The benefits of seed banking for red maple (*Acer rubrum*): maximizing seedling recruitment

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Abstract: Seed banking is assumed to be unimportant for temperate trees, because their seeds are short-lived in soils. However, even short-term seed banking could increase recruitment and affect population dynamics of seed-banking trees. To investigate this possibility, we examined early life-history stages of red maple (*Acer rubrum* L.), an abundant seed-banking tree in eastern forests. We found that seed banking benefits red maple by increasing germination when seedling survival is likely. Most red maple seeds germinate soon after spring dispersal, when seedling survival is high, or postpone germination to the following growing season, once seedling survival becomes less likely late in the summer. This occurs because seed dormancy increases during the growing season, matching a concurrent decrease in seedling survival. Our results and those of other studies suggest seed dormancy is increased by the same environmental factors (low light and low moisture) that also decrease seedling survival. We speculate that early life-history traits, including seed banking, may have contributed to this species' increased abundance in eastern deciduous forests in the last century.

Résumé : L'entreposage de graines n'est pas présumé important pour les arbres des forêts tempérées parce que leurs semences ne demeurent pas viables longtemps dans le sol. Cependant, même l'entreposage de graines à faible longévité pourrait augmenter le recrutement et affecter la dynamique des populations d'arbres qui entreposent leurs semences. Pour vérifier cette possibilité, les auteurs ont examiné les premières étapes du cycle biologique de l'érable rouge (*Acer rubrum* L.), un arbre qui entrepose ses semences et qui est abondant dans les forêts de l'Est. Ils ont trouvé que l'entreposage des graines profitait à l'érable rouge en augmentant la germination lorsque les chances de survie des semis sont bonnes. La germination des semences d'érable rouge survient principalement tôt après la dispersion printanière, quand la survie des semis est forte, ou est reportée à la saison de croissance suivante lorsque les chances de survie des semis deviennent plus risquées tard pendant l'été. Ce phénomène survient parce que la dormance des graines augmente au cours de la saison de croissance concurremment à une diminution de la survie des semis. Leurs résultats ainsi que ceux d'autres études suggèrent que la dormance des semences est augmentée par les mêmes facteurs environnementaux (faible lumière et faible humidité) que ceux qui diminuent le taux de survie des semis. Ils croient que les caractéristiques des premières étapes du cycle biologique, ce qui inclut l'entreposage des graines, peuvent avoir contribué à l'augmentation de l'abondance de cette espèce dans les forêts décidues de l'Est au cours du dernier siècle.

[Traduit par la Rédaction]

Introduction

Seed banking, the retention of viable seeds in the soil for more than one growing season prior to germination, is not thought to strongly affect population dynamics of temperate forest trees (Matlack and Good 1990; Schiffman and Carter-Johnson 1992; Yorks et al. 2000; but see Marks 1974; Peterson and Carson 1996; Hille Ris Lambers et al. 2004). This idea is fostered by two observations. First, tree seeds are generally at low densities in forest soils in comparison to seeds of other life forms (Roberts and Vankat 1991; Schiffman and Carter-Johnson 1992; Yorks et al. 2000), implying that trees rely more on recently dispersed seeds and less on seed banks for recruitment than do co-occurring species (e.g., annual forbs, herbaceous perennials, shrubs). Second, studies have found that temperate tree seeds are short-lived in forest soils relative to tree life-spans (Pickett and McDonnell 1989; Thompson 1992; Haywood 1994), particularly in comparison to annuals, whose seeds often remain viable in soils for many years before germination. Both these observations imply that seed banks of trees do not significantly buffer aboveground populations from local extinction (as persistent seed banks of annuals do; Rees 1994).

The growing realization that early life-history stages can critically affect forest dynamics has caused some to reconsider the role that seed banking might play in forests (Grubb 1988; Clark et al. 1998; Hille Ris Lambers et al. 2004). Although temperate forest seed banks do not prevent local extinction of tree populations (with the exception of aerial seed banks of fire-adapted pine species), seed banking of temperate trees could still buffer recruitment from annual fluctuations in seed production and (or) unfavorable recruitment opportunities (Rees 1994; Hille Ris Lambers et al. 2004). Because differences among tree species in recruitment may drive succession, gap-phase dynamics, and species diversity, persistent seed banks may critically affect the population dynamics of seed-banking temperate tree species (Marks 1974; Houle 1994; Peroni 1995).

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Unfortunately, there are few studies that document the benefits of seed banking for temperate forest trees by carefully quantifying the appropriate demographic processes (e.g., seed dormancy, germination, survival; but see Marks 1974; Houle 1994; Hille Ris Lambers et al. 2004). In this paper, we use observational data to ask how and whether seed banking might benefit red maple (*Acer rubrum* L.) seedling recruitment. Red maple provides an interesting example of a seed-banking temperate tree species (Marquis 1975; Houle 1994; Peroni 1995), because the longevity of this species' seeds in the soil is not much longer than that of co-occurring species that do not possess persistent seed banks (e.g., *Carya* spp., *Quercus* spp.). Red maple seeds are dispersed in the spring; those seeds that do not germinate the summer after dispersal emerge from seed banks the following growing season (10–15 months later). Such short seed longevity in soils (often less than 1 year) may seem difficult to reconcile with any significant benefits of seed banking for seedling recruitment.

However, short-term seed banking can increase seedling recruitment of red maple by allowing this species to cope with two types of variation: annual variability in seed production and seasonal variation in seedling survival. Seed banking can serve as a hedge against recruitment failure when seed production is temporally variable (Rees 1994; Clark et al. 1998), as explored for red maple (and other seed-banking trees) in a previous study (Hille Ris Lambers et al. 2004). Less appreciated is that short-term seed banking may also improve red maple seedling recruitment by timing seedling emergence to coincide with conditions that are favorable for seedling recruitment. Studies suggest that seedling survival of red maple may depend on when seeds germinate; seedlings that emerge late in the growing season experience higher mortality than do seedlings that emerge early (Jones and Sharitz 1989; Jones et al. 1997). Postponing germination for even just one growing season may therefore be advantageous by reducing germination late in the growing season, when environmental conditions can be unfavorable for seedling survival (Canham and Marks 1985; Tremblay et al. 1996). To assess the latter possibility, we quantified (1) the dormancy of freshly dispersed red maple seeds as affected by time since dispersal and maternal light environment, (2) the relationship between emergence date and seedling survival of red maple seedlings, and (3) the density of freshly dispersed red maple seeds relative to seed-bank densities and seedling recruitment. We also discuss how early life-history traits, including seed banking, may have contributed to the increased abundance of red maple (relative to other species) in eastern forests during the last century.

Materials and methods

Study species

Red maple is a common tree in temperate deciduous forests of North America (Burns and Honkala 1990; Abrams 1998). Red maple seeds are dispersed in early spring, with some seeds germinating in the growing season following dispersal, while other seeds remain dormant in the soil for at least a year before germinating (Peroni 1995; Tremblay et al. 1996; Anella and Whitlow 1998). Because this species sets seed in the spring (unlike the majority of temperate forest tree species that set seed in the fall), seeds of this species that germinate immediately avoid overwintering in the soil as dormant seeds; it is this dual strategy (of immediate germination or overwintering) that is the focus of this study. Like other temperate tree species, annual seed production of this species varies dramatically from year to year, resulting in seed densities that range from 1 to >50 seeds/m^2 following dispersal (Clark et al. 1998, 2004). Red maple has received much attention recently because of its high abundance in eastern deciduous forests. Red maple was not an important component of presettlement forests, but has increased in abundance across a broad range of eastern deciduous forests in the last century (Lorimer 1984; Abrams 1998; in the Midwest: Larsen 1953; Zhang et al. 2000; Dyer 2001; the Northeast: Gerhardt and Foster 2002; Whitney and DeCant 2003; and in the Southeast: Christensen 1977; Orwig and Abrams 1994; Shumway et al. 2001). Early life-history stages are thought to have contributed to this species' dramatic increase in abundance (Abrams 1998).

Seed dormancy

We quantified seed dormancy of red maple with respect to time since the start of the growing season and light availability. We collected seeds (as they were dispersing) from 105 trees in four state parks and research stations throughout North Carolina (the Coweeta Hydrologic Laboratory in Macon County, Duke Forest in Orange County, Hanging Rock State Park in Stokes County, and Pilot Mountain State Park in Surry County) in April, May, and June of 1997 and 1998. At all sites (spanning a range of elevations), we collected seeds from trees located in secondary forests (Duke Forest: 100–150 m; Hanging Rock: 225–525 m; Pilot Mountain: 425–550 m; Coweeta: 600–900 m). Seeds were either collected directly from maternal trees (from multiple branches) or from the forest floor immediately below the tree. We only collected seeds in the latter manner when maternal trees were isolated from other red maple trees by at least 40 m, to ensure that seeds originated from one maternal tree. For seeds collected from trees in Duke Forest (24 trees), we noted whether trees from which we collected seeds were in open-canopy (i.e., part of the upper canopy) or closed-canopy (i.e., entirely below the upper canopy) conditions.

To quantify the proportion of seeds from each maternal tree that are dormant, we planted 20 seeds from each tree in high-light and high-moisture conditions (within 2–3 days of seed collection) and monitored germination on a biweekly basis. We considered seeds that had not germinated after 2 months to be dormant. We confirmed that seeds were dormant and viable, not dead, by dissecting seeds and checking for the presence of living tissue. For a subset of trees (46 trees) from Coweeta Hydrologic Laboratory and Duke Forest, we also determined how seed dormancy changes after dispersal by planting a second batch of seeds (10 seeds instead of 20 seeds) in high-light and high-moisture conditions 1 month after seed collection and monitoring germination on a biweekly basis.

Seedling survival

We followed the fates of red maple seedlings in four permanent vegetation plots at the Coweeta Hydrologic Laboratory (Macon County, North Carolina) during three growing seasons to determine whether seedling survival is affected by date of emergence. In each plot, we laid out twenty 1-m^2 quadrats in the spring of 1997 (for a total of 80 quadrats). From 1997 to 2000, we quantified seedling emergence and survival throughout the summer by tagging (with uniquely colored toothpicks) and recensusing red maple seedlings in these seedling quadrats. Seedlings were relocated using the tag and location of the seedling (we recorded the x and y coordinates of each seedling in each quadrat). Seedling censuses were performed roughly every 4 weeks each summer (16 June, 17 July, 6 August, and 26 August in 1997; 1 May, 26 May, 10 June, 15 July, 18 August, and 14 September in 1998; 4 June, 10 July, 1 August, and 9 September in 1999). In early June of 2000, we tagged no new seedlings, but recorded the fate of all previously tagged seedlings. In total, we noted the emergence and survival (or death) of 1875 seedlings over 4 years. We considered seedlings to be dead if they could not be relocated in three consecutive censuses.

Rhododendron maximum, an ericaceous shrub, affects light, soil moisture, soil pH, soil nutrients, and is known to depress red maple seedling densities (Clinton and Boring 1994; Beckage et al. 2000; Lei et al. 2002). We therefore quantified the cover of this shrub in each seedling quadrat to include as a covariate in analyses of seedling survival. Other understory shrubs (e.g., *Kalmia latifolia*) are also present in the southern Appalachians, but are not abundant in these vegetation plots. We estimated the leaf area index (LAI) of *Rhododendron maximum* for each seedling quadrat by counting the average number of leaves touching a 2-m pole held vertically at the four corners of the seedling quadrat. Poles were extended to the top of the *Rhododendron maximum* canopy if these shrubs were taller than 2 m.

Seed-rain, seedling, and seed-bank densities

We determined seed-rain, seedling, and seed bank densities in 1997, 1998, and 1999 in the same vegetation plots at Coweeta Hydrologic Laboratory in which we quantified seedling survival. We quantified seed-rain densities by identifying and counting all red maple seeds collected from eighty 0.1764-m^2 seed traps (20 per plot, adjacent to each seedling quadrat) each spring. We used the total number of first-year seedlings censused in seedling quadrats as an estimate of first-year seedling emergence. Finally, we estimated the density of viable seeds remaining in the soil seed bank each fall (after seedling emergence in the summer) by counting the number of red maple seedlings emerging from eighty 62.1-cm^2 soil cores removed from an area adjacent to each seedling quadrat in late August of each year. Soil cores were stratified at 4 °C for 8 weeks after collection and planted over sterile potting soil in Duke University greenhouses. Seedling emergence was monitored for 8 months, long after red maple seedlings ceased to emerge.

Statistical analysis

Seed dormancy

We used maximum likelihood to determine whether seed dormancy of freshly dispersed seeds increases during the growing season. In our model, the proportion of dormant seed produced by each maternal tree i (p_i) depends on the time at which seeds from tree i are collected (t_i, number of days since 1 April, April being the earliest month that we collected seed) and two fitted parameters: g_0, the proportion of seeds ready to germinate (i.e., not dormant) on 1 April, and k, the rate at which dormancy levels saturate to one:

$$[1] \qquad p_i = 1 - g_0 e^{k t_i}$$

The proportion of seeds that are dormant (p_i) is calculated from the number of dormant seeds (d_i) in each lot of seeds planted (n_i) of i = 1, 2, …, m trees. We used the binomial likelihood

$$[2] \qquad L(p_i | d_i, n_i) \propto \prod_{i=1}^{m} p_i^{d_i} (1 - p_i)^{(n_i - d_i)}$$

to fit our data to eq. 1 and to test whether dormancy levels change over time; that is, if $k < 0$ (when $k = 0$, seed dormancy is $1 - g_0$ at all times during the growing season). We fit eqs. 1 and 2 to data from Coweeta Hydrologic Laboratory and Duke Forest separately (the two sites for which seeds were collected at several times throughout the growing season) to verify that qualitative results (i.e., whether parameter k is significantly less than zero) did not depend on collection site.

We next determined whether seed dormancy increases over time once seeds are dispersed and whether seed dormancy depended on the light environment seeds matured in. In both cases, we used maximum likelihood to test for differences in dormancy of seeds (1) immediately after dispersal and of those same seeds 1 month later (for 46 trees) and (2) collected from trees in closed-canopy versus open-canopy conditions (for seeds collected from 24 trees in Duke Forest). We fit two models to both these data, the first with a common dormancy (p_{null}) for seeds tested immediately as well as 1 month after dispersal and collected from trees in both closed-canopy and open-canopy conditions (this is our null model). Our second model had two dormancy parameters (p_1 and p_2, and p_o and p_c) corresponding to time since dispersal (none vs. 1 month) and to canopy condition (open vs. closed). We used a binomial likelihood (eq. 2) and likelihood ratio tests to determine which of these two models best fit the data.

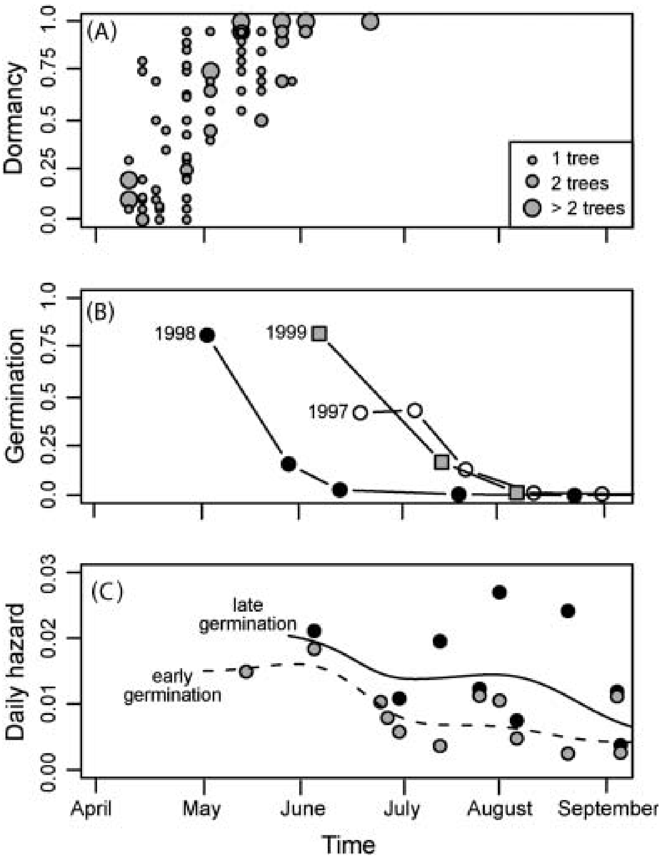
Seedling emergence and survival

For each of 3 years of data, we fit log-normal distributions to counts of seed germination dates, to estimate mean date of emergence and 95% confidence intervals on the average date of germination. To determine whether the date of seedling emergence and the leaf area of *Rhododendron maximum* affect long-term seedling survival, we used a log-normal survival function ($S(t)$, the probability that a seedling survives beyond t days) to analyze seedling survival data:

$$[3] \qquad S(t) = 1 - \Phi\left\{\frac{\log t - (\mu + \gamma^t \mathbf{Z})}{\sigma}\right\}$$

where Φ is the cumulative normal distribution, log(t) is the logarithm of time to seedling death, μ is mean seedling survival time, σ is the standard deviation of the log-normal distribution (a measure of variance in the data), γ is a vector of regression coefficients, and $\mathbf{Z}$ is a vector of explanatory variables (Klein and Moeschberger 1997). The log-normal distribution was selected from several possible distributions (the Weibull,

Fig. 1. Seed dormancy (A), cumulative germination (B), and the daily probability of seedling mortality for early-emerging and late-emerging seedlings of red maple over the course of one growing season. In (A), symbols are scaled in size to the number of maternal tree sources with equivalent seed dormancy levels collected at the same time. In (B), black circles are from 1998 censuses, clear circles from 1997 censuses, and grey squares from 1999 censuses. In (C), black circles and solid lines represent raw data and smoothed hazard rates from late-germinating seeds, while grey circles and broken lines represent raw data and smoothed hazard rates from early-germinating seeds.



exponential, log-logistic) based on model selection using Aikaike's information criterion (AIC).

We included plot, year, *Rhododendron maximum* LAI, and date of emergence as explanatory variables. These variables were modeled as fixed effects. We accounted for right and interval censoring of survival data using the function CensorReg in S-Plus. We used sequential likelihood ratio tests (adding parameters one at a time and excluding individual parameters) to determine which explanatory variables affected the survival of red maple seedlings. The total time seedling survival was monitored was 1, 2, or 3 years from germination, depending on the seedling cohort censused (1999, 1998, and 1997 respectively).

We also used a nonparametric smoothing method to quantify the daily probability of mortality (the hazard function) for early-emerging and late-emerging seedlings during the growing season. We smoothed step functions describing the average daily probability of death at census intervals (for all the 3 years) for seeds germinating prior to our first census each year (early emerging, prior to 16 June for all years) and for all seedlings emerging at all other censuses (late emerging). We weighted the contribution of each step by the number of seedlings tagged during the census interval.

Seed-rain, seed-bank, and seedling densities

We used 3 years' worth of data on seed-rain, seedling, and seed-bank densities (from seed traps, seedling quadrats, and soil cores, respectively) collected from the four vegetation plots to determine whether germination strongly decreases the availability of seeds for germination in the following growing season (i.e., in the seed bank) and how strongly seed-bank densities in the fall and seedling emergence in the summer depend on the magnitude of seed production in the spring. We did this by comparing the average density of red maple recruits in spring (from seed densities in seed traps), summer (from the total number of emerged seedlings in quadrats), and the fall (from densities of viable seeds in soil cores). We then used simple correlations to determine whether seedling and seed-bank densities (per plot and year) are correlated with seed-rain densities.

Results

Seed dormancy

Seed dormancy levels of freshly dispersed seeds increased over time ($p < 0.0001$ for a likelihood ratio test against no effect of time; $k < 0$; Fig. 1A), and statistical models explained 65% of the variation in seed dormancy (R^2 between observed seed dormancy levels and seed dormancy levels predicted from eq. 1 and fitted parameters, as in Clark et al. 1998). Statistical models fit to Coweeta and Duke Forest data separately, although yielding slightly different values of g_0 and k, also indicated that seed dormancy levels of freshly dispersed seeds increased over time at these sites ($p < 0.0001$ for both likelihood ratio tests against no effect of time). Seed dormancy of seeds continued to increase after dispersal, and the average increase in dormancy 1 month after seed dispersal is 31.4% (from 50.4% to 81.8%, $p < 0.0001$; Fig. 2A). Dormancy of seeds collected from trees in open-canopy conditions was lower than that of seeds collected from trees in closed-canopy conditions (18% vs. 43%, $p < 0.0001$; Fig. 2B).

Seedling emergence and survival

Mean emergence dates for the three cohorts of seedlings were 28 June, 6 April, and 10 June for 1997, 1998, and 1999 respectively. For all years, 95% of all germination occurred before the middle of July (19 July 1997, 22 May 1998, 3 July 1999; Fig. 1B). Seedling survival was significantly affected by plot, year, *Rhododendron maximum* LAI, and date of emergence ($p < 0.0001$ for all likelihood ratio tests). Survival varied among plots (highest in plot 2, lowest in plot 3; Table 1) and was lowest for seedlings emerging in 1998. Seedling survival was lower in quadrats with high *Rhododendron maximum* LAI and lower for seedlings that emerged later in the growing season (Table 1). One unit of *Rhododendron maximum* LAI increases the probability of seedling mortality by a factor of 1.11 (LAI ranges from 0 to 4.8). Each day that seed germination is postponed increases the probability of mortality by a factor of 1.01 (Table 1; equivalent to a 1.34 greater chance of mortality for each month that germination is postponed). The hazard rate for seedlings (daily probability of mortality) was always higher for late-emerging seedlings than for early-emerging seedlings (Fig. 1C).

Seed-rain, seed-bank, and seedling densities

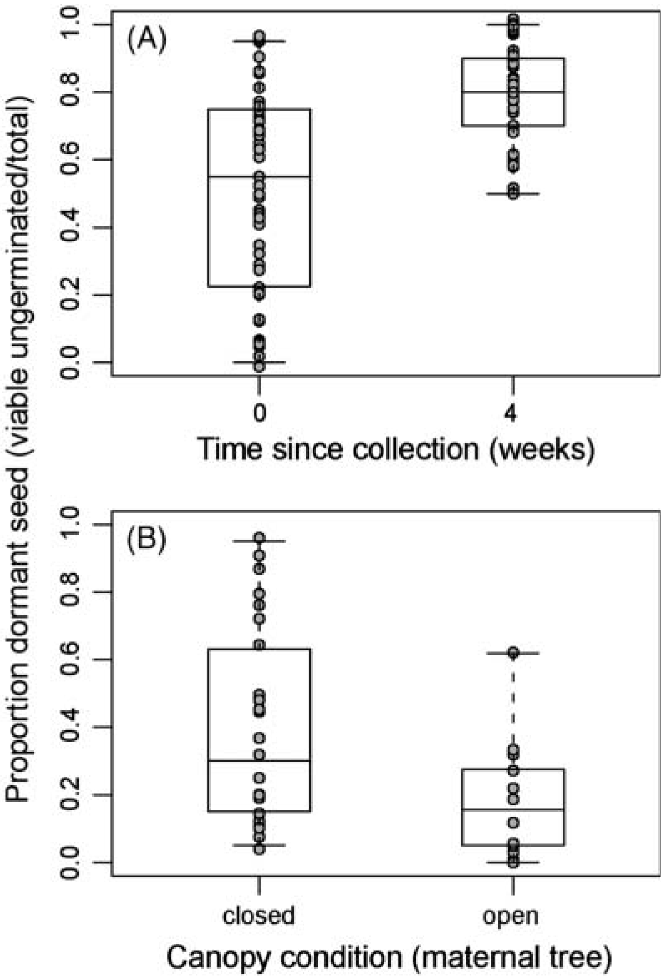
Seed-rain, seed-bank, and seedling densities vary from site to site and year to year (Table 1). Seed-bank densities in August are generally greater than the total density of emerging seedlings observed during censuses ($p < 0.0001$ in a one-way analysis of variance). Thus, late-season germination appears limited by increasing seed dormancy, not by the depletion of seed banks. The density of seeds dispersed in spring is strongly correlated with the density of seeds in seed banks in fall (Pearson's $r = 0.735$, $p = 0.0064$), but not with the cumulative density of emerging seedlings throughout the growing season (Pearson's $r = -0.232$, $p = 0.489$).

Discussion

Our results suggest that seed banking may increase seedling recruitment of red maple by maximizing the chance that seedlings experience conditions conducive to seedling survival. At our sites, few red maple seeds are dormant following dispersal (Fig. 1A), when conditions are relatively favorable for seedling survival (Fig. 1C). Seedlings emerging late in the growing season are less likely to survive (Table 1, Fig. 1C; Jones and Sharitz 1989; Jones et al. 1997), but by then fewer seeds germinate (Fig. 1B). This occurs because seed dormancy increases as the growing season progresses (Fig. 1A), that of both freshly dispersed seeds and seeds on the forest floor (Figs. 1C, 2A). Postponing germination for 1 year appears to be a common phenomenon; the autumn density of seeds in seed banks as compared to spring seed rain and summer seedling densities suggests that a significant number of red maple seedlings recruit from persistent seed banks (Table 2; Peroni 1995). When seeds in persistent seed banks germinate at the beginning of the following growing season, they once again experience conditions that are relatively favorable for seedling survival (Fig. 1C). Thus, red maples' flexible seed dormancy strategy (immediate germination or delayed germination if conditions are unfavorable for seedling survival) may substantially increase seedling recruitment for this species (Canham and Marks 1985).

We were not able to identify which factors cause seedling survival of late-emerging seedlings to be less than that of early-emerging seedlings, but several possibilities are suggested by other studies. First, red maple seedling mortality may be greater late in the growing season because host-specific predators or pathogens, to which red maple appears to be susceptible (Hille Ris Lambers et al. 2002), accumulate to levels at which they negatively impact seedling survival. Second, seedling survival may decline because light levels decrease in the forest understory following canopy closure in late spring (George and Bazzaz 1999*b*), which occurs around the same time that red maple seeds are dispersed. Finally, survival of emerging seedlings may be negatively affected by lower water availability late in the growing season (Swift et al. 1988; Helvey and Petric 1988; caused by declining precipitation and increasing evapotranspiration due to higher temperatures). These three possibilities are not mutually exclusive, although the fact that red maple seedling survival is negatively correlated with *Rhododendron maximum* cover (Table 1) tends to support the latter two possibilities, as the forest floor under this evergreen shrub is associated with lower levels of both light and moisture (Clinton 2003).

Fig. 2. (A) The proportion of dormant seeds from freshly dispersed seeds and those same seeds 1 month later, and (B) the proportion of dormant seeds collected from red maple trees in open- and closed-canopy conditions. Each symbol represents the proportion of dormant seeds (from 10 seeds in (A), 20 seeds in (B)) for seeds from one maternal tree. Points were jittered (i.e., a small amount of random noise added) in the *y*-direction so that sample size is obvious. The superimposed boxplots represents the mean, 95% error bars, and range for dormancy levels.



Does changing seed dormancy allow seed germination to track conditions favorable for seedling survival? Our data and those of other studies suggest that the environmental variables that reduce seedling survival may also cause seeds to become dormant. Low light (closed-canopy conditions), which decreases seedling survival, appears to increase seed dormancy during seed maturation (Fig. 2). Other studies indicate that low moisture, which also affects seedling survival negatively, acts in a similar manner (Anella and Whitlow 1998). Thus, seeds might be dispersed with lower levels of seed dormancy when seeds are exposed to conditions favorable for seedling survival (in gaps or moist microsites). Seed dormancy also continues to change after dispersal (Peroni 1995), increasing over the course of the growing season as seedling

Table 1. Effects of *Rhododendron maximum*, date of emergence, plot, and year on red maple seedling survival.

Parameter	Coefficient (95% C.I.)	Standard error	*p* value	Relative odds
Intercept	4.520 (4.25, 4.79)	0.138	<0.0001	na
Rhododendron maximum LAI	–0.190 (–0.265, –0.115)	0.0383	<0.0001	1.11
Date of germination (first date censused)	–0.023 (–0.299, –0.0166)	0.0034	<0.0001	1.01
Plot (2)	0.999 (0.861, 1.14)	0.070	<0.0001	na
Plot (3)	–0.318 (–0.405, –0.231)	0.0445	<0.0001	na
Plot (4)	–0.113 (–0.172, –0.0699)	0.0261	<0.0001	na
Year (1998)	–0.770 (–0.990, –0.548)	0.113	<0.0001	na
Year (1999)	0.076 (–0.015, 0.167)	0.0463	0.102	na

Note: Coefficients are from a parametric regression with a log-normal distribution. Relative odds (for *Rhododendron maximum* and date of seedling emergence) indicate the relative increase in risk of mortality associated with one extra unit of *Rhododendron maximum* leaf area index, or germinating 1 day later (from a nonparametric model, fit using Cox proportional hazards). na, not applicable.

Table 2. The average density and standard errors (in parentheses) of red maple during early life-history stages.

Plot	Year	Seed rain (m^{-2})	Seedling emergence (m^{-2})	Seed bank (m^{-2})
1	1997	99.49 (16.92)	1.350 (0.378)	19.53 (8.88)
1	1998	15.87 (4.77)	7.650 (1.103)	7.493 (4.54)
1	1999	44.22 (7.91)	0.400 (0.183)	0 (0)
2	1997	183.4 (21.93)	2.00 (0.465)	53.70 (12.70)
2	1998	76.25 (6.40)	35.90 (5.196)	13.11 (4.78)
2	1999	102.6 (15.17)	3.95 (0.667)	0 (0)
3	1997	198.1 (24.74)	0.850 (0.350)	63.46 (11.99)
3	1998	105.4 (10.73)	16.85 (2.473)	37.47 (9.10)
3	1999	112.0 (19.49)	1.10 (0.390)	16.11 (7.74)
4	1997	425.5 (41.70)	3.40 (0.642)	56.14 (11.27)
4	1998	133.5 (19.22)	14.85 (1.534)	20.61 (6.95)
4	1999	151.6 (17.75)	5.45 (1.075)	44.30 (12.88)

Note: Seed rain: dispersed seeds in the spring; seedling emergence: the total density of emerged seedlings during the summer; seed bank: viable seeds remaining in the seed bank the following fall.

survival becomes less likely (Figs. 1A and 1C, Fig. 2A). It is possible that seed dormancy continues to respond to light and moisture levels after dispersal (George and Bazzaz 1999*a*), but other factors may also play a role. Changing seed dormancy could either be controlled by maternal trees that are affected by light and (or) moisture (or other environmental variables) or by seeds responding directly to these environmental variables both during and after dispersal; regardless, red maple seeds appear to germinate soon after dispersal, when conditions for seedling survival are relatively high, or they postpone germination to the following growing season, when local environments are unfavorable for seedling survival. Whether or not this pattern of seed dormancy has evolved in red maple to increase seedling recruitment is an interesting question that is beyond the scope of this study.

Red maples' flexible germination strategy (i.e., immediate germination early in the growing season vs. postponement late in the growing season, when seedling survival is less likely) differentiates this species from co-occurring species, many of which do not possess seed banks and most of which set seed in the fall (Burns and Honkala 1990; Abrams 1998). Other traits that differentiate red maple from co-occurring species include early reproductive maturation (Burns and Honkala 1990, 2004) and high fecundity (Clark et al. 1998, 2004). It is worth noting these differences, because red maples' dramatic increase in abundance in eastern forests cannot easily be explained by leaf physiology or adult demography (Abrams 1998; Wyckoff and Clark 2002). However, early life-history traits such as high fecundity, early maturation, and seed banking may have allowed red maple seedling recruitment to exceed that of co-occurring species following the extensive disturbance experienced by eastern forests in the last century (logging, the conversion of agricultural lands to secondary forest, the virtual extinction of the overstory dominant *Castanea dentata*, and fire suppression; Whitney 1994; Fuller et al. 1998; Gerhardt and Foster 2002; Whitney and DeCant 2003). If so, the current abundance of red maple in eastern deciduous forests may be a transient phenomenon resulting from differential recruitment by tree species following 19th century disturbance and land-use change in eastern forests.

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