IMPLICATIONS OF SEED BANKING FOR RECRUITMENT OF SOUTHERN APPALACHIAN WOODY SPECIES

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Abstract. Seed dormancy is assumed to be unimportant for population dynamics of temperate woody species, because seeds occur at low densities and are short lived in forest soils. However, low soil seed densities may result from low seed production, and even modest seed longevity can buffer against fluctuating seed production, potentially limiting density-dependent mortality and ensuring that seeds are available for germination when recruitment success is likely. To investigate whether seed banking affects woody seedling dynamics in the southern Appalachians, we monitored seed rain, seed bank, and seedling densities to (1) determine the prevalence of seed banking among southern Appalachian woody species, (2) quantify annual seed mortality rates for three seed-banking species using a Bayesian statistical approach, and (3) assess whether or not the ability to seed bank affects recruitment rates. We found that the seeds of eight woody taxa (*Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*, *Nyssa sylvatica*, *Robinia pseudoacacia*, *Rubus* spp., *Sassafras albidum*, and *Vitis* sp.) remain viable in the soil for more than one year. Seeds of six taxa (*Amelanchier* spp., *Acer pennsylvanicum*, *Carya* spp., *Quercus prinus*, *Quercus rubra*, and *Tsuga canadensis*) were never found in the soil seed bank, despite high seed production and germination. For three species, a substantial proportion of seeds available for germination came from dispersal events two or more years in the past (*Acer rubrum* 12–37%, *Betula* spp. 59–73%, *Liriodendron tulipifera* 40–76%), even though annual seed mortality was high (*Acer rubrum* 70–98%, *Betula* spp. 21–81%, *Liriodendron tulipifera* 12–59%). In years when no seeds fall in local microsites (approximately one in five years), seed banks are the only source of seedling recruitment for these species. Comparing our results to those of previous studies led to valuable insights: first, that seeds of *Acer rubrum* and *Betula* spp. suffer high mortality while being incorporated into the seed bank; and second, that seed decay varies greatly over relatively small spatial scales (i.e., within a watershed). Taken together, these results demonstrate that seed banking may play a critical role during woody seedling recruitment in temperate forests.

Key words: Bayesian statistics; bet hedging; recruitment limitation; seed banking; seed dormancy; Southern Appalachian forests; species coexistence.

INTRODUCTION

Seed banking, the ability of seeds to remain dormant in the soil for several years following dispersal, can be crucial for the maintenance of plant populations. Spreading reproduction over time acts as a hedge against reproductive failure, especially for desert annuals experiencing unpredictable rainfall regimes (Philippi 1993, Pake and Venable 1995, 1996). Following disturbance, pioneer tree species often recruit from dormant seed, long after mature plants have disappeared with successional change (Marks 1974, Dalling et al. 1997, 1998, Tierney and Fahey 1998). Regeneration of many chaparral species depends on fire; seeds of these species remain dormant in the seed bank until germi-

nation is stimulated by exposure to heat or smoke (Keeley and Keeley 1988, Keeley and Fotheringham 1998).

Seed banking is often assumed to be unimportant for temperate woody species, despite evidence that seeds of many woody species persist in the soil for several years (Clark and Boyce 1964, Marks 1974, Marquis 1975, Wendel 1977, Haywood 1994, Houle 1994, Peroni 1995). There are a number of reasons for this view. In comparison with herbaceous species (especially annuals), seeds of woody species are not abundant in temperate forest soils (Matlack and Good 1990, Mladenoff 1990, Roberts and Vankat 1991, Schiffman and Carter-Johnson 1992, Thompson 1992, Yorks et al. 2000, Baskin and Baskin 2001) and they are generally short lived (<5 years: Clark and Boyce 1964, Wendel *1977, Granstrom and Fries 1985, Granstrom 1987, Houle 1992, 1994). Theory has shown that long-lived adult stages can buffer against periods of low recruitment (Cohen 1966, Warner and Chesson 1985, Chesson

TABLE 1.   Dominant tree taxa and site characteristics of five plots used in study.

Stand vegetation type and dominant taxa†	Elevation (m)	Max.–min. mean temp.‡ (°C)	Light level (% solar radiation at forest floor)§	Soil moisture (%)‖
Plot 1: ridgetop				
Pinus rigida, Quercus coccinea, Acer rubrum, Oxydendrum arboreum, Carya glabra	775	21.4–3.5	7.6	17.8
Plot 2: cove				
Liriodendron tulipifera, Acer rubrum, Carya glabra, Quercus prinus, Betula lenta	830	21.1–2.3	4.3	31.0
Plot 3: mixed oak 1				
Quercus prinus, Acer rubrum, Carya glabra, Oxydendrum arboreum, Nyssa sylvatica	870	21.8–2.7	3.8	23.9
Plot 4: mixed oak 2				
Quercus prinus, Acer rubrum, Quercus rubra, Oxydendrum arborea, Nyssa sylvatica	1100	19.7–2.0	4.6	21.0
Plot 5: northern hardwood				
Quercus rubra, Betula allegheniensis, Betula lenta, Tilia americana, Acer saccharum	1380	18.4–0.4	3.0	25.3

† Dominant taxa are shown in decreasing order of basal area.
‡ Average July (max.) and January (min.) temperatures from hourly data sets recorded at microclimate station from 1991 to present.
§ Averages from 20+ canopy photos, analyzed using Hemiview (Delta-T, Cambridge, UK).
‖ Averages of monthly soil moisture data recorded from 1991 to present, taken at 5-cm soil depth using TDR.

2000), which makes seed dormancy seem unnecessary for long-lived woody perennials.

The importance of seed banks for temperate woody perennials may be underrated, and based, in part, on limited data. Low seed bank densities can result from low seed production, while still accounting for a substantial fraction of seedling recruitment in any given year. Even modest seed dormancy can enhance seedling recruitment, because both seed production and environmental conditions favorable for seed germination vary widely from year to year (Houle 1994, Tapper 1996, Clark et al. 1998, 2004). Unfortunately, determining the extent to which seed banking can buffer recruitment of woody species against fluctuations in seed production and uncertain germination opportunities requires both long-term seed production data and seed mortality estimates, which are rarely collected simultaneously (Pickett and McDonnell 1989).

In this paper, we determine the contribution of seed banking to recruitment of temperate woody perennials in western North Carolina. We first identify seed-banking and non-seed-banking species using long-term seed rain, seed-bank, and seedling data collected at the Coweeta Hydrologic Laboratory in North Carolina, USA. We then use these data to quantify seed mortality of three seed-banking taxa, *Acer rubrum*, *Betula* spp. and *Liriodendron tulipifera*, using Markov Chain Monte Carlo (MCMC) model fitting and a Bayesian approach. Finally, we use seed mortality estimates and seed rain observations to estimate the contribution seed banking makes to seedling recruitment for these species. These estimates demonstrate that seed banking can provide an important hedge against environmental variability during early life history stages of southern Appalachian woody species.

METHODS

Study site

Coweeta Hydrologic Laboratory is located in the Southern Appalachians of western North Carolina (35°03′ N, 83°27′ W), and ranges in elevation from 500 to 1500 m. Precipitation is high throughout the year, with a maximum of 200 mm in March and a minimum of 110 mm in October. Average monthly temperatures range from 3°C in January to 22°C in July (Swift et al. 1988). Forests are secondary and have remained relatively undisturbed since the chestnut blight in the mid-1930s.

Forest composition varies with elevation (Whittaker 1956). *Betula allegheniensis*, *Liriodendron tulipifera*, and *Magnolia frasierii* dominate mesic low-elevation coves, while *Kalmia latifolia*, *Pinus rigida*, *Quercus velutina*, and *Sassafras albidum* are dominants on xeric ridge tops. *Carya glabra*, *Nyssa sylvatica*, *Oxydendrum arboreum*, *Rhododendron maximum*, and *Quercus prinus* are generally found on low- to mid-elevation slopes. Northern hardwood forests are found at upper elevations, with *Acer pennsylvanicum*, *Acer saccharum*, *Betula lenta*, *Fagus grandifolia*, and *Tilia americana* as dominants. *Acer rubrum* and *Quercus rubra* are common at all elevations. Five permanent vegetation plots were established in these forests at the Coweeta Hydrologic Laboratory in 1991. Sites were chosen to represent a range of communities and environmental conditions found in southern Appalachian

TABLE 2. Seed-banking status, dispersal vectors, seed rain, and seed bank densities (averages across all sites) of taxa surveyed.

Taxon	Persistent seed bank? (yes/no)	Dispersal vector	Seed rain (seeds·m^{-2}·yr^{-1}) [mean (95% CI)]	Seed bank (seeds·m^{-2}·yr^{-1}) [mean (95% CI)]
Acer pennsylvanicum	no	wind	3.49 (2.558–4.60)	0
Acer rubrum	yes†,‡	wind	71.91 (63.30–82.95)	16.51 (14.12–19.02)
Amelanchier spp.	no	bird	0.099 (0.0972–0.220)	0
Betula spp.	yes†,§	wind	1964 (1922–3404)	136.7 (124.7–148.2)
Carya spp.	no	mammal	0.719 (0.590–0.856)	0
Fraxinus americana	?†	wind	1.801 (1.241–2.42)	0
Kalmia latifolia	?	passive/wind	NA‖	56.72 (45.30–69.49)
Liriodendron tulipifera	yes†	wind	77.44 (65.14–91.70)	31.77 (26.63–35.36)
Nyssa sylvatica	yes¶	bird	2.18 (0.692–4.33)	0.432 (0.173–0.777)
Quercus rubra	no#,††	mammal/bird	7.048 (5.889–8.569)	0
Quercus prinus	no††	mammal/bird	7.048 (5.889–8.569)	0
Rhododendron maximum	?	passive/wind	NA‖	176.0 (160.3–192.5)
Robinia pseudoacacia	yes§,¶	?	0.057 (0.0063–0.120)	0.907 (0.432–1.381)
Rubus spp.	yes†	bird	NA‖	168.27 (153.35–182.51)
Sassafras albidum	yes†,¶	bird	0.0063 (0–0.0189)	0.176 (0–0.432)
Tsuga canadensis	no	wind	0.4661 (0.340–0.598)	0
Vitis spp.	yes†,¶	wind	0.8574 (0.106–1.757)	12.45 (10.10–14.93)

† Seeds remain viable for more than one year in buried bags (Marquis 1975, Wendel 1977, Haywood 1994).
‡ Seedling germination in spring occurs before seed set in spring (J. Hille Ris Lambers, *personal observation*).
§ Seeds remain viable in storage for more than five years (Burns and Honkala 1990; National Tree Seed Laboratory, *unpublished data*).
‖ Seeds not captured in traps: seeds too small (*Kalmia* and *Rhododendron*) or traps too high (*Rubus*).
¶ Seed bank densities in some, or all, years were greater than seed rain densities.
# Buried bag studies find seed longevity is less than one year (Marquis 1975, Haywood 1994).
†† All viable seeds germinate in less than one year after dispersal (J. Hille Ris Lambers, *personal observation*; National Tree Seed Laboratory, *unpublished data*).

forests (Table 1). Seed rain, seed bank, and seedling censuses were conducted in these five stands (designated ridge, cove, mixed oak 1, mixed oak 2, and northern hardwood [Table 1]).

Seed rain, seed bank, seedling censusing

Seed rain densities have been censused in all plots since 1991 (Clark et al. 1998, 1999, 2004). Within each plot, 20 seed traps are distributed as two transects of 10 traps (~30 m apart), with traps within transects separated by 5 m. Seed traps are 42 by 42 cm laundry baskets suspended on pvc stilts, lined with mosquito mesh and covered with coarse wire to deter rodent predation. Seeds are collected from traps three or four times annually, are identified to species, counted and archived (Clark et al. 1998, 1999, 2004).

We censused seed bank densities in late August, from 1995 to 1999 (except for the Ridge stand, which was sampled only from 1997 to 1999). Each year we removed between 40 and 86 7.5 cm diameter soil cores (to 5 cm depth) from each plot. Soil cores were stratified at 4°C for two months, and then spread over sterile potting soil in Duke University greenhouses after removing litter, rocks, and roots. Pots were watered daily, fertilized monthly, and natural lighting was supplemented by artificial light in the greenhouse. We found low densities of viable seeds in control pots (pots filled with sterile potting soil only), and no seedlings of the woody species we focus on (Table 2), indicating that contamination from seed sources near the greenhouse

was minimal. Each emerging seedling was identified and counted, and total seedling counts were used to estimate the density of viable seeds in the soil. Soil cores were monitored twice monthly for eight months, well after new seedlings ceased to germinate. By collecting soil cores after peak seed germination, but before seed dispersal of most species, the likelihood of sampling species that accumulate seeds in the soil is high (Thompson and Grime 1979).

Seedlings were censused at the same locations as seed bank censuses in July of each year beginning in 1996. Seedling plots consist of 86 1 × 1 m seedling quadrats. Seedlings were identified as first-year and second-year (or older) cohorts based on the presence of cotyledons and the absence of stem woodiness.

ANALYSIS

Identifying seed-banking species

We determined seed-banking status for species present in plots as adult trees, as dispersed seeds, and as viable seeds in the seed bank or as first-year seedlings (~17 of the >30 woody taxa present in our plots). All temperate woody seeds at our site reside on or in the soil between seed dispersal (occurring in autumn for most species) and germination in the spring (Baskin and Baskin 2001: Fig. 1). Thus, species with viable seeds in the soil had to fulfill one of two additional criteria for us to designate them as ''seed banking.'' If seed bank densities in any plot/year combination ex-

ceeded seed densities of the most recent dispersal event (we used bootstrapped confidence intervals to determine significance), then it is likely that some of those seeds must have originated from prior dispersal events. This is a conservative test, because our estimates of seed bank densities are based on viable seeds, while our seed rain estimates are based on the density of all seeds in seed traps, many of which may not be viable (Burns and Honkala 1990; National Tree Seed Laboratory, *unpublished data*; Appendix Fig. A1). Second, we used published accounts of buried seed studies to identify species with seed longevities that exceed one year. We used the following criteria to identify species that do not seed bank: species that are present as seeds *and* as first-year seedlings the following growing season, but absent from seed banks. We also used published buried seed studies to verify that these species have seed longevities that do not exceed one year.

Estimating seed mortality

We estimated seed mortality rates of three seed-banking species that had sufficiently high seed rain and seed bank densities to perform statistical analyses (*Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*). To estimate seed mortality rates (including losses due to germination) we developed a model relating annual seed rain to seed bank densities. We modeled seed decay as an exponential loss of seed viability over time, because that is consistent with data from several seed burial studies (Appendix Fig. A2, e.g., Clark and Boyce 1964, Granstrom 1987, Haywood 1994, Baskin and Baskin 2001). We assumed that seed bank densities (B_{jk}; the average density of viable seeds per square meter) in plot j and at time k depend on average seed rain inputs over the past T years ($s_{j(k-1)}$ to $s_{j(k-T)}$), the proportion of those seeds that are incorporated into the soil after one growing season (v_j), and a plot-specific annual mortality rate (d_j):

$$B_{jk} = v_j s_{j(k-1)} + \sum_{l=2}^{T} v_j s_{j(k-l)}(1 - d_j)^{(l-1)}. \quad (1)$$

Seeds from dispersal events more than one year in the past (from $l = 2$ to T years in Eq. 1) are part of the persistent seed bank. Our seed rain data do not distinguish between viable and inviable seeds; thus, parameter v_j represents the proportion of freshly dispersed seeds that are viable *and* survive to become incorporated into the seed bank. Because our model does not include a parameter for seed germination, the decay parameter (d_j) includes losses from the seed bank that are due to mortality as well as losses due to seed germination ($d = m + g$ in Fig. 1A). However, we believe annual seed mortality most influences the decay parameter (d_j), because first-year seedling densities for *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera* are orders of magnitude less than seed bank densities (Hille Ris Lambers and Clark 2003), and germination
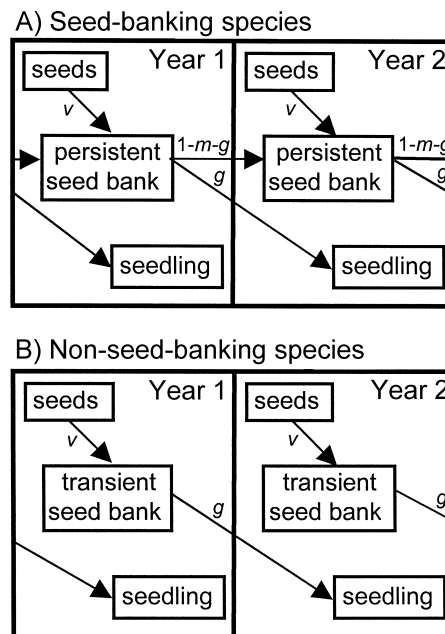

FIG. 1. Transitions across early life history stages for temperate woody species that (A) can and (B) cannot accumulate viable seeds in the soil. Non-seed-banking species possess a transient seed bank; seeds are present in the soil (the product of v and seed rain) between dispersal and seed germination (g). Seeds of seed-banking species can die (at rate m), germinate (at rate g), or remain viable in the soil for another year (with transition $1 - m - g$), forming a persistent seed bank.

rates (estimated from multiple censuses of tagged seedlings during the growing season) are much lower than our estimates of d_j (J. Hille Ris Lambers, *unpublished data*).

We used $T = 5$ yr for two reasons. First, seed burial studies for these species indicate that >90% of seeds lose viability after five years (Clark and Boyce 1964, Wendel 1977, Granstrom 1987, Haywood 1994). Second, our seed rain data only extend five years before our first seed bank sampling year. To check that this assumption did not unduly affect our parameter estimates, we also estimated both v_j and d_j with values of T ranging from one to five. At lower values of T (one or two), v_j values became higher and d_j values lower. Estimates of v_j and d_j were insensitive to values of T between three and five years, presumably due to high annual variability in seed rain and high seed mortality rates (results not shown).

We did not use standard analytical techniques for parameter estimation because the spatial location of seed traps and soil cores do not coincide, and we wished to incorporate this uncertainty in our parameter estimates. This was not possible using classical analytical methods such as maximum likelihood. We therefore used Markov chain Monte Carlo (MCMC) simulation to estimate seed incorporation (v_j values) and plot-specific decay rates (d_j values). We also employed a Bayes-

ian approach to model fitting because it allowed us to incorporate information from previous studies (in the form of probability distributions called ''priors'') into our estimation of v_j and d_j (means of the so-called ''posterior'' distributions). In addition, the parameters of interest in our statistical models (v_j and d_j) are correlated when model fitting, and we hoped that the inclusion of prior information for v_j would help constrain estimates of d_j. We compared parameters (posteriors) from analyses with diffuse priors (i.e., flat or uninformative priors) to those incorporating priors constructed from estimates of seed viability for v_j (from the National Tree Seed Laboratory; for *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*) and seed mortality (from published seed burial studies; for *Betula* spp. and *Liriodendron tulipifera*) for d_j. We used the software BUGS (Bayesian inference Using Gibbs Sampling) for model fitting (*available online*);[5] the methodology is described in the Appendix.

Implications of seed banking for recruitment limitation

To determine the extent to which seed dormancy buffers seedling recruitment against fluctuations in seed rain, we combined posterior estimates of seed incorporation in the soil (v_j) and annual seed mortality rates (d_j) with seed rain data of *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*. For each species, we randomly selected a seed trap (i) within a plot (j), and five years of seed rain densities from the nine years of seed rain data from that trap ($st_{ij1}:st_{ij5}$). Next, we randomly sampled an incorporation (v_j) and mortality (d_j) estimate from the appropriate plot-specific posterior samples. We used binomial realizations from these posterior samples to estimate the number of seeds that remain viable in the seed bank at location i and plot j from each of the previous years of previous seed rain (b_{ijk}; $k = 1$ to 5):

$$b_{ijk} = rbinom[rbinom(st_{ijk}, v_j), (d_j)^{(k-1)}]. \quad (2)$$

The sum of these values ($\Sigma^5_{k=1} b_{ijk}$) represents the total density of seeds available for germination in year k. We then calculated the proportion of these seeds that originated from the persistent seed bank (i.e., from seed rain events >1 year in the past; $\Sigma^5_{k=2} b_{ijk}/\Sigma^5_{k=1} b_{ijk}$). We repeated these simulations 1000 times per plot per species. From these 1000 simulations, we also calculated the proportion of years that no seeds fall locally but seeds from prior dispersal events were available for germination ($b_{ij1} = 0$ and $\Sigma^5_{k=2} b_{ijk} > 0$). In these years, all seedling germination must come from the persistent seed bank. We used posteriors of v_j and d_j from analyses with diffuse priors for these calculations.
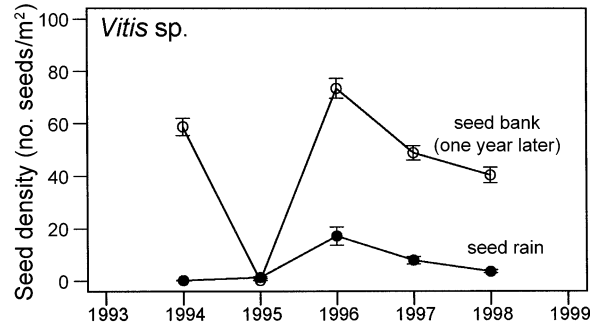
FIG. 2. Time series of annual seed rain inputs and seed bank densities of *Vitis* seeds in plot 2; error bars represent ± 1 SE. Note that seed bank densities are greater than the density of seeds deposited during the most recent dispersal event in four of five years.

RESULTS

Seed-banking species in southern Appalachian forests

We found evidence that eight woody species present as viable seeds in the soil at Coweeta hydrologic laboratory possess persistent seed banks (*Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*, *Nyssa sylvatica*, *Robinia pseudoacacia*, *Rubus* spp., *Sassafras albidum*, *Vitis* spp.). Seed burial studies confirm that seeds of several of these species can survive in the soil for >1 year (*Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*, *Rubus* spp., *Sassafras albidum*, *Vitis* spp. [Clark and Boyce 1964, Marquis 1975, Haywood 1994, Houle 1994, Peroni 1995]). Soil seed densities of some species were greater than annual seed rain densities in some plots (*Nyssa sylvatica*, *Robinia pseudoacacia*, *Sassafras albidum*, *Vitis* sp.; Fig. 2, Table 2), suggesting that soils contain seeds from several previous years of seed rain for these species. Because our seed traps do not capture the small seeds of *Kalmia latifolia* and *Rhododendron maximum*, we could not unequivocally determine whether these species (both having high densities of viable seeds in soil) possess persistent seed banks.

Six taxa found as dispersed seeds in seed traps and first-year seedlings were never found in soil seed banks (Table 2; *Acer pennsylvanicum*, *Carya* spp., *Amelanchier arboretum*, *Quercus prinus*, *Quercus rubra*, *Tsuga canadensis*). Although *Fraxinus americana* has previously been reported capable of accumulating seeds in soil (Marquis 1975), we found no viable seeds of this species in our seed bank samples, in spite of abundant seed rain and first-year seedling densities of this species in our northern hardwood stand. Seed burial studies confirm that *Quercus rubra* and *Tsuga canadensis* do not seed bank (Marquis 1975). Because $>90\%$ of *Quercus prinus* and *Quercus rubra* seeds germinate in early spring regardless of environmental conditions (Farmer 1997; J. Hille Ris Lambers, *personal*

TABLE 3. Estimates (and 95% confidence intervals) of seed bank incorporation and annual seed mortality rates based on uninformed priors, priors on the parameter of interest, and priors on both parameters (v_j and d_j).

| Species and plot no. | Incorporation, v_j† | | | Mortality, d_j‡ (yr^{-1}) | | |
	Uninformed prior	Informed prior (v_j)	Informed priors (v_j, d_j)	Uninformed prior	Informed prior (d_j)	Informed priors (v_j, d_j)
Acer rubrum§						
1	0.162 (0.067–0.289)	0.217 (0.111–0.354)	NA	0.698 (0.152–0.982)	NA	0.793 (0.440–0.985)
2	0.166 (0.107–0.235)	0.181 (0.123–0.251)	NA	0.936 (0.780–0.998)	NA	0.946 (0.805–0.999)
3	0.200 (0.104–0.273)	0.222 (0.149–0.297)	NA	0.821 (0.346–0.994)	NA	0.873 (0.596–0.996)
4	0.133 (0.090–0.179)	0.145 (0.100–0.188)	NA	0.987 (0.650–0.997)	NA	0.920 (0.735–0.998)
Betula spp.						
1	0.377 (0.097–0.869)	0.756 (0.451–0.986)	0.793 (0.512–0.984)	0.434 (0.057–0.789)	0.576 (0.253–0.878)	0.811 (0.721–0.891)
2	0.118 (0.097–0.141)	0.142 (0.123–0.163)	0.143 (0.125–0.163)	0.507 (0.414–0.594)	0.513 (0.423–0.595)	0.632 (0.571–0.690)
3	0.177 (0.140–0.216)	0.259 (0.244–0.296)	0.262 (0.227–0.301)	0.210 (0.116–0.292)	0.219 (0.132–0.297)	0.413 (0.361–0.467)
4	0.293 (0.192–0.408)	0.516 (0.414–0.634)	0.529 (0.425–0.655)	0.259 (0.086–0.415)	0.282 (0.116–0.429)	0.609 (0.532–0.685)
5	0.011 (0.009–0.013)	0.014 (0.012–0.015)	0.014 (0.012–0.016)	0.515 (0.352–0.634)	0.532 (0.381–0.647)	0.671 (0.610–0.728)
Liriodendron tulipifera						
1	0.193 (0.034–0.505)	0.159 (0.025–0.440)	0.127 (0.021–0.335)	0.589 (0.041–0.982)	0.358 (0.140–0.616)	0.342 (0.126–0.604)
2	0.076 (0.057–0.107)	0.074 (0.056–0.106)	0.087 (0.066–0.116)	0.118 (0.004–0.319)	0.211 (0.081–0.370)	0.209 (0.081–0.361)
3	0.423 (0.220–0.658)	0.403 (0.210–0.628)	0.379 (0.247–0.544)	0.451 (0.041–0.731)	0.399 (0.161–0.610)	0.389 (0.148–0.597)
4	0.293 (0.112–0.579)	0.265 (0.106–0.525)	0.220 (0.111–0.376)	0.511 (0.057–0.886)	0.376 (0.145–0.632)	0.368 (0.146–0.614)

† Proportion of dispersed seeds incorporated into the seed bank.
‡ Proportion of seeds in the seed bank losing viability annually.
§ For *Acer rubrum*, we used informed priors only for v_j; values for d_j in column 5 come from models with informed priors on v_j.

observation), we conclude that seeds of these species are not likely to accumulate in the soil.

Seed incorporation (v_j) and seed decay (d_j) of Acer rubrum, Betula *spp., and* Liriodendron tulipifera

We found that the proportion of dispersed seeds that are viable and incorporated into soil seed banks (i.e., v_j) annually is low (Table 3, columns 2 and 3). With the exception of *Liriodendron tulipifera*, the parameter v_j is much lower than are the seed viability estimates from the National Tree Seed Laboratory for these taxa (means of seed viability priors are 0.815 for *Acer rubrum*, 0.72 for *Betula* spp., and 0.309 for *Liriodendron tulipifera*; see Appendix). Seed incorporation varied little from plot to plot for *Acer rubrum*, but varied substantially for *Betula* spp. and *Liriodendron tulipifera*. Priors had little effect on posterior densities of seed incorporation, with the exception of two plot-specific estimates from *Betula* spp. (plots 1 and 4, Table 3). Although posterior densities of v_j are correlated with those of d_j (see Appendix), the inclusion of informed priors for d_j in statistical model fitting did not strongly

affect posteriors of v_j (Table 3, column 4 vs. column 3).

Annual seed mortality in the soil is highest for *Acer rubrum* and lower for both *Betula* spp. and *Liriodendron tulipifera* (Table 3). Annual seed mortality estimates from Markov Chain Monte Carlo simulations using noninformative priors are variable from plot to plot (Table 3). Posteriors of plot-specific mortality rates were strongly affected by informative priors for *Liriodendron tulipifera*, but only slightly so for *Betula* spp. (column 6 vs. column 5 in Table 3; see Appendix). Priors had greatest effects on posterior densities for plots having limited data, and thus, broad posteriors when priors are uninformed (plots 1 and 4 for both *Liriodendron tulipifera* and *Betula* spp.; Table 3; see Appendix). Priors for v_j affected posterior densities of d_j of *Betula* spp. but not of *Liriodendron tulipifera* (Table 3; column 7 vs. column 6).

Implications for recruitment limitation

For both *Liriodendron tulipifera* and *Betula* spp., >40% of seeds available for germination in all plots

TABLE 4. The consequence of a persistent seed bank for seedling recruitment; the average proportion of seeds available for germination each year that come from persistent seed banks (column 2), and the temporal frequency with which seed dispersal fails locally and all germination comes from persistent seed banks (column 3).

Species and plot no.	Proportion of seeds from seed banks	Proportion of time seeds come only from seed banks
Acer rubrum		
1	0.373	0.149
2	0.123	0.057
3	0.245	0.114
4	0.176	0.077
Betula spp.		
1	0.593	0.304
2	0.622	0.302
3	0.730	0.365
4	0.721	0.425
5	0.618	0.329
Liriodendron tulipifera		
1	0.398	0.087
2	0.762	0.274
3	0.572	0.220
4	0.501	0.218

come from a persistent seed bank, and >10% of *Acer rubrum* seeds available for germination annually originate from seeds dispersed more than one year in the past (Table 4). Based on our calculations (Eq. 2), persistent seed banks were the sole source of seeds in years when local microsites (the size of seed traps) received no seeds, approximately one in three years for *Betula* spp., one in five years for *Liriodendron tulipifera*, and one in 10 years for *Acer rubrum* (Table 4).

DISCUSSION

The prevalence of seed banking in temperate deciduous forests

Our results indicate that potentially more woody species (eight) seed bank than do not (six; Table 2), implying that seed banking may play a more important role in the recruitment of temperate woody species than previously thought (Matlack and Good 1990, Mladenoff 1990, Roberts and Vankat 1991, Schiffman and Carter-Johnson 1992, Thompson 1992, Yorks et al. 2000). The life history traits of these woody species are varied. Seeds of wind-dispersed taxa (*Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*) and bird-dispersed taxa (*Nyssa sylvatica*, *Robinia pseudoacacia*, *Rubus* spp., *Sassafras albidum*, *Vitis* sp.) were found in persistent seed banks. Seed-banking species include shrub (*Rubus* spp., possibly *Kalmia latifolia*, *Rhododendron maximum*), vine (*Vitis* sp.), and early- to mid-successional tree species (*Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*, *Nyssa sylvatica*, *Robinia pseudoacacia*, *Sassafras albidum*).

Only large-seeded, late-successional species are consistently absent from southern Appalachian seed banks (Table 2). *Carya* species and *Quercus* species were never found in seed banks, despite an abundance of adult trees, seeds, and seedlings (Clark et al. 1998, Hille Ris

Lambers and Clark 2003, and Tables 1 and 2). Seeds of these species may not accumulate in the soil, because virtually all viable seeds germinate in the spring regardless of environmental conditions (>90% for *Quercus rubra* and *Quercus prinus* [Farmer 1997; J. Hille Ris Lambers, *personal observation*]). A comparison of oak seed survival (<5%/yr due to high seed predation Burns and Honkala 1990; B. Beckage, *personal communication*) and seedling survival rates (>30%/yr; J. Hille Ris Lambers, *unpublished data*) suggests that seed banking may not be advantageous for these species. In contrast, seed-banking species have much higher seedling mortality rates (>85%/yr for *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*) than seed mortality rates (Table 3). The greater risk of mortality at seed than at seedling stages for large-seeded species may provide an evolutionary explanation for their absence from temperate forest seed banks (Louda 1989). For these large-seeded species, ''seedling banks'' rather than seed banks may buffer seedling recruitment against variable seed production and unpredictable recruitment opportunities.

How does seed banking of woody temperate species compare with that of other species? It is unlikely that the short-term seed banking of temperate woody species (<5 years) is important for the long-term persistence of these species, unlike many desert annuals or crop weeds that rely on dormant seeds to survive in the soil until conditions are favorable for maintaining aboveground populations (Pake and Venable 1995, 1996, Baskin and Baskin 2001). The costs of short-term seed banking for long-lived woody species are probably primarily related to protecting seeds against agents of mortality, unlike annual species, which also experience significantly reduced population growth rates by postponing germination. Unlike chaparral spe-

cies, seeds of temperate woody species do not appear to require specific cues such as fire or NO_3 for germination (Keely and Keely 1988, Keely and Fotheringham 1998; but see Marks 1974), and all seeds may germinate when conditions are favorable for seedling survival (J. Hille Ris Lambers, *personal observation*). However, in common with crop weeds, desert annuals, and chaparral species, seed banking allows temperate woody species to cope with the temporal uncertainty these species experience, both due to annually fluctuating seed production or unpredictable opportunities for seed germination and seedling survival.

Benefits of seed banking for temperate woody species

The advantage of a short-term persistent seed bank for *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera* results from high year-to-year variability in seed production. If seed production were constant, first-year seedlings would predominately originate from recently dispersed seeds. Instead, a high proportion of seeds available for germination have survived more than one year in the soil, and when seed production fails locally (more than one in five years for *Betula* spp. and *Liriodendron tulipifera*), all seedling recruitment comes from seeds that originate from prior dispersal events (Table 4). Thus, persistent seed banks can make a large contribution to seedling recruitment, despite high decay rates of *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera* seeds, because seed banking buffers seedling recruitment from annually variable seed production.

How might buffering recruitment from extreme fluctuations in seed supply be beneficial? One possibility is that the density-dependent effects of host-specific predators and pathogens on seedlings is limited by reducing germination in years when seed production is high (Ellner 1985). Density-dependent mortality at seedling stages is high for these three species (Hille Ris Lambers et al. 2002), and seed banking may thus allow these species to avoid the density-dependent effects of host-specific predators and pathogens on seedlings. However, seed banking may also increase the risk of density-dependent mortality by host-specific predators and pathogens at seed stages (Connell 1970, Wright 1983), which these three species also experience (Hille Ris Lambers et al. 2002). Whether or not seed banking is beneficial because it limits density-dependent mortality will thus depend on the relative effects of host-specific predators and pathogens on seed vs. seedling stages.

Seed banks may also enhance fitness for these three species (*Acer rubrum*, *Betula* spp., *Liriodendron tulipifera*) because it increases recruitment in years when seed production is low but conditions are favorable for germination and seedling survival (Cohen 1966). For example, high light and moisture increase seedling survival of all three species (Burns and Honkala 1990, Burton and Bazzaz 1991, Carlton and Bazzaz 1998),

and both light and moisture vary spatially and temporally in forest understories (Beckage et al. 2000, Masaki and Nakashizuki 2002, Clinton 2003). Persistent seed banks thus increase the probability that seeds will be available when conditions are favorable for seedling survival (Table 4). For spring-seeding species (such as *Acer rubrum*), seed banking may also allow seeds to germinate prior to canopy closure and the dispersal of that year's seed crop, thus avoiding the higher mortality risk frequently associated with germinating later in the growing season (Canham and Marks 1985, Jones and Sharitz 1989, Peroni 1995).

Presumably, seed dormancy benefits other seed-banking woody species at our site, because the conditions that make seed banking beneficial for *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera* are shared by others. Seed production fluctuates annually for most species (Houle 1994, Tapper 1996, Clark et al. 1998, 2004). Density-dependent mortality at early life history stages is prevalent among temperate forest tree species (Streng et al. 1989, Jones et al. 1994, Hille Ris Lambers et al. 2002), as are spatially and temporally varying abiotic factors that affect recruitment (Burton and Bazzaz 1991, Beckage et al. 2000). Thus, seed banking may generally decrease density-dependent mortality when seed production is high, and enhance recruitment of seed-banking species in years when seed production fails and conditions are favorable for seedling survival.

It is even possible that other species rely even more heavily on seed banking as a buffer against variable seed production and unpredictable germination opportunities than do *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*. Seed banking enhances seedling recruitment of *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera* (Table 4), despite relatively high annual mortality of seeds in the soil ($>50\%$ annual mortality in some plots; Table 3). High seed bank densities relative to seed rain densities of *Nyssa sylvatica*, *Robinia pseudoacacia*, *Sassafras albidum*, and *Vitis* sp. (in comparison to *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*) imply that these species have much lower annual seed mortality rates than do *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*. Greater seed longevity could mean that seed banks of these species buffer seedling recruitment from temporal variability more than seed banks of *Acer rubrum*, *Betula* spp., and *Liriodendron tulipifera*.

The utility of a Bayesian framework in estimating seed bank dynamics

The results from any study must be evaluated in light of previous knowledge; Bayesian statistics afford us the opportunity to do so in a rigorous and quantitative way (Clark and Lavine 2001). Our Bayesian approach allowed us to determine how previous knowledge (such as prior distributions) affected our estimation of the processes of interest; incorporation into the seed bank

(v_j) and annual seed mortality (d_j). At first glance, our priors do not appear to contribute much to our estimation of these parameters. Priors of v_j were so different from posterior estimates for two species (*Acer rubrum* and *Liriodendron tulipifera*, see Appendix) that their appropriateness as priors is questionable. Because the priors for v_j did not have much weight (i.e., the information content of our data was much stronger than that of the priors), they had little effect on posteriors of v_j (Table 3; see Appendix). Priors did affect d_j for *Liriodendron tulipifera*, but did not significantly narrow confidence intervals of plot-specific seed mortality rates for *Betula* spp., which are very variable from plot to plot (Table 3; see Appendix).

What insights did we gain from our Bayesian approach? First, the fact that seed viabilities from prior estimates are much higher than our estimates of v_j (seed incorporation into the soil) for two species (v_j; *Acer rubrum* and *Betula* spp.) tells us that seed mortality between the time of dispersal and seed bank sampling is great for these species, much greater than we had expected. This suggests that for these two species, processes such as seed predation and pathogen damage affect seeds immediately after dispersal and prior to incorporation into the seed bank (Granstrom 1987, Houle and Payette 1990, Tanaka 1995). Our plot-specific estimates of annual seed mortality with diffuse priors differ from one another, and together, span estimates from buried bag studies (the prior), suggesting that on average, seed decay at Coweeta Hydrologic Laboratory is comparable to seed decay at other locations in Eastern forests. However, several of our plot-specific estimates of annual seed mortality fall far outside of the prior distributions (e.g., plots 3 and 4 for *Betula* spp.), suggesting that seed decay can vary as much within one watershed as it does across Eastern deciduous forests, perhaps in response to environmental variables (Table 1). In short, although the inclusion of prior information did not aid in parameter estimation by narrowing confidence intervals of v_j and d_j, the quantitative comparison of our data to prior information (a direct consequence of our Bayesian statistical approach) did lead to valuable insights on the processes that may affect seed banking of these temperate woody species.

Implications of seed banking for dynamics of temperate forests

Differences among species in their ability to seed bank (Table 2) may importantly affect community dynamics in temperate deciduous forests. In theory, trade-offs between competition and colonization promote species diversity in plant communities by allowing less competitive species to capture space from more competitive species by forfeit (Shmida and Ellner 1984, Tilman 1994, Pacala and Rees 1998). Large-seeded species were not found in seed banks (Table 2), and seedling survival rates are generally positively correlated with seed size (Jurado and Westoby 1992, Greene and Johnson 1998; J. Hille Ris Lambers, *unpublished data*). If seed-banking species can better capitalize on temporally unpredictable recruitment opportunities than large-seeded species can, seed banking may allow species with lower seedling survival to coexist with large-seeded species that do not seed bank. Many large-seeded species in the Southern Appalachians (such as *Quercus* spp. and *Carya* spp.) may rely on "seedling banks" to buffer unpredictable recruitment opportunities. However, (a) the much lower fecundity of these large-seeded species relative to small-seeded species (Smith and Fretwell 1974, Clark et al. 1998), (b) low seed to seedling transition rates due to high seed predation (Burns and Honkala 1990), and (c) less widely dispersed seedlings than small-seeded species (due to shorter seed dispersal distances [Hille Ris Lambers and Clark 2003]) suggest that these "seedling banks" may be less effective at buffering species from variable seed production and recruitment opportunities than seed banks are.

CONCLUSIONS

Contrary to expectation, seed banking is common in temperate forests and may determine recruitment success of many woody species. Although seed survival rates are low in comparison to those of some annual plant species, seed banking substantially boosts recruitment rates of seed-banking woody species and serves as a hedge against years when seed production fails. Seed banking can allow species to avoid density-dependent mortality when seed production is high, and capitalize on temporally unpredictable opportunities for successful recruitment when seed production is low. Differences among species in seed banking can also have implications for community composition; the ability to seed bank (disperse through time) may trade off with competitive ability of seedlings, and thus promote diversity.

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APPENDIX

A description (including a table and figures) of estimating seed decay and incorporation into the soil seed bank using a Bayesian statistical approach is available in ESA's Electronic Data Archive: *Ecological Archives* E086-005-A1.