effect on population dynamics. This conclusion appears to come more from a perceived paucity of woody plant seeds in comparison with herbaceous plants than it does from analysis of seed bank contribution to demography. Few seed bank studies produce data pertaining to dynamics—

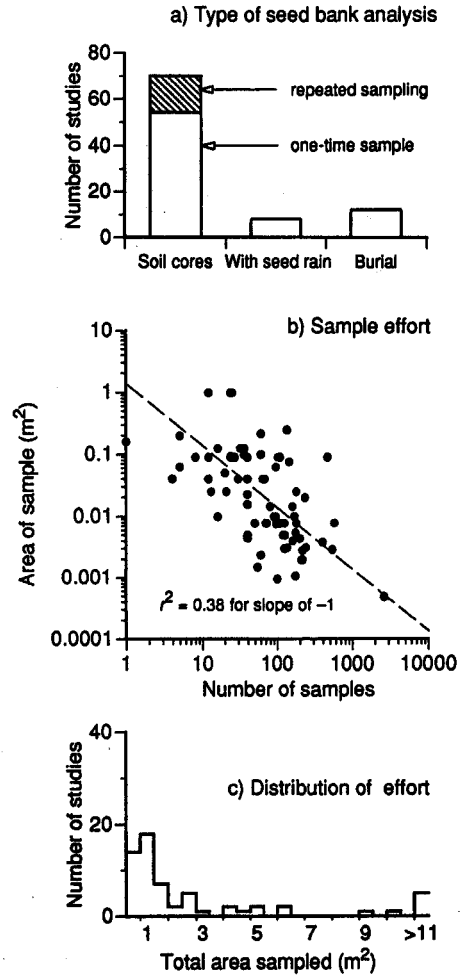

Fig. 3. Sampling of seed banks from the survey of literature. Most studies are from soil cores, few of which include repeated samples or comparisons with incoming seed rain (a). The proportionate decline in area per sample with increasing sample number is represented by the slope of −1 on the log-log plot, which explains 78% of the scatter (b). Most studies sample <0.2 m^2 of the soil surface (c).

most examine only density. Burial experiments (to determine rates of viability loss) and comparisons of densities with incoming seed rain are few (we encountered 12 seed burial studies and eight studies combining seed rain and seed banks).

Although often rare in comparison with herbaceous seeds, seed banks appear important for a number of woody perennials. *Rubus* (at least six species) was common in North America (e.g., Whitney, 1986; Morgan and Neuenschwander, 1988) and Europe (Granstrom, 1987) and in at least one study each from Australia (Hopkins and Graham, 1987) and Japan (Higo, Shinohara, and Kodama, 1995). *Betula* (at least four species) was found in 16 studies from North America (e.g., Marquis, 1975; Houle, 1994), Europe (Granstrom and Fries, 1985; Granstrom, 1987) and temperate Asia (Osumi and Sakurai, 1997). Seed banks of the New World Tropics often include *Cecropia* (e.g., Holthuijzen and Boerboom, 1982; Alvarez-Buylla and Martinez-Ramos, 1990; Dalling, Swaine, and Garwood, 1995), and those in Australia commonly include *Acacia* (e.g., Vlahos and Bell, 1987; Auld and O'Connell, 1989). In general, early-successional species have higher seed bank densities in temperate forests than do late-successional species (Morgan and Neuenschwander, 1988; Peterson and Carson, 1996).

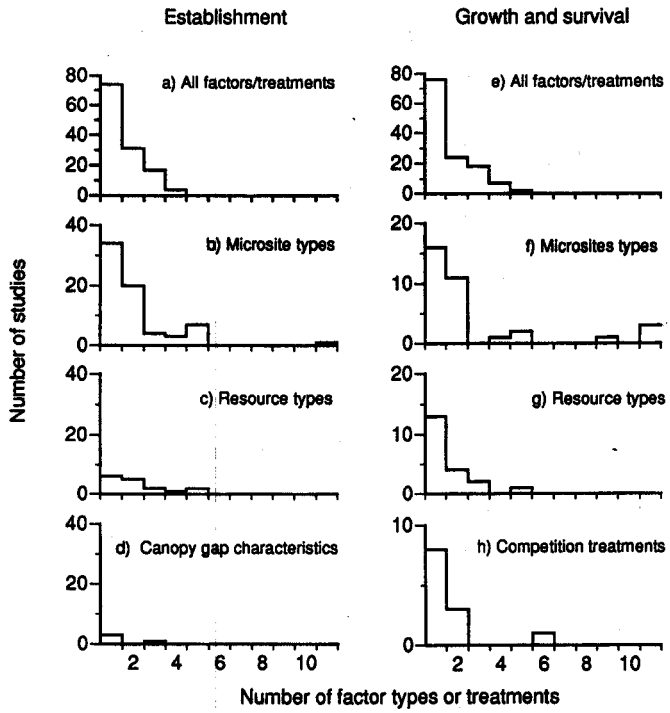

Fig. 4. Numbers of factors and factor types or treatments examined in studies of seedling "establishment" (left) and "growth and survival" (right). Factors in (a) and (e) include microsites, predation, canopy gaps, resources, competition, and predation.

Seedling establishment and growth—Studies of establishment and growth and survival most often considered a single factor (i.e., microsites, predation, gaps, resources, competition, or pathogens), but some included five or more factors (e.g., Chapin et al., 1994; Goldberg, 1985) (Fig. 4). Moreover, upon breaking factors down into factor types, we found that studies typically reported on a single type (Fig. 4b, c, d, f, g, h). Microsites were the most popular (~50%) factor of study (Fig. 5a, c). Analyses of microsite effects typically considered the effects of a single microsite type, and studies considering more than two microsite types were rare (Fig. 4b). The most popular microsite types were related to fire, pit and mound topography, and nurse logs. Huenneke and Sharitz (1986) considered an unusually large number of microsite types (16 in Fig. 4f).

Next in popularity after microsites were predation, canopy gaps, resources, competition, and pathogens, respectively (Fig. 5a, c). Most predation studies examined loss of seed from feeding stations located in specific microsite types (e.g., Gill and Marks, 1991; Augspurger and Kitajima, 1992). Less common were studies employing experimental exclosures (e.g., DeSteven, 1991) or manipulating predator densities (e.g., Ostfeld, Manson, and Canham, 1997). Few gap studies examined more than one canopy gap type, although an exceptional study (Sork, 1985) included four types (Fig. 4d). As with other factors, resource studies tended to focus on a single resource (Fig. 5c, g), but studies were rather uniformly distributed among the six categories of resource types we used (Fig. 5b, d). Factorial studies rarely included more than three resources. Competition studies were more common for the growth and survival phase than they were for establishment (Fig. 5a, c). A few studies considered competition for two resources (Fig. 4h).

Duration of early recruitment studies—Analyses of recruitment are short lived. While there are exceptional seed rain studies lasting more than a decade, most studies span a single year, and few exceed 5 yr (Fig. 6a). Some of the longest studies suffer from inconsistent estimation procedures (e.g., Hagner, 1965). Studies of seed banks from soil

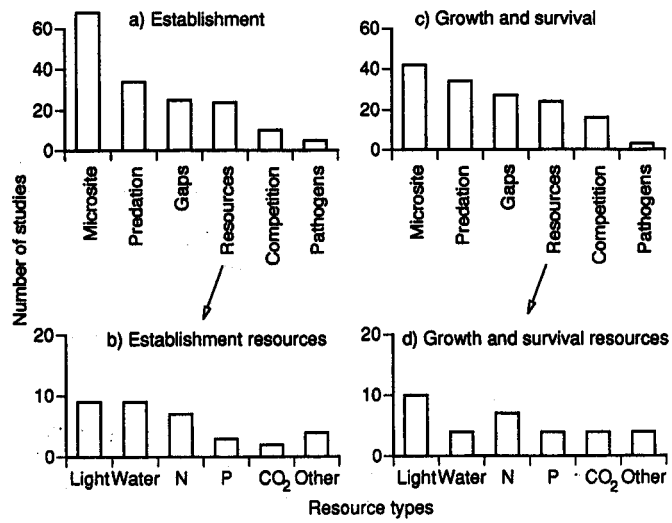

Fig. 5. Distributions of studies among factors (above) and a breakdown of resource studies into resource types (below).

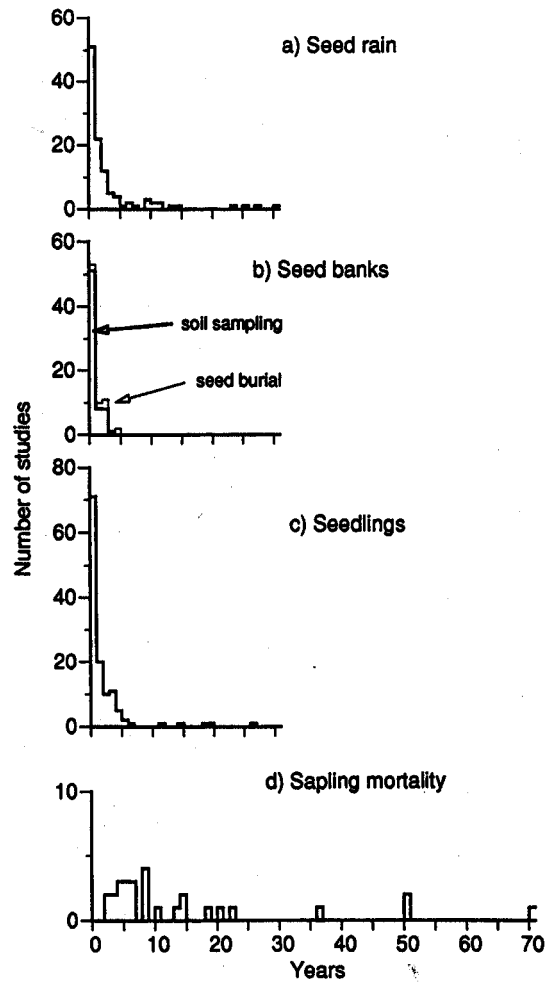

Fig. 6. Distributions of durations of studies in the literature survey.

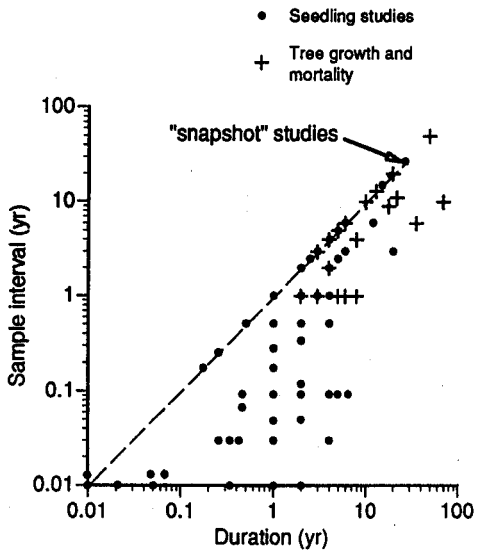

Fig. 7. The relationship between study duration and mean sample interval for seedling and tree growth and mortality studies.

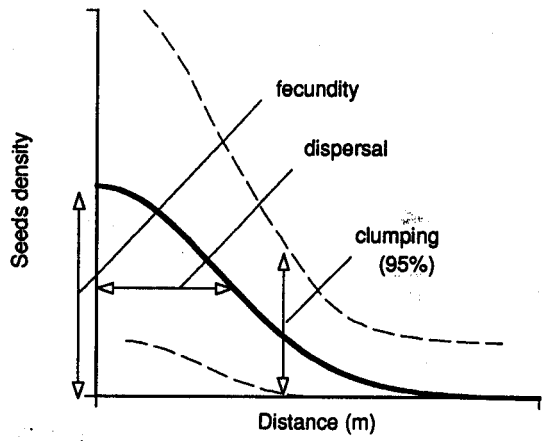

Fig. 8. Seed rain parameters include fecundity (seed production per unit basal area) and dispersal (m). The clumping index is the fitted shape parameter of the negative binomial error distribution. High values tend to a spatial Poisson process. Low values indicate clumped data.

cores are mostly single samples (i.e., "0" yr in Fig. 6b), and we found none exceeding 2 yr. Seed burial studies are few, but they tend to last >1 yr. Studies of seedling establishment, growth, and survival tended to last longer than seed bank studies, but the vast majority spanned <2 yr (Fig. 6c). As for seed rain studies, there were a few exceptionally long studies. There was substantial variability in sampling intensity (Fig. 7). The longest studies tended to come from a single census interval. No studies lasting more than a decade sampled at greater than annual frequency. We did find a number of seedling studies lasting >1 yr that sampled more than once a year.

Sapling growth and mortality—We considered only growth and mortality studies that exceeded 1 yr. Fifty-three studies spanned a continuum from intensive short-term studies of growth and mortality as a function of resource availability (e.g., Pacala et al., 1994) to extensive long-term studies where growth and mortality were studied without reference to causal mechanism [e.g., the U.S. Forest Service's Forest Inventory Analysis (FIA)]. Short-term (<5 yr) studies tended to focus on saplings and smaller trees, while long-term (>10 yr) studies were mostly limited to canopy and large understory trees. Studies that include detailed resource measurements had smaller sample sizes (75–1800 individuals) than did long-term census data. Most studies reported diameter growth rates determined by tree ring analysis or from repeated censuses of permanent plots. Some short-term studies of saplings reported height or internode growth. Studies spanned a broad range of durations (Fig. 6d) due in large part to recensuses of "historic" data sets by investigators other than those who initially established plots.

The FIA represents the largest and most extensive data set. Data are collected in all 50 states on permanent plots established as far back as the 1930s. Plots are resampled every 5–15 yr. Growth data are available for trees >2.54 cm in dbh (diameter at breast height), but mortality come only from trees >12.7 cm dbh. Spatial and environmental data are lacking for most plots (Hansen et al., 1992). Ecologists have made little use of FIA data (Rudis, 1991), preferring instead to design studies tailored to ecological questions (Harcombe and Marks, 1983; Hubbell and Foster, 1986a, b; Clark and Clark, 1992).

Short-term, intensive studies examined effects of light availability on growth and mortality. Some studies reported correlations between growth rates and light availability in the understory. Although a number of studies correlated sapling growth rates and light availability, our survey encountered only seven studies that reported regressions of growth rates and light (Hix and Lorimer, 1990; King, 1991, 1994; Lieffers and Stadt, 1994; Pacala et al., 1994; Kobe et al., 1995; Chen, Klinka, and Kayahara, 1996). With the exception of Hix and Lorimer (1990), all of these studies considered only small (<5 cm dbh) saplings. Hix and Lorimer (1990) reported growth as a function of canopy exposure for large trees.

Few studies examined the relationship between nutrient availability and growth of individual trees. A single paper in our survey reporting regressions of nutrient level and individual tree growth (Mitchell and Chandler, 1939) focused on nitrogen. The fact that recent models (including Pastor and Post, 1985) use the nitrogen function developed by Aber, Botkin, and Melillo (1979) from Mitchell and Chandler (1939) reflects lack of data on nutrient effects at the individual tree level. Lack of study relating nutrient levels to individual tree growth contrasts with a large literature relating nutrient levels to stand level processes (e.g., biomass per hectare, net primary production) (e.g., Binkley and Högberg, 1997; Magill et al., 1997; Reich et al., 1997).

In summary, we find a tendency for short-term studies that concentrate on sampling of a few factors at a particular spatial scale. Whether the existing approaches are sufficient basis for estimating recruitment demography depends on variability across these scales of space and time. In the next section we examine parameter estimation at these scales.

IS THE SAMPLING EFFORT SUFFICIENT?

We used an extensive, long-term set of experiments and permanent plots to assess how sampling efforts described by our literature survey affects the ability to estimate the vital rates in Fig. 1. The data sets come from five stands that vary in moisture status and elevation in the southern Appalachians (Clark, Macklin, and Wood, 1998). Experiments and monitoring span 7 yr (1991–1998) and each of the life history stages in Fig. 1. Our strategy was to estimate parameters for subsets of this data set comparable to those we found in the literature and to compare estimates with those we obtain using the full data set.

Analysis—Fecundity and dispersal—To analyze how sampling effort affects estimates of seed rain we used data from 100 seed traps from our five stands collected over 7 yr. Clark, Macklin, and Wood (1998) and Clark

(1998) use a 6-yr portion of these data to determine seed shadows, including parameter estimates, confidence intervals, and power curves. The method uses the spatial relationships between trees and seed traps to estimate fecundity, dispersal, and clumping (Fig. 8). The model assumes that seed shadows have a Gaussian shape and depend on fecundity (seed production per square meter basal area) and on dispersal distance, represented by a distance parameter.

Confident estimates of seed shadows depend on having sufficiently large maps of trees to insure that most of the seed arriving in a seed trap emanate from trees that are included in the sample. Unfortunately, censusing of trees is time consuming, so there are limited numbers of such plots, and the areas of mapped plots might not be sufficient to insure good seed shadow estimates. We asked how the sizes of the mapped plots affects our ability to accurately estimate dispersal parameters. To assess this size effect, we used Clark, Macklin, and Wood's (1998) statistical model with negative binomial error, but modified the area of the mapped stand to include potential source trees in increasingly wide buffer distances surrounding the central area where seed traps were located. For each buffer width we determined maximum likelihood (ML) estimates for fecundity, dispersal distance, and clumping (Fig. 8) with bootstrapped confidence intervals.

We then asked how the duration of the study affected parameter estimates. Beginning with seed rain data from our first sample year (1991–1992), we estimated seed shadow parameters from Fig. 8. We determined how parameter estimates changed as we increased the duration of the study by bootstrapping parameters with each additional year of data up to the full 7-yr data set.

Finally, we determined how the inclusion of different stand types affects estimates of fecundity and dispersal. Seed shadows were estimated individually for each of several stands and compared with the seed shadows estimated from the composite data set.

Seed banks—Most studies suggest that seed banks are highly variable, but we were unable to determine from the published literature how much sampling is needed in temperate forests to obtain an accurate estimate of density (for herbaceous communities, see Benoit, Kenkel, and Cavers, 1989; Gross, 1990). To determine how seed bank estimates change with sampling effort, we estimated seed banks for subsets of our data set, which included 66 soil cores per stand from four stands in 1995, three stands in 1996, and five stands in 1997 (HilleRisLamber and Clark, unpublished data). To examine differences among stands and among years, we estimated mean densities with Bayesian confidence intervals. To determine how estimates and confidence intervals are affected by numbers of cores per stand, we bootstrapped 100 estimates for each of 12 year-and-stand combinations.

Data analysis was motivated by theoretical expectation, empirical observation, and convenience. We assumed seed density to be a spatial Poisson process, but with a mean (parameter) of the Poisson varying among samples according to a gamma distribution. Together, these assumptions imply that the marginal distribution of seed density is a negative binomial distribution. The Poisson embodies the notion that seed location is spatially stochastic. Distributions of mean values obtained from our data were well described by a gamma distribution (Beckage et al., unpublished data). The negative binomial is consistent with the clumped distributions observed for seed and seedling distributions (Clark, Macklin, and Wood, 1998). The gamma prior and Poisson likelihood represent a convenient combination, because the conjugate gamma prior allows for sequential analysis as the data set is enlarged to include new plots and/or additional sample years. Our gamma prior was extremely weak, having a weight equivalent to 1/1000 of a 1-m^2 soil core.

Seedling establishment—To determine the spatial and temporal extent of samples needed to estimate recruitment of new seedlings, we examined how estimates changed with sampling effort. Our data set consisted of 60 1-m^2 seedling subplots distributed over five stands and censused annually for 6 yr (Beckage et al., unpublished data). Each new (1st-yr) seedling was censused in subplots and used to estimate annual recruitment rates (number of seedlings per square metre per year). We used methods described for seed banks to determine mean estimates and Bayesian confidence intervals for subsets of the full data set, including individual years, individual stands, and numbers of 1-m^2 subplots within stands. We determined how estimates and confidence intervals changed as we sequentially enlarged our sample sizes to include the full data set.

Sapling and tree mortality—Sampling effort is deemed important for mortality studies, because mortality rates tend to be low. We asked how estimates of tree mortality are affected by sampling effort using data from three censuses from five 0.64-ha permanent plots, with census intervals spanning 1991–1993, 1993–1995, and 1995–1996. Our Bayesian estimation method (Wyckoff and Clark, unpublished data) starts with a prior beta density of mortality parameterized with numbers of live and dead stems encountered while walking transects in the five stands. Prior mortality rates were calculated from these data by dividing the ratio of dead to total trees by an estimate of the length of time dead trees remain on the landscape (Kobe et al., 1995). Together with a binomial likelihood, we generated successive beta posterior densities of mortality rate as the basis for Bayesian confidence intervals as the data set was enlarged to include additional censuses.

How data limitation affects estimation—Seed rain—Estimates of seed shadows depend on the survey area in which source trees are mapped. By expanding the area from which trees are sampled around our seed traps we changed our estimates of seed production (fecundity parameter in Fig. 9a) and dispersal distance (Fig. 9b). When too small an area is used to estimate the sources of seeds (Fig. 9a), fecundity is overestimated, because seeds in seed traps or seedlings in sample plots may derive from trees outside the sampled area. Only at buffer widths >10 m did we obtain stable estimates of the dispersal parameter. In a broader survey of sampling effects on dispersal estimates Clark, Macklin, and Wood (1998) found that dispersal estimates stabilized at consistent val-

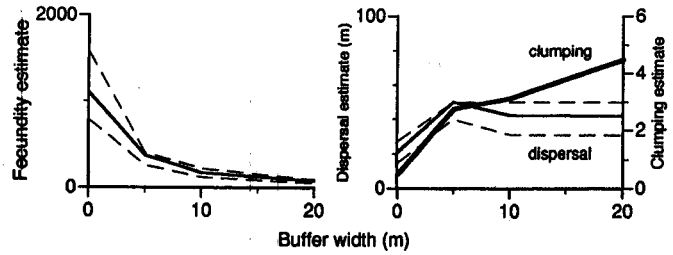

Fig. 9. Effect of plot size on fecundity and dispersal estimates from Fig. 8. Parameter estimates stabilize as buffer around the center area containing seed traps is extended to 10–20 m. Fecundity has units of seeds·m^{-2} basal area·yr^{-1}.

ues when buffer widths approached the value of the parameter itself. The dispersal estimate of 20 m in Fig. 9b is accurately estimated as the buffer width is extended beyond 10 m.

The explanation for the declining estimate of clumping (indicated by an increase in the clumping parameter in Fig. 9b) with plot size is more complex. In some respects, clumping can be viewed as variability among plots that cannot be explained by the source trees. Small survey plots leave out trees that contribute seed, which results in an overestimate of clumping. As plots are enlarged, more of the variance in the data is explained by the dispersal model and, hence, the data appear less clumped.

Large differences in fecundity across different stand types means that samples from single stands may not be representative. Figure 10 shows examples of seed shadows from three species fitted to seed rain in individual stands (left side) contrasted with those obtained when fitted to all stands simultaneously (right side). *Nyssa* and *Betula* showed extreme differences among stands in fecundity (left side) and, consequently, large error in seed shadows for composite data sets (right side). *Acer* showed rather uniform fecundities among sites and thus was well summarized by the composite estimate. In general, we have found that fecundity varies more strongly among stands than does dispersal distance (Clark, Macklin, and Wood, 1998). The 95% confidence intervals on composite seed shadows (dashed lines) are especially wide close to the source, indicating relatively large uncertainty in fecundity, rather than dispersal distance.

Long-term data were needed to obtain reliable estimates of seed shadows. The two examples we include in Fig. 11 show parameter bias and large uncertainty with data obtained from short time series. Scatter plots of bootstrapped parameter estimates (above) show negative parameter correlations for both species with data sets spanning <3 yr ("1991–1992"). With 3 yr of data ("1991–1993"), a positive correlation in *Acer* estimates develops. Not until the 1995 data collection does the dispersal parameter estimate stabilize and confidence intervals fall to acceptable levels (Fig. 11c). After 6 yr of data the *Acer* fecundity estimate still had not stabilized (Fig. 11b). The fecundity estimate for *Nyssa* varies widely across the first 4 yr of data, stabilizing by the 5th yr (Fig. 11d). Error in dispersal estimates for *Nyssa* decline to stable values over the first 3 yr (Fig. 11e).

Seed banks—Seed bank densities varied more among

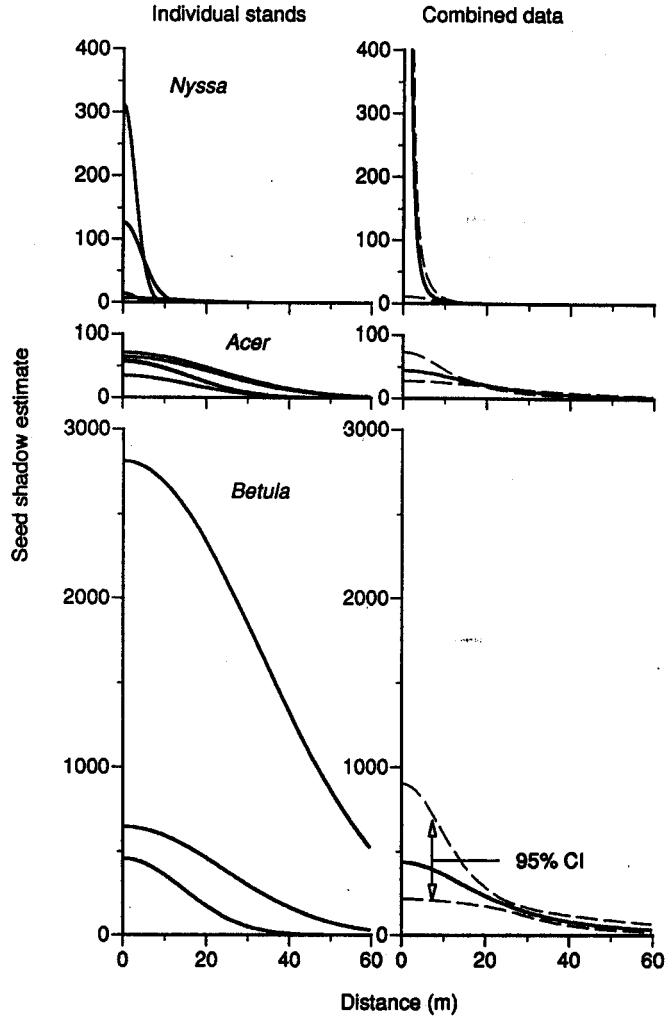

Fig. 10. Seed shadow estimates for individual stands (left-hand side) and for data from all stands simultaneously (right-hand side). Dashed lines on right are 95% confidence intervals determined by propagating parameter error and correlation (Clark, 1998). The seed shadow has units of seeds·m^{-2}·yr^{-1}.

stands than they did among years (Fig. 12). Tight Bayesian confidence intervals indicate that variability among stands and years is not due to inadequate sample sizes. The examples for *Betula* and *Vitis* demonstrate seed bank patterns that match differences in stand composition (Fig. 12a). Although *Vitis* was rare in 1996, variability among years is otherwise low (Fig. 12b); estimates of densities using the cumulative data set do not show strong trends (Fig. 12c).

Sample size affected how well we could estimate seed bank density within stands. *Betula* seed, which is abundant and evenly dispersed in our study area (Clark, Macklin, and Wood, 1998), obtained stable estimates with only 20 soil cores (Fig. 12d). *Vitis* represents a more typical pattern, where seed is less dense and clumped. For most species >60 soil cores were needed to obtain stable estimates (Fig. 12e). Limited ability to estimate seed banks results from use of small diameter soil cores and from several sources of variability in the data that cause a high degree of clumping. Seed bank densities tend to be high

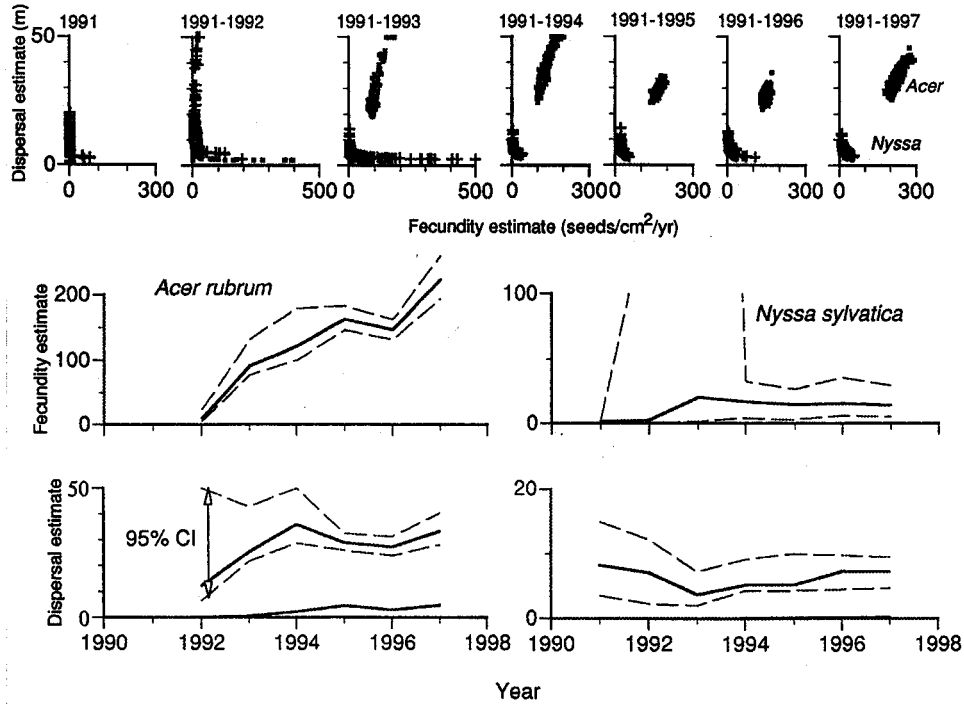

Fig. 11. Effect of study duration on parameter estimates from Fig. 8. Upper series shows scatter of bootstrapped parameter estimates as the data set is enlarged to include from 1 to 7 yr of seed rain data. Initially there is large negative correlation between parameters, which decreases with several years of data. Below shows how parameter estimates from Fig. 8 with their confidence intervals change for the same interval. Fecundity has units of seeds·m^{-2} basal area·yr^{-1}. Dispersal has units of m.

near source trees. Superimposed on the variation produced by locations of parent trees is clumping at a fine (square metre) spatial scale. This fine-scale variation is produced by secondary dispersal of seed and microrelief (Matlack, 1989; Carlton and Bazzaz, 1998).

Germination and establishment—We found large year-to-year, stand-to-stand, and within-stand variability in seedling recruitment that was not well characterized by estimates from single years or from single stands (Fig. 13). As with seed banks, tight Bayesian confidence intervals indicate sample sizes are large enough to accurately describe recruitment rates in any one stand (Fig. 13a) or year (Fig. 13b). But the estimates are unique to a particular time and place, fluctuating widely among stands and years. For example, *Acer* showed unusually high recruitment rates in 1995 (Fig. 13b) and in a cove hardwood stand (stand 2 in Fig. 13a). *Quercus* had substantial recruitment following the single mast year that occurred during our sample interval (Fig. 13b), which was limited to high elevations (stands 4 and 5 in Fig. 13a). Within any one year or stand, we found that the number of 1-m^2 subplots needed to gain a confident estimate of the mean recruitment rate depended on abundance. For the rather abundant *Acer rubrum* we found that 30 subplots were sufficient (Fig. 13d), but larger numbers of plots are needed for most species.

If we were to sample continuously over time, how long would we need to sample to achieve consistent estimates of recruitment? We cannot answer this question from our data sets, but 6 yr is not enough (Fig. 13c). Unlike seed banks, where variance among stands dominates, seedling establishment shows high year-to-year variability (Fig. 13b, c). This variability suggests that confident estimates of mean and variance might require up to a decade.

Sapling and tree mortality—Confidence in mortality estimates increased with increasing numbers of censuses, but progressive contraction in Bayesian confidence intervals converged only slowly after the first census. Prior estimates of *Acer rubrum* and *Cornus florida* mortality rates overlapped, but the estimates became distinct with the addition of census data. By the third census, which occurred in year 5, the rate of contraction suggests that additional censuses would cause modest change in parameter estimates and confidence intervals.

EXISTING DATA IN THE CONTEXT OF ANALYSIS

Ideally, we strive for experiments and sampling schedules tailored to the variability in data. Prior estimates of variance are the basis for sample number and their distribution in space and time, across the relevant sources of variability. In the absence of prior information, we begin with our best guess as to response variability, but each new analysis can help refine that knowledge.

Despite a long tradition in ecology that could provide the background to guide sampling designs, the literature contains few studies with sufficient scope to permit confident estimates of recruitment parameters. Moreover, we sense little attention in recruitment studies to building on what is already known from this tradition. We do not imply that sampling is routinely inadequate for the spe-

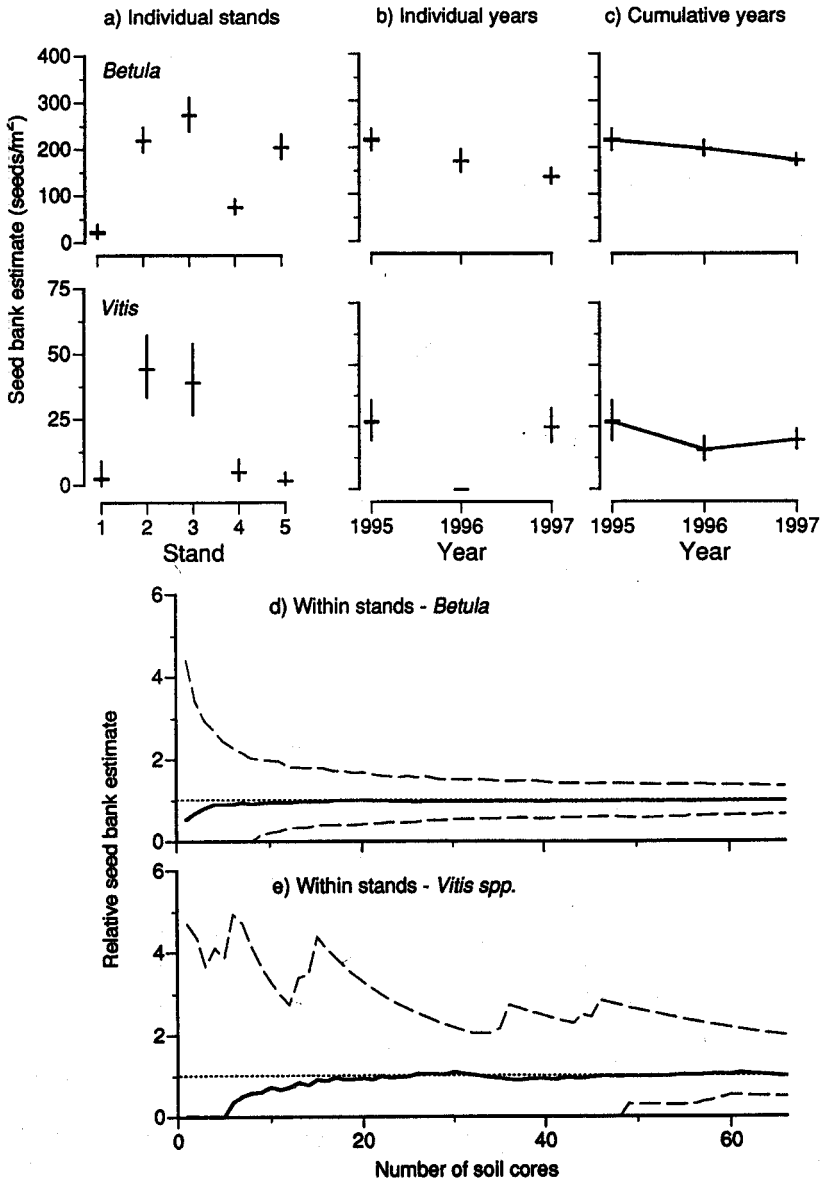

Fig. 12. Effect of numbers of samples (a) and of years (b and c) on seed bank estimates. Vertical lines are 95% Bayesian confidence intervals. Parts (d) and (e) show progressive change in parameter estimates using a cumulative data set. The relative estimates in (d) and (e) are expressed as a ratio of the estimate for a given number of cores relative to that obtained with the full data set.

cific goals of individual experiments. Nor do we argue that the questions asked by individual studies ignore results of previous work (the Connell-Janzen hypothesis is addressed repeatedly). Rather, the goals may be too narrow to shed much light on recruitment limitation in general.

Where and when sampling effort is inadequate—Our analysis demonstrates a gulf between sampling effort typical of recruitment studies and that needed to estimate recruitment parameters. The legacy of seed rain studies, for example, could have alerted us by now to the inadequacy of single-fruiting season estimates (Downs and McQuilkin, 1944; Fowells and Schubert, 1956; Daubenmire, 1960; Hagner, 1965; Lester, 1967; Alexander, 1969; Gashwiler, 1969; Harris, 1969; Larson and Schubert, 1970; Zasada and Viereck, 1970; Rehfeldt, Stage, and Bingham, 1971; Godman and Mattson, 1976; Noble and Ronco, 1978; MacDonald, 1992; Graber and Leak, 1992; Hofgaard, 1993; Sork, Bramble, and Sexton, 1993; Koenig et al., 1994). While the fact that few studies extend beyond 5 yr will come as news to few ecologists, we were surprised by the preponderance of effort devoted to single-year (or less) analysis. The tendency to sample few stands for a single year and to avoid true replication at several spatial scales makes the literature on recruitment inadequate for assessing simple questions of broad interest. Examples include the frequency and geographic coherence of mast cycles (Rehfeldt, Stage, and Bingham, 1971; Sork, Bramble, and Sexton, 1993) and recruitment success (Clark, Macklin, and Wood, 1998) and the relative importances of vital rates in Fig. 1 (Nakashizuka et al., 1995).

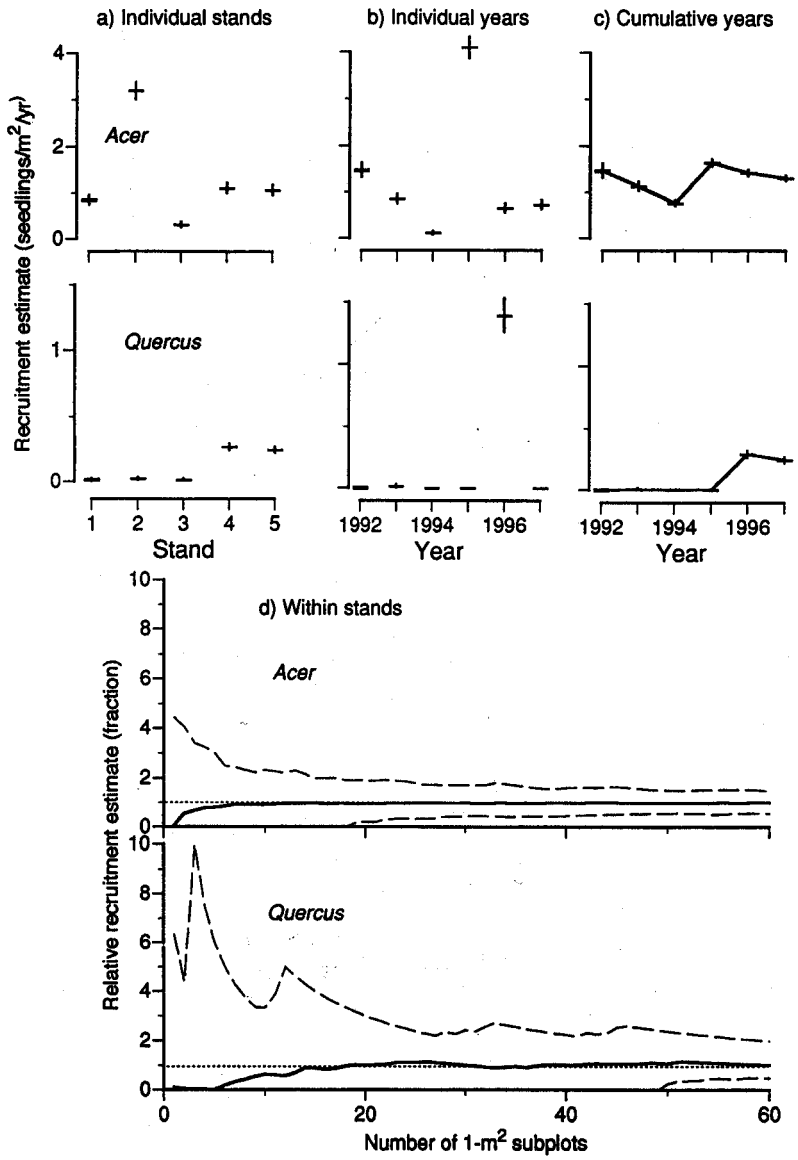

Fig. 13. Effect of numbers of samples (a) and of years (b and c) on recruitment estimates. Vertical lines are 95% Bayesian confidence intervals. Part (d) shows progressive change in parameter estimates using a cumulative data set. The relative estimates in (d) are expressed as a ratio of the estimate for a given number of cores relative to that obtained with the full data set.

The bias toward single-stand studies is actually worse than it appears from Fig. 2a owing to the fact that multiple-stand studies included there often are sampled inconsistently. Studies of seed rain are especially prone to intensive sampling at fine scales, often with many dozens of samples (Fig. 2b) concentrated in small areas (Fig. 2a). Seed banks and seedlings are likewise sampled at fine scales. Fine-scale variability makes this intensive effort valuable. Sample plots must include enough samples (Fig. 12) distributed over sufficient areas (Fig. 9) to capture effects of seed source, primary and secondary dispersal, and microtopography. But the variability in forest composition across landscapes is captured by sampling from different types of stands. Although seed dispersal distances can be rather consistent from stand to stand (Carkin et al., 1978; Clark, Macklin, and Wood, 1998) (despite differences between closed forest and open environments), fecundities can vary widely (Hagner, 1965). The order of magnitude differences in fecundities that we estimate across four stands in a single watershed for *Nyssa* and *Betula* (Fig. 10) (see also Rehfeldt, Stage, and Bingham, 1971) is but one example. Large differences among stands in recruitment rates (Fig. 13c, d) point to the importance of these differences in fecundities and to other factors that vary across landscapes. The tendency to sample single stands makes it difficult to generalize from the existing literature on any of the vital rates in Fig. 1.

We do not yet know the consequences of the small area of forest floor sampled in the course of most recruitment studies, but we can identify reasons why it might be cause for concern. The total area sampled during a typical seed bank study (median of 0.9 m^2) is equal to the basal area of a single 1.7 m diameter tree. The trade-off between sample size and number (Fig. 3b) sug-

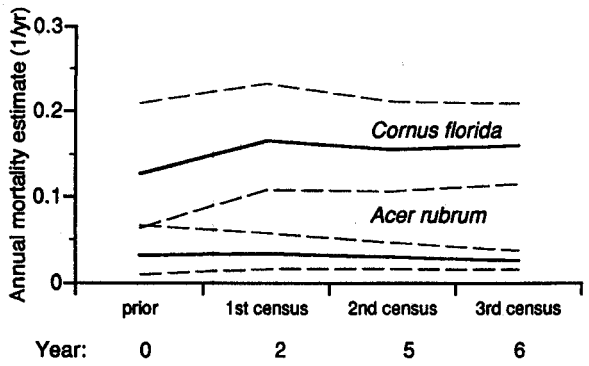

Fig. 14. Bayesian estimates and confidence intervals for mortality across successive censuses of permanent mapped plots.

gests that labor and time constrain sample effort. Simply deploying more samples of smaller size is not the answer because high noise levels in small samples (Fig. 12) ultimately necessitate averaging. Seed densities of most species are too low to allow confident estimates from extremely small samples (Fig. 12). Although soil seed banks in temperate forests are usually dominated by herbaceous taxa, seed dormancy is common for a number of early- to mid-successional arboreal species. Because seed banks are dynamic, spatially variable, and influenced by microclimates, soils, seed predators, all of which vary among stands, creative ways to obtain more representative data sets would be valuable.

Although we lack seed burial data of our own to analyze for effects of study duration, the few data sets that exceed 1 yr suggest most data sets fall short. After 2 yr of burial in Australian rainforest, Hopkins and Graham (1987) found viabilities of >50% for two *Acacia* species, >80% for *Smilax*, and >90% for *Rubus*. The longest seed burial study in our survey found >50% viability for *Betula* and >90% viability for *Rubus* after 5 yr (Granstrom, 1987). Variation in seed banks among seasons (Thompson and Grime, 1979) and with soil depth (Dalling, Swaine, and Garwood, 1995) further hint at our poor understanding of seed bank parameters.

The failure to obtain data sets of adequate duration is most extreme where the long-term data are needed most. Seed rain, seed banks, and seedlings, which are most often studied for a year or less (Fig. 6) and rarely span a typical mast cycle, have the highest spatial and temporal variability. These earliest stages of recruitment require ≥5 yr of data to obtain acceptable estimates (Figs. 11, 13a, b). By contrast, although tree mortality can be episodic (Harmon et al., 1986), mortality rate is the least variable of the vital rates we consider here (Fig. 14) (Wyckoff and Clark, unpublished data). Yet mortality is the parameter that has been most often estimated from long-term data (Fig. 6d), such as the Duke Forest Plots (Christensen and Peet, 1984), FIA, and the Barro Colorado Island plots (Condit, Hubble, and Foster, 1995). These studies provide key insights into the dynamics of mortality and growth, but low variability in mortality means that each additional year of data adds less new information than it would for the highly variable fecundity and seedling establishment. This is evident from the small changes in mortality estimates (Fig. 14) in contrast to large changes in fecundity (Fig. 11) and seedling establishment (Fig. 13a)—the benefit from each additional year of recruitment data, in terms of improved parameter estimates (Figs. 11, 13), makes increased sample length of value. Whereas a 1-yr extension of a sapling mortality study is unlikely to yield much change in our estimates (unless it spans an unusually high mortality year), a similar extension of a recruitment study could substantially modify estimates (Figs. 11, 13). Long-term data sets for mortality of sapling and larger size trees are likely to be most valuable for capturing the relatively rare catastrophic mortality that attends storms and insect or pathogen outbreaks. The short-term payoff of such studies is likely to be low in terms of improved mortality estimates (Fig. 14).

The focus on single-factor studies means that generalization requires piecing together many different studies. This approach has disadvantages, because (1) there are few commonalities in terms of sampling design that would permit close comparison, and (2) the many variables that differ among studies interact. Thus, the response to resources may depend on predation pressure (Lichter, unpublished data). This sort of interaction cannot be pieced together from the single-factor studies that dominate the literature (Fig. 4a, e), because covariances over space and time are unknown.

Just as important as the analysis of multiple factors is the need for multiple stages. The limitations on recruitment in Fig. 1 result from different causes, and the limitation at one stage can result from dynamics in another. The commonly discussed interaction between fecundity and seed predation (Sork, 1993; Crawley and Long, 1995; Shibata, Tanaka, and Nakashizuka, 1998) is a dominant control on seedling recruitment in experimental gaps in the southern Appalachians (Beckage et al., unpublished data). In the absence of seed rain estimates that study would have found little environmental control over *Quercus* recruitment in gaps. Effects of light availability, soil moisture, and soil temperature were only apparent after year-to-year variability in seed rain was taken into account.

How much detail is needed?—Population models based on Fig. 1a and parameterized with data used in our analyses indicate that most southern Appalachian tree populations at a given time and place are usually in decline (Clark et al., unpublished data). Across much of the forest understory recruitment rates are too low to permit canopy replacement. Analyses of stage-structured matrix models yield growth rates <1, and elasticities are dominated by sapling survivorship. The dominant contribution of survivorship is typical for populations in decline, because only survival of established individuals staves off population collapse (Caswell, 1985). Fecundity elasticities are low, because too few seeds become established and survive to sustain population growth—recruitment limits population growth much of the time. By partitioning the effects of fecundity and dispersal on the probability of seed arrival, Clark, Macklin, and Wood (1998) found that most of the forest floor fails to receive seed in a typical year, despite presence of adults. Low fecundity, limited dispersal, and clumping together result in poor coverage of the forest floor (Fig. 15). Depending on

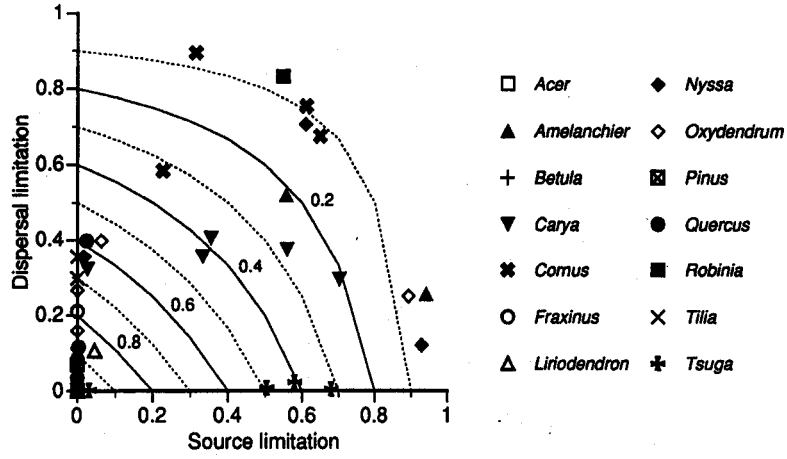

Fig. 15. Seed production and dispersal limitation in southern Appalachian forests. Contours represent the fraction of 1-m² patches on the forest floor expected to receive seed in a given year. The horizontal axis isolates the effect of seed production. Source limitation is the expected fraction of patches receiving seed if dispersal were not limiting, i.e., a spatial Poisson process limited only by seed production. A value of zero means no limitation–all patches are expected to receive seed. The vertical axis isolates the effect of seed dispersal. Dispersal limitation is relative difference between seed arrival given estimated seed shadows and levels of clumping vs that realized under unlimited dispersal with Poisson arrivals. A large number of species are limited by both seed production and by dispersal (from Clark, Macklin, and Wood 1998).

specific assumptions, the "Sapling immigration" view in Fig. 1b is represented either by the origin or by the horizontal axis in Fig. 15. If recruitment did not depend on seed production and dispersal, all points on Fig. 15 would lie at the origin. Our scatter of points across this coordinate space indicates limited seed production and dispersal for many species. We have found fecundity elasticities to be low everywhere except in large blowdowns, where recruitment can be so large as to offset population decline that prevails across most of the landscape most of the time. The stages of limitation vary among species and among stands (Clark, Macklin, and Wood, 1998; Beckage et al., unpublished data). Thus, in order to understand why some species are rare we needed to consider much of the detail in Fig. 1a and we needed to do so in different parts of the landscape.

Our analyses suggest (1) that the level of detail needed to identify the role of recruitment limitation is close to that summarized in Fig. 1a and (2) that the sampling effort needed to characterize that detail is beyond most studies now in the literature. Although more extensive sampling is clearly needed to estimate demography associated with recruitment, the solution is not simply one of impossibly large and long-term experiments. Indeed, creative approaches that minimize time-consuming field work is preferred. Insights gained from models that adopt simplistic views (e.g., Fig. 1b) demonstrate the value of pushing forward in the absence of ideal data sets. Attention to novel statistical approaches yield greater insights into dispersal pattern than previously available. In closed stands where seed shadows overlap, for instance, inverse modeling has provided parameter confidence and correlation (Ribbens, Silander, and Pacala, 1994; Clark, Macklin, and Wood, 1998), confidence in the seed shadow itself (propagation of parameter error) (Clark, 1998; Clark et al., 1999), the distribution of fine-scale variability (clumping) around estimated seed shadows (Clark, Macklin, and Wood, 1998), and power in dispersal estimates (Clark, 1998).

Nonetheless, longer term data sets are needed to estimate fecundity, seed bank dynamics, and early seedling growth and establishment. Long-term data sets are less critical for seed dispersal (because dispersal is more constant from year to year than is fecundity) and for mature tree mortality (because variability is low in contrast with other transitions in Fig. 1). Spatially extensive sampling is needed for most aspects of recruitment, because landscape diversity is controlled by the effects of environmental variability on transitions in Fig. 1. Although dispersal and mortality of saplings and large trees are relatively constant from year to year, variability from stand to stand is probably large. The interactions of factors that affect recruitment need better characterization. Taken together, the combination of existing sampling effort and analysis of how that effort contributes to parameter confidence suggest sampling at a broader scale, over longer durations, and of the interactions of forces that limit recruitment.

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