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DENSITY OF INTRASPECIFIC COMPETITORS DETERMINES THE OCCURRENCE AND BENEFITS OF ACCELERATED GERMINATION[1]

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Germination is a key process in plant recruitment and population dynamics, and seeds are expected to be under strong selection pressure to germinate under conditions that maximize subsequent plant survival. Increased rates of germination (i.e., accelerated germination) may occur in competitive environments. We examined the effects of conspecific density on the timing of germination of seeds of a bird-dispersed plant, *Phytolacca americana* (Phytolaccaceae, L.), in three different competitive environments. By comparing germination of seeds sown at the same time at different densities, we quantify the benefits of accelerated germination under conditions in which differences in performance among seedlings are attributable to germination timing only, and not to being sown at different times. We find that although the probability of germination is unchanged, the time to initiation of germination is significantly shorter when competition is greater. We also show that plants that germinate earlier are larger and have higher growth rates because they have more time to grow without competitors. Our work demonstrates that shifts in germination timing in response to competition can yield significant dividends for seeds that germinate earliest, but we caution that the magnitude and consequences of accelerated germination will likely depend on the competitive neighborhood.

Key words: accelerated germination; dormancy; intraspecific competition; seedling growth.

Seed germination can affect many aspects of plant ecology. The timing of seed germination affects individual plant fitness (Rees, 1997; Baskin and Baskin, 1998), survival (Ross and Harper, 1972; Jones et al., 1997), population dynamics (Rees, 1997; Cabin et al., 2000), and competitive interactions (Haizel and Harper, 1973; Rice and Dyer, 2001). Therefore, understanding the cues that seeds use to germinate is important for understanding the ecology and evolution of plants. A large body of work illustrates the importance of abiotic cues such as temperature and light in affecting germination (Rees, 1997; Baskin and Baskin, 1998). However, whether conditions are optimal for germination may depend on biotic characteristics of a seed's environment, such as the presence of potential competitors. In both interspecific (Bergelson and Perry, 1989) and intraspecific (Black and Wilkinson, 1963) seed mixtures, early germination may allow seedlings to grow larger (Black and Wilkinson, 1963) and maintain competitive dominance over seeds that germinate later (Ross and Harper, 1972; but see Turkington et al., 2005). On the other hand, seeds may also delay germination until subsequent growing seasons in competitive environments (Turkington et al., 2005). Empirical studies show that seeds may either delay or accelerate their germination in response to the presence of other seeds or seedlings (e.g., Palmblad, 1968; Linhart, 1976; Inouye, 1980; Bergelson and Perry, 1989; Dyer et al., 2000; Turkington et al., 2005; Tielbörger and Prasse, 2009), and the magnitude of selection for earlier germination can increase as density of conspecifics in the seedbank increases (Miller et al., 1994). However, accelerated germination is also likely to carry a cost, because seeds that germinate early have less time to integrate other cues of environmental suitability before emergence, such that accelerated germination in variable environments could expose seedlings to suboptimal conditions (e.g., Rice, 1985; Clauss and Venable, 2000). These costs and benefits predict that accelerated germination should be employed only in very competitive environments, in which it is predicted to yield the greatest benefit; otherwise, employing accelerated germination risks exposing seedlings to harsh conditions.

Despite the potential importance of accelerated germination, it remains unclear whether accelerated germination confers an advantage in competitive neighborhoods. To understand whether accelerated germination confers a benefit, it is important to document the potential benefit under conditions in which only accelerated germination creates differences in emergence times in competitive neighborhoods (i.e., situations in which the benefits of accelerated germination are not potentially confounded by differences in sowing time). However, previous investigations either have not examined the effects of competitor density on germination rates (Ross and Harper, 1972), have not measured the competitive benefits of accelerated germination (Bergelson and Perry, 1989; Dyer et al., 2000), or have measured the benefits but manipulated the timing of seed germination by planting seeds at different times (e.g., Black and Wilkinson, 1963). Because shifts in germination timing may be on the order of 1–2 d, the benefits of accelerated germination may be more difficult to observe in studies of community-level germination patterns in which it is feasible to monitor seedling cohorts only on longer timescales, such as two or three times per month (Turkington et al., 2005). Moreover, although seeds of animal-dispersed species might become highly concentrated

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in animal feces and preferred defecation sites (Howe, 1986; Loiselle, 1990), and thus be under strong selection for accelerated germination (Miller et al., 1994), none of the 34 species examined in previous studies are primarily dispersed by endozoochory (Ballard, 1958; Black and Wilkinson, 1963; Palmblad, 1968; Ross and Harper, 1972; Linhart, 1976; Waite and Hutchings, 1978; Bergelson and Perry, 1989; Dyer et al., 2000).

We used an experimental approach to explicitly evaluate the consequences of accelerated germination under the most ecologically realistic scenario: interactions among seeds, not experimentally manipulated planting times, determining both the rate of germination and the performance of seeds after they germinate. We focused on intraspecific competition, thus avoiding the potential confounding effects of comparing native and nonnative seeds (Turkington et al., 2005). Our study species is the endozoochorous, early-successional *Phytolacca americana*. Although it is unknown whether density affects germination in *P. americana*, this species is well suited for examining the benefits of accelerated germination because endozoochorous seeds may experience highly competitive environments. Our study examines (1) whether seeds of *P. americana* exhibit accelerated germination in more competitive neighborhoods and (2) whether accelerated germination within highly competitive neighborhoods yields benefits, as measured by seedling growth.

MATERIALS AND METHODS

We collected fruit of *P. americana* in August 2003 from naturally occurring plants growing at the Savannah River Site, a National Environmental Research Park located near Aiken, South Carolina. We extracted the seeds, thoroughly washed them with tap water to remove all debris and pulp, and stored them in a dry container at room temperature. Seeds of *P. americana* are 2.5–3 mm long and weigh ~0.01 g (Armesto et al., 1983). On 1 June 2004, the seeds were haphazardly placed on the surface of a 2:1 mix of potting soil and sand, a mixture chosen to replicate the relatively sandy soils in the region where they were collected. The placement of the seeds on the soil surface matched field conditions in which *P. americana* is most often encountered (i.e., recently disturbed microsites), and experiments have confirmed that burial greatly reduces germination of *P. americana* (Orrock et al., 2006). Each seed was randomly allocated to one of three density treatments within a cell 7 × 5 cm wide in a plastic greenhouse container. Each cell was 8 cm deep and had drainage holes in the bottom. Low-density treatments had 5 seeds, medium-density treatments had 10 seeds, and high-density treatments had 25 seeds, yielding densities of 0.143 seeds/cm^2, 0.286 seeds/cm^2, and 0.714 seeds/cm^2, respectively. There were 18 replicates of each density treatment.

Trays were randomly arranged along a single level within a Percival PGC 15.5 growth chamber (approximate light output 1000 μmol/m^2/s from cool white fluorescent and incandescent bulbs). The growth chamber was set to 14 h day:10 h night photoperiod, with temperatures of 34°C and 27°C, respectively. This regime reflects conditions used in other germination studies of *P. americana* (Farmer and Hall, 1970; Edwards et al., 1988; Orrock et al., 2003, 2006). Seeds were checked daily, and distilled water was added as necessary to maintain soil moisture. We considered seeds to have germinated when the radicle was >1 mm in length (Farmer and Hall, 1970). Upon germination, each seedling was marked by placing a colored wire in the soil near the seedling. We concluded the study on 30 June 2004, quantifying height and number of leaves and harvesting aboveground seedling biomass. After harvest, individual seedlings were dried at 50°C for 12 h and weighed to determine biomass.

Statistical analyses—We used a generalized linear model with a binomial response distribution to examine whether competition treatments altered the proportion of seeds that germinated during the course of the experiment. Cells were used in this analysis regardless of whether any seeds germinated in them, because we were interested in testing the overall effects of competition treatment on germination; a cell in which no seedlings germinated provides relevant information regarding overall germination rates. However, we used only data from cells in which at least one seedling germinated to analyze how competitor density affects the timing of germination and subsequent growth of seedlings, because examining the timing of germination requires that germination occurred. Although there were 18 initial replicates of each density treatment, differences in germination yielded realized replication of 14, 14, and 16 cells in which at least one seed had germinated for low-, medium-, and high-density treatments, respectively.

We used survival analysis to determine differences in germination timing across density treatments, because it is a robust approach for modeling time-to-event data such as germination data (Scott et al., 1984). Because accelerated germination is likely to be most important for seeds that germinate first, we focus on timing of only the first germinants in each density treatment (i.e., the first seed in each replicate to exhibit radicle emergence), using Cox's proportional hazard regression conducted in R (R Development Core Team, 2009). Our data met the proportionality assumptions of this nonparametric procedure. Because we were focusing on the fate of seeds that germinated, we used only noncensored data in our proportional hazards analysis (i.e., only cases in which seeds germinated during the experiment), although we note that identical statistical patterns were observed if censored data were used.

We used analysis of variance to examine how final seedling mass was affected by competitor density and germination cohort of the seedling (i.e., whether it germinated first or subsequently). "Subsequent germinants" are any seeds that did not germinate first (e.g., third and fourth germinants within a replicate are both subsequent germinants). We focused on seedling mass because it directly quantifies seedling growth and was also strongly related to other measures of seedling performance, such as height at the end of our experiment ($r^2 = 0.74$, $F = 272.93$, df = 1 and 97, $P < 0.001$) and the number of leaves per seedling ($r^2 = 0.74$, $F = 275.64$, df = 1 and 97, $P < 0.001$). The analysis of variance (ANOVA) model was constructed in agreement with the split-plot design of our experiment, whereby the treatment of competitor density was applied to the cell (i.e., the main plot), and germination order arose within each cell (i.e., the subplot). To more fully explore how germination order affected seedling growth in highly competitive environments and incorporate differences in seedling age into overall growth, we also used ANOVA to examine the effect of germination order on the relative growth rates of seedlings, calculated as ln[biomass (mg) / age in days] for seedlings (Gibson, 2002) from the high-density treatment. These analyses were conducted in SAS (Littell et al., 2006) and R (R Development Core Team, 2009).

RESULTS

Effects of competitor density on timing of seed germination—Across all cells, including cells in which no seeds germinated, the proportion of seeds that germinated over the course of the experiment did not differ among competition treatments ($F = 0.82$, df = 2 and 51, $P = 0.44$; mean proportion of seeds that germinated was 0.21 ± 0.02 SE) and was similar to overall germination rates observed in other studies of *P. americana* that used nonstratified seeds (Orrock et al., 2006). In the cells used to examine germination timing (i.e., cells in which at least one seedling germinated), our density treatments were successful in increasing the competitive environment by increasing the absolute number of seedlings at the end of the experiment (generalized linear model with Poisson distribution, $\chi^2 = 33.23$, df = 2, $P < 0.001$). On average, there were 1.57 ± 0.47 seedlings in the low-density treatments, 2.27 ± 0.46 seedlings in the medium-density treatments, and 5.06 ± 0.44 seedlings in the high-density treatments.

The rate at which first seeds germinated responded to the density of competitors (Wald $\chi^2 = 10.7$, df = 2, $P < 0.01$; Fig. 1). Germination rate accelerated as the competitive environment became more dense, making the difference in germination rate greatest between low- and high-density treatments ($z = -3.27$, $P = 0.001$). Although there was a trend of more rapid germination in medium-density treatments than in low-density treatments, this difference was not significant ($z = 1.39$, $P = 0.16$). Similarly, there was a trend of faster germination of high- vs. medium-density treatments, but this trend was not significant

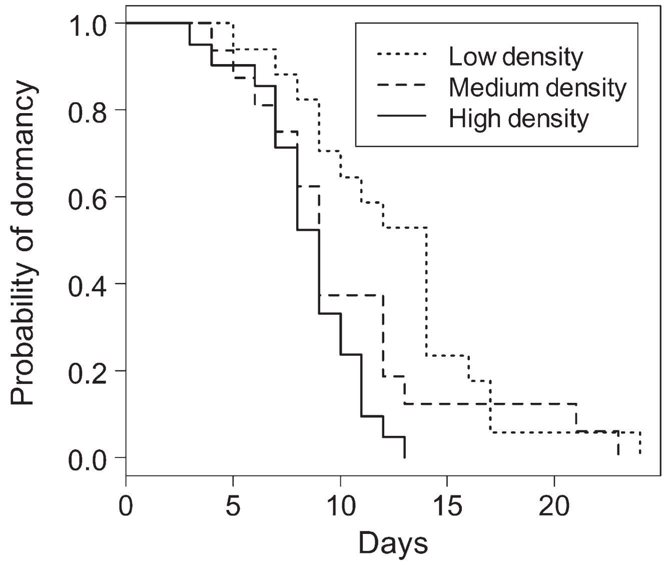

Fig. 1. Germination curves calculated from proportional hazards analysis using competitor density as a fixed effect. The *y* axis indicates the complement of the probability of germination (i.e., the probability of remaining dormant). More steeply decreasing curves indicate treatments in which seeds exhibited more rapid germination.

($z = -1.45$, $P = 0.15$). These statistical trends are supported by 95% confidence limits for median day of germination for the low-density treatment (10–16 d), medium-density treatment (8–13 d), and high-density treatment (8–11 d).

Benefits of earlier germination—When the biomass of first germinants and subsequent germinants was compared across density treatments, the order in which seeds germinated significantly affected the amount of biomass accrued by seedlings (Fig. 2; $F = 44.33$, df = 1 and 75, $P < 0.001$). Although there was no main effect of competitor density averaged across both germination cohorts (density treatment main effect, $F = 1.40$, df = 1 and 38, $P = 0.26$), there was a significant interaction between the effect of germination cohort and competitive environment (cohort × density interaction, $F = 4.23$, df = 1 and 75, $P < 0.02$; Fig. 2). The interaction between germination cohort and competitor density was attributable to differences in biomass among first germinants (linear contrast $F = 5.41$, df = 2 and 75, $P < 0.01$). Specifically, first germinants from low- and medium- density treatments had 32% less biomass than first germinants from high-density competitive neighborhoods (linear contrast, $F = 10.75$, df = 1 and 75, $P < 0.002$). There was no significant difference in biomass attributable to competitor density when only the subsequent germinants were examined (linear contrast $F = 0.21$, df = 2 and 75, $P = 0.81$; Fig. 2). When the benefits of accelerated germination were quantified as the difference in biomass between first germinants and subsequent germinants, the difference in biomass was significantly greater in high-density treatments than in low- and medium-density treatments ($F = 7.70$, df = 1 and 75, $P < 0.01$), although this trend was weaker when only the difference between low-density and high-density treatments was examined ($F = 3.67$, df = 1 and 75, $P < 0.06$). Examination of growth rate suggests that differences in biomass among treatments were largely attributable to accelerated germination (i.e., more time for growth), rather than to faster growth rates in a particular density treatment, given that there was no significant main effect of density treatment ($F = 0.82$, df = 1 and 38, $P = 0.45$), no interaction between density treatment and germination cohorts ($F = 1.67$, df = 1 and 75, $P = 0.19$), but a strong main effect of germination cohort ($F = 11.32$, df = 1 and 75, $P = 0.001$).

The relative growth rate achieved by a seedling in the high-density treatment was a function of the number of competitors present when the seedling germinated ($F = 10.14$, df = 5 and 51,

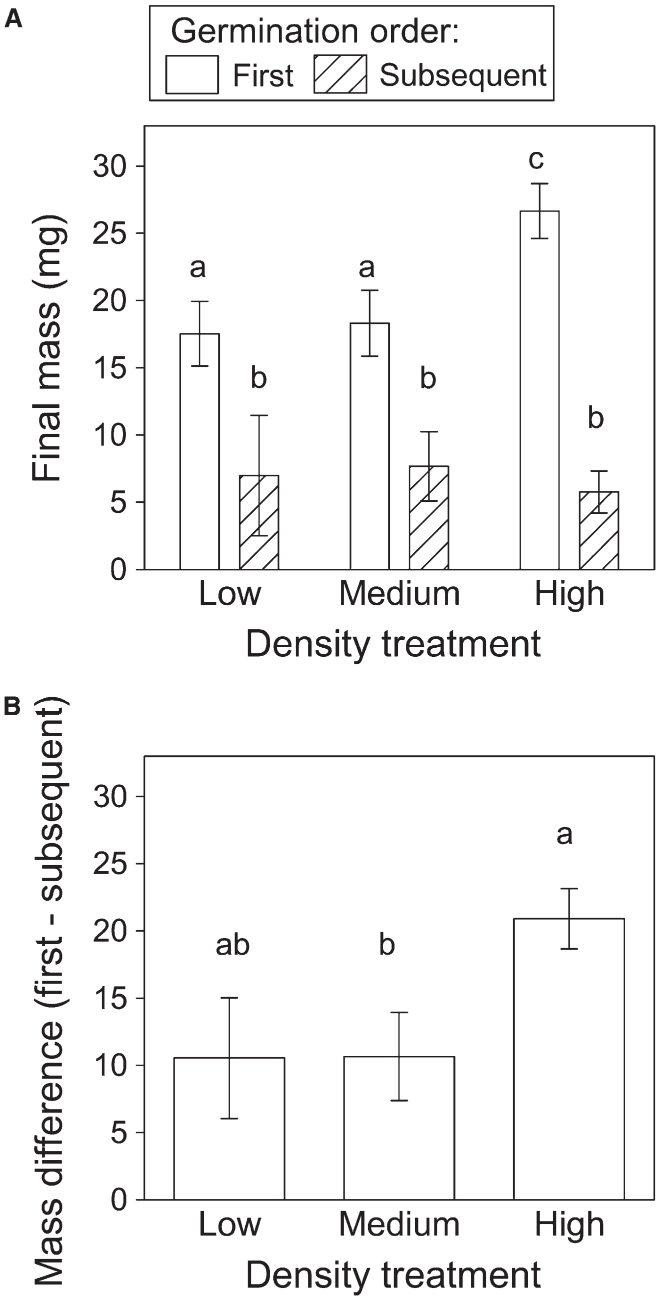

Fig. 2. (A) Seedling mass (± SE) in relation to the competitive environment and germination cohort (i.e., whether a seed was a first or a subsequent germinant). Low-density treatments had 5 total seeds, medium-density treatments had 10 seeds, and high-density treatments had 25 seeds. (B) Differences in seedling mass among density treatments. Within each panel, values with different letters are significantly different by linear contrast ($P < 0.05$).

$P < 0.001$; Fig. 3). Seedlings that germinated first had greater relative growth rates than all other germination orders (linear contrast; $F = 32.01$, df = 1 and 51, $P < 0.001$). Moreover, the majority of variation in mean relative growth rate was inversely related to the order in which a seed germinated ($r^2 = 0.72$, $F = 10.43$, df = 1 and 4, $P = 0.03$; Fig. 3).

DISCUSSION

Because the timing of seed germination can influence seedling survival, understanding the cues that alter germination rates is important for gaining insight into the dynamics of plant persistence, community composition, and the selective forces that govern plant evolution. Although many factors affect germination timing (Rees, 1997; Baskin and Baskin, 1998) and subsequent plant survival (Crawley, 1997), seeds that exhibit adaptive use of germination cues should accelerate germination if the competitive environment warrants it, and only when accelerated germination yields quantifiable benefits. Evidence for both of these predictions was observed in our study: germination of *P. americana* was accelerated as seed densities increased (Fig. 1), and the order in which seeds germinated significantly affected seedling size and growth rate (Figs. 2–3), especially when competitor densities were high (Fig. 2).

Our work builds on previous demonstrations of accelerated germination in response to competitive environment (Bergelson and Perry, 1989; Miller et al., 1994; Dyer et al., 2000; Tielbörger and Prasse, 2009) by demonstrating that seed-mediated changes in germination timing affect seedling performance (Fig. 2). Moreover, our data suggest that early germination is advantageous only if the probability of future competition is sufficiently high. At low competitor densities, resources are less likely to be limiting and earlier germination is less likely to provide a net benefit, especially in light of the potential costs of accelerated germination (e.g., having less information about environmental variability before germinating). Comparison of relative growth rates suggests that the differences in final mass attained by seedlings that germinated first in different competitive neighborhoods (Fig. 2) were largely a function of the additional time for growth afforded by accelerated germination, given that competitive neighborhood had no effect in relative growth rates. Although the relative growth rates of first germinants did not differ among density treatments, it is important to note that first germinants had significantly greater relative growth rates than subsequent germinants (Fig. 3). As suggested by Ross and Harper (1972), this benefit of first germination is likely attributable to the disproportionate accumulation of resources by seedlings that germinate first.

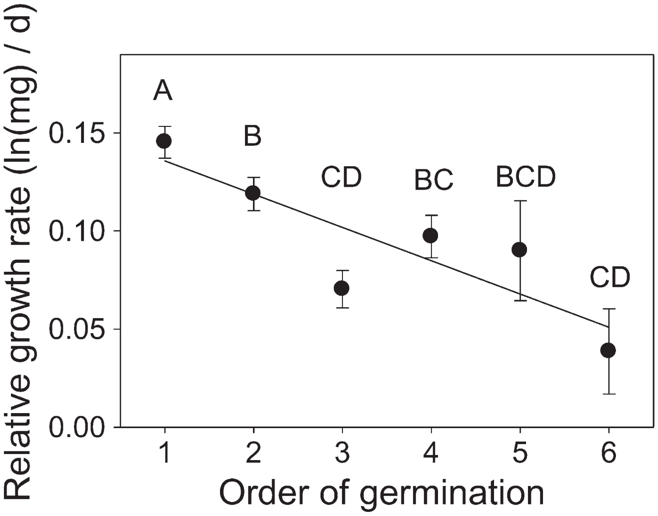

Fig. 3. Relative growth rate as a function of the order in which seeds germinated in high-density treatments (25 seeds replicate^{-1}; e.g., seeds with germination order = 3 germinated after two seeds in that replicate had already germinated). A negative relationship describes mean relative growth rate as a function of germination order; the best-fit line was estimated using least-squares regression. Standard error bars are shown; means that do not share a letter are significantly different ($P < 0.05$).

Ultimately, the evolution of germination timing is likely determined by natural selection operating over evolutionary timescales. Many factors can influence the evolution of germination timing (Rees, 1997; Baskin and Baskin, 1998), but we will discuss only competitive and variable germination environments, because these are the factors that have been examined in previous studies.

Species with seeds that may experience highly competitive neighborhoods over evolutionary timescales may also exhibit accelerated germination in response to seed density. For example, seeds of bird-dispersed species may encounter high levels of intraspecific competition in deposition sites (Howe, 1986; Loiselle, 1990) and often exhibit altered germination behavior (Loiselle, 1990; Travaset and Verdu, 2002; Orrock, 2005). Because *P. americana* is often dispersed by birds, future work is needed to determine whether the shift in germination timing that we observed in unconsumed *P. americana* seeds (Fig. 1) is altered by passage through a bird's digestive system. Similarly, California grasslands are often dominated by annual grasses that produce large quantities of seeds, which may create highly competitive neighborhoods and affect germination rates (Dyer et al., 2000). Other mechanisms that create highly competitive seedling neighborhoods may also select for accelerated germination. For example, *P. americana* may reduce germination of conspecific seeds by allelopathy (Edwards et al., 1988); seeds that do not germinate quickly may be prevented from germinating at all (Tielbörger and Prasse, 2009). Ultimately, future laboratory and field studies are needed to examine whether labile germination strategies are common mechanisms to escape allelopathic inhibition.

Environmental variability experienced by a species in evolutionary time may also play an important role in the degree to which seeds use biotic cues to alter germination. In harsh and variable environments, the costs associated with competitor-mediated accelerated germination, such as emerging into an unsuitable environment, may outweigh the benefits of emerging before competitors. Under these conditions, adaptive delay of germination may become a more effective strategy. For example, Turkington et al. (2005) found that dicot germination rate was negatively correlated with seedbank density of arid sand dunes, and timing of germination had little effect on subsequent seedling growth or survival. Growth of plants in the arid dune systems examined by Turkington et al. (2005) is inhibited by low temperatures until 3 to 4 weeks before the end of the growing season, when seedlings quickly accelerate their growth (Turkington et al., 2005). Thus, accelerated germination in response to competitor density may not be a viable strategy because it confers no benefits. However, species that have evolved in environments in which many species initiate germination and growth at the onset of a well-defined rainy season (e.g., grasslands in Mediterranean climates) may be more sensitive to the competitive environment, increasing the benefit of accelerated germination (Dyer et al., 2000). Therefore, the contrasting results of our study and those of Turkington et al. (2005) may indicate the presence of a gradient in the costs and benefits of density-dependent accelerated germination, with higher relative costs predicted for species living in relatively unpredictable environments and greater relative benefits for species found in more predictable environments.

Although highly competitive neighborhoods and constant environments may select for germination timing on the basis of competitor densities, it is important to realize that other constraints likely affect the evolution of germination timing. Because many other abiotic and biotic conditions also determine seedling survival, density of competitors may not be the most important agent of selection on germination timing. For example, obligate annual species or species with seeds that are unable to persist in the soil because of high rates of attack by soil pathogens (e.g., Orrock and Hoisington-López, 2009) are effectively constrained to germinate before seed death, regardless of the competitive environment. Species that can persist in the soil for extended periods may use germination cues to be more selective in their germination environment. For example, *P. americana* can remain viable in the seed bank for ≤40 yr (Toole and Brown, 1946) and has a generally labile germination strategy (Fig. 1; Armesto et al., 1983).

A large body of literature attests to the importance of abiotic germination cues (Rees, 1997; Baskin and Baskin, 1998), and a growing number of studies, including this one, have demonstrated that biotic cues in the environment are also important. Our results emphasize the value of germination timing for seedling growth in competitive neighborhoods and suggest that the timing of germination is essentially a decision (Karban, 2008) that is based, in some part, on information about the density of conspecifics (e.g., Linhart, 1976). These effects could ultimately alter the composition of plant communities if responses to competitor density are different for different plant groups within the same community (Turkington et al., 2005) and could lead to community-level regulation of plant density, particularly when resources are limiting (Shilo-Volin et al., 2005). Moreover, competitive and facilitative germination cueing effects may be highly species-specific (Lortie and Turkington, 2002). Future work examining the relative importance of abiotic and biotic cues in determining germination—and the importance of germination timing compared with other components that affect plant success—will be essential for gaining greater insight into the ecological and evolutionary significance of dormancy.

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