

Notes and Comments

Long-Term Persistence of Pioneer Species in Tropical Rain Forest Soil Seed Banks

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ABSTRACT: In tropical forests, pioneer tree species regenerate from seeds dispersed directly into canopy gaps and from seeds that persisted in soil seed banks before gap formation. Life-history models have suggested that selection for the long-term persistence of tree seeds in the soil should be weak because persistence potentially reduces population growth rate by extending generation time and because adult life spans may exceed the return interval of favorable recruitment sites. Here we use accelerator mass spectrometry to carbon-date seeds of three pioneer tree species extracted from undisturbed seed banks in seasonally moist lowland Neotropical forest. We show that seeds of *Croton billbergianus*, *Trema micrantha*, and *Zanthoxylum ekmannii* germinate successfully from surface soil microsites after 38, 31, and 18 years, respectively. Decades-long persistence may be common in large-seeded tropical pioneers and appears to be unrelated to specific regeneration requirements.

Keywords: carbon dating, pioneer species, seed survival, forest regeneration.

Introduction

Up to 15% of tree species in old-growth tropical forests have been classified as pioneers that require high-light conditions for successful seedling recruitment (Hubbell et al. 1999; Molino and Sabatier 2001). In most forests, these conditions are found in treefall gaps that occur infrequently and at largely unpredictable locations and that usually persist for only a few years before canopy closure (Hartshorn 1990; Young and Hubbell 1991; Schnitzer et al. 2000). As a consequence, pioneer life histories are usually characterized by traits associated with a high colonization ability, that is, prolific seed production, high seed dispersibility, and disturbance-cued germination from soil seed banks (Whitmore 1983; Swaine and Whitmore 1988).

While most of these life-history traits have now been described in detail, the contribution of persistent seed banks to pioneer colonization remains unclear. Detailed demographic studies of common, small-seeded pioneers have generally shown that seed persistence (i.e., the capacity to survive in the soil, generally in a nondormant state) is short, lasting for a few years at most (Alvarez-Buylla and Martínez-Ramos 1990; Dalling et al. 1998). Nonetheless, a few species have been shown to retain high viability for at least 3 years, even when exposed to predators and decomposer organisms (Hopkins and Graham 1987; Dalling et al. 1997; Murray and Garcia 2002).

The adaptive value of seed persistence is to reduce the impact on plant recruitment of temporal variation in the favorability of habitat conditions (Venable and Brown 1988). In arid environments, where recruitment conditions fluctuate strongly, seed persistence coupled with variable duration of seed dormancy can provide a means of “bet hedging” to ensure that some seeds avoid germinating in years that are unfavorable for seedling establishment (Cohen 1966; Venable 2007). In these environments, seed persistence is an important trait preventing local extinction of short-lived or semelparous species (Kalisz and McPeck 1993). In contrast, long-term seed persistence is apparently rare for long-lived perennials and has not been reported for European temperate mature forest trees (Thompson 2000). The apparent absence of seed persistence in temperate tree communities has been interpreted as a consequence of the added fitness cost that results from delayed reproduction (Venable and Brown 1988). Additionally, for long-lived organisms, the adult reproductive life span may exceed the interval between favorable recruitment sites becoming available (Rees 1994; Thompson 2000). Temperate woodland herbs, by comparison, frequently show persistent seed banks, with germination cued by small-scale disturbances to litter or the herbaceous vegetation layer (Jankowska-Blaszczuk and Grubb 1997).

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In this study, we provide a first step in describing the capacity for long-term seed persistence among pioneer trees of lowland Neotropical forest. We use accelerator mass spectrometry (AMS) to carbon-date naturally dispersed seeds present in surface soil layers where successful seedling emergence can take place.

Study Site and Methods

We measured how long seeds of pioneer species remain viable in the soil beneath seasonally moist lowland tropical forest on Barro Colorado Island (BCI), Panama (9°10'N, 79°51'W). Rainfall on BCI averages 2,600 mm/year, with a pronounced dry season from January to April (Windsor 1990). Seeds were collected in May 2002 from soil cores taken within old-growth forest in the 50-ha forest dynamics plot in the center of the island (Hubbell and Foster 1983). Only surface soil layers (0–3 cm depth) were sampled to ensure that seeds were collected from burial depths from which emergence can successfully occur (Pearson et al. 2002). Seeds were extracted from the soil by wet sieving, identified to species, and germinated in sand in individual petri dishes. To increase the probability of encountering “old” seeds, we used plot data to sample locations where reproductive-sized individuals of focal tree species had occurred over the previous 20 years.

We targeted three relatively large-seeded pioneer species shown to retain high viability over 2 years in seed burial experiments (Dalling et al. 1997). *Croton billbergianus* (Euphorbiaceae), air-dried seed mass 24 mg, is a ballistically dispersed subcanopy tree with a median dispersal distance of 2.2 m (Dalling et al. 2002). *Croton* is among the commonest pioneers on BCI, with 367 reproductive-sized individuals recorded in the 1995 census of the 50-ha plot. *Trema micrantha* (Celtidaceae), seed mass 3.9 mg, is a bird-dispersed canopy tree with year-round seed production. *Trema* is rare in old-growth forest on BCI; 11 reproductive-sized individuals were recorded in the 1995 plot census. *Zanthoxylum ekmannii* (Rutaceae), seed mass 11 mg, is the most abundant of four congeneric dioecious canopy trees on BCI; 108 reproductive individuals were recorded in the 1995 plot census. Median dispersal of *Zanthoxylum* spp. was estimated at 0.8 m (Dalling et al. 2002). *Zanthoxylum* fruits are semidehiscent follicles; seeds are reportedly dispersed by primates (Hladik and Hladik 1969).

Samples of seed coat material from 32 seeds that germinated (table A1 in the online edition of the *American Naturalist*) were cleaned and dated using AMS at the Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory. AMS yields high-precision measurements of $^{14}\text{C}/^{13}\text{C}$ based on very small amounts of carbon (<100 μg) by providing counts of individual isotope atoms (Donahue et al. 1990; Donahue 1995; Moriuchi

et al. 2000). Dates of carbon fixation for the samples were determined by regressing the sample F^{14}C value (the fraction of a value expected for material from 1950; Reimer et al. 2004) against a long-term atmospheric record for Northern Hemisphere zone 2 (Hua and Barbetti 2004). Seed dates obtained with this technique are conservative because we assume that carbon fixation occurred during the period of declining $^{14}\text{C}/^{13}\text{C}$ (post-1963) rather than ascending $^{14}\text{C}/^{13}\text{C}$ (1953–1963). As an independent check of our ability to accurately date seeds, we analyzed fruit and seed wall material from dated herbarium specimens collected and stored on BCI. Specimens used were *Ficus insipida*, *Hamelia axillaris*, *Miconia lonchophylla*, *Ochroma pyramidale*, *Simarouba amara*, *Stemmadenia grandiflora*, *Stenospermaton angustifolium*, and *Tabebuia rosea*, collected between August 1967 and August 1996.

Results and Discussion

AMS carbon dating of herbarium seed material of known age (fig. 1) shows that predicted ages for field-collected seeds are likely to be accurate within <2 years. With one exception, predicted seed ages and seed collection dates differed by <18 months. Seeds of *Stenospermaton angustifolium*, an epiphytic aroid collected in 1997, however, were predicted to be >4 years older than observed. The age discrepancy for this species probably indicates long-term storage of fixed carbon in rhizomes used for infrequent reproduction.

Application of AMS dating to field-collected seeds in-

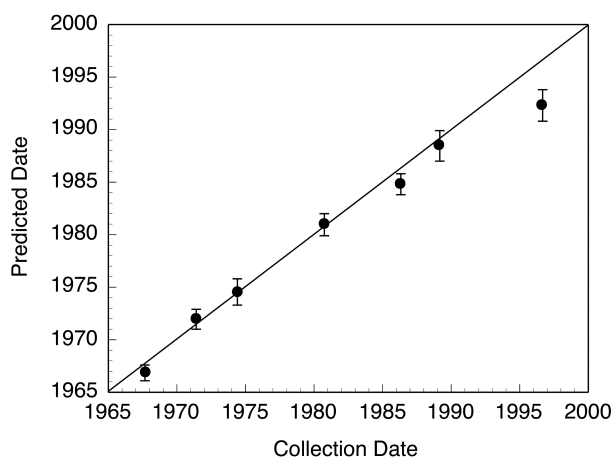


Figure 1: Correlation of date of seed production derived from ^{14}C dating with date of seed collection for eight liana and tree species sampled from herbarium sheets. Correlation $r = 0.99$. Error bars are 95% confidence intervals for the regression of the isotopic ^{14}C ratio, determined by mass spectrometry and the atmospheric F^{14}C record for Northern Hemisphere zone 2 (Hua and Barbetti 2004; Reimer et al. 2004).

dicates that seeds of the three pioneer species tested are capable of persisting in the soil for decades (fig. 2; table A1). Germinable seeds were recovered from surface soil layers after up to 18 years (*Zanthoxylum*), 31 years (*Trema*), and 38 years (*Croton*) in the soil seed bank. These persistence times are remarkable, given the rapid decomposition rates of woody material on the soil surface in tropical forests (Chambers et al. 2000).

The cost of AMS prevents dating of sufficient samples to construct survivorship curves for seeds in the seed bank. Nonetheless, the relatively high viability of seeds isolated from the same soil cores from which seeds were dated suggests that long-term persistence is likely to be common for these species (table A1). For *Zanthoxylum*, three seeds dated from one soil core gave consistent ages of 15–16 years; 59 of 535 seeds recovered from the same core (11%) were germinable. For *Trema*, five seeds dated from one core gave ages ranging from 20 to 31 years; 12 of 100 seeds recovered from the same core were germinable. For *Croton*, a subcanopy tree with very low estimated fecundity (2.6 seeds/cm² basal area; Dalling et al. 2002), only 10 seeds were recovered from the soil, seven of which were germinable.

The seed ages reported here greatly extend the measured duration of seed persistence times for tropical pioneers. These data, however, are consistent with inferred seed persistence times calculated as the ratio of seed bank density to average annual seed rain. Repeated measurements of seed rain and soil seed densities made in a montane forest in Costa Rica yielded a median seed bank to seed rain ratio of 8.4 for 23 species (Murray and Garcia 2002). Several species common in the seed bank, including *Trema micrantha*, were not observed in seed rain over 3 years, while a pioneer shrub, *Bocconia frutescens*, accumulated a seed bank equivalent to 85 years of seed rain. Estimates of seed persistence based on seed bank to seed rain ratios are sensitive to sampling methods and are unlikely to meet assumptions of spatial homogeneity and temporal equilibrium of seed rain and seed banks (Garwood 1989; Murray and Garcia 2002). Nonetheless, the combination of direct seed dating and inferred seed residence times in the soil strongly suggests that long-term seed persistence is common for tropical pioneer trees and shrubs.

In contrast to field data, population growth models predict that selection for long-term seed persistence should be weak (Murray 1988). This is because seeds that germinate after a long period in the soil contribute less to population growth than those that arrive directly in gaps or germinate soon after dispersal. Long-term seed persistence, however, may arise even if it is not under direct selection. Risk of mortality for seeds is highest shortly after dispersal, when seeds are exposed to predators and pathogens on the soil surface (Estrada and Coates-Estrada

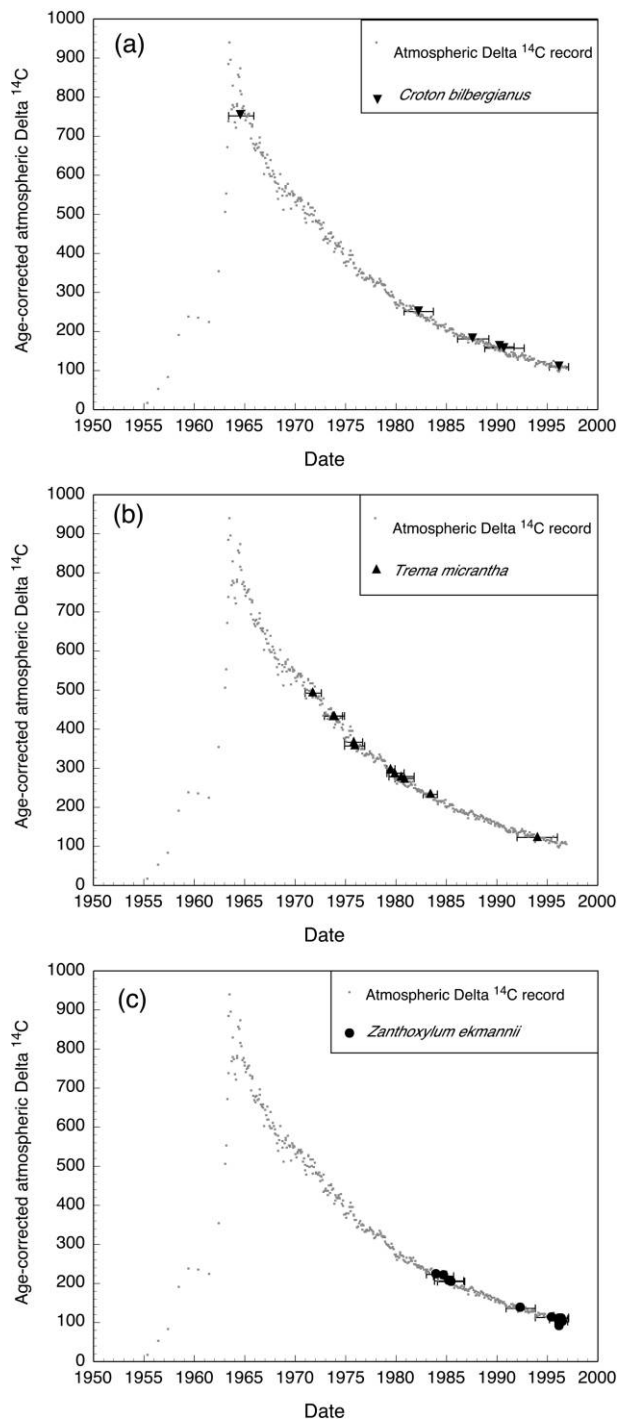


Figure 2: Atmospheric record of $F^{14}C$ for Northern Hemisphere zone 2 (gray points) and predicted dates and their 95% confidence intervals for the production of individual seeds of (a) *Croton bilbergianus* ($n = 6$), (b) *Trema micrantha* ($n = 11$), and (c) *Zanthoxylum ekmanii* ($n = 15$) recovered from surface soils in lowland wet tropical forest. Dates for seeds were determined from regressions of seed $F^{14}C$ with the atmospheric record.

1991; Dalling et al. 1997). Physical and chemical traits that provide sufficient protection for seeds to become incorporated into the soil may incidentally also confer long-term persistence.

Although species included in this study have among the largest seed masses of Neotropical pioneers, they differ in other important respects. *Croton* is relatively slow growing, disperses seeds only a few meters, and regenerates in a wide range of gap sizes (Pearson et al. 2003). Seed trap data suggest that *Zanthoxylum* has similarly short-distance dispersal but is among the fastest-growing species in the forest (Condit et al. 1993; Dalling et al. 2002). *Trema* is rare on BCI and is restricted to very large treefall gaps that occur infrequently in old-growth forest (Brokaw 1987; Pearson et al. 2003). Thus, long-term seed persistence does not appear to be restricted to pioneers that share a single combination of life-history traits.

Finally, our observations suggest that some additional consequences of maintaining a persistent seed bank also apply to this functional group. In common with annual plants and copepods (Brown and Venable 1986; Hairston and De Stasio 1988), seed banks that persist longer than adult life spans may maintain genotypes absent from other life stages, increase effective population size, and reduce the effects of short-term variation in selection (Templeton and Levin 1979; Tonsor et al. 1993). Seed banks may therefore be critical to the long-term survival of pioneer populations in habitat fragments and may contribute to the maintenance of pioneer diversity through temporal niche partitioning if long-term persistence is coupled with interspecific variation in germination requirements (Chesson 2000; Facelli et al. 2005).

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