GERMINATION ECOLOGY OF NEOTROPICAL PIONEERS: INTERACTING EFFECTS OF ENVIRONMENTAL CONDITIONS AND SEED SIZE

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Abstract. Germination provides many potentially unrecognized sources of variation in the regeneration niche. In this study we relate germination requirements and seed size for 16 species of pioneer trees to microclimatic conditions present in gaps in semi-deciduous rain forest in Panama. We found that, whereas increased duration of direct irradiance can be an effective indicator of the presence of a canopy gap across all scales of canopy openness, diel fluctuations in soil temperature effectively discriminate both understory sites and small gaps (25 m^2) from larger gaps. Germination response was significantly related to seed size. Small-seeded species (seed mass <2 mg) showed significantly greater germination in response to irradiance of 22.3 μmol·m^{-2}·s^{-1} than in complete darkness. Their germination was unaffected by an increasing magnitude of diel temperature fluctuation up to a species-specific threshold, above which it declined. Large-seeded species (seed mass >2 mg) germinated equally in light and darkness (with one exception) and either showed a positive germination response to an increasing magnitude of temperature fluctuation (four species) or no significant response (four species). The maximum seed burial depth from which seedlings could emerge successfully was strongly positively associated with seed mass. We conclude that photoblastic germination of tropical pioneer trees results in small-seeded species germinating in gaps only when seeds are located in microsites that are suitable for seedling emergence. A positive germination response to increasing temperature fluctuation can stimulate germination of larger-seeded species in larger gaps and when they are buried beneath an opaque soil or litter layer. Therefore, seed size differences constrain the physiological mechanisms of canopy gap detection in tropical pioneer trees and might contribute to observed differences in the distribution of adult plants in relation to canopy gap size.

Key words: Barro Colorado Island, Panama; emergence potential; germination cue; niche differentiation; pioneer species; tropical diversity.

INTRODUCTION

Many processes contribute to the maintenance of tree diversity in tropical forests. Recently studied processes include density and frequency-dependent recruitment success (e.g., Harms et al. 2000), dispersal limitation (e.g., Hubbell et al. 1999), and niche differentiation or resource partitioning during early recruitment (Grubb 1996). Although considerable attention has been given to seedling responses to resource availability, particularly irradiance (e.g., Metcalfe and Grubb 1997), the roles of other potential differences between species have not been examined in detail.

Here we examine the importance for pioneer species of different germination responses to the environmental signals that indicate the presence of a canopy gap. Tropical pioneer trees have been defined as species requiring high irradiance for establishment and growth to maturity (Swaine and Whitmore 1988). Germination requirements are likely to be under strong selection pressure as early colonization leads to early growth in a situation where larger plants have a disproportional advantage in competition for irradiance (Weiner 1990).

Studies of cues to germination in tropical pioneers have examined irradiance, but largely neglected alternative cues and the role of seed size. Although many pioneers are sensitive to irradiance, published results are not representative of pioneers in general because work has been biased toward small-seeded species (Vázquez-Yanes and Orozco-Segovia 1993). Temperature has rarely been considered as a germination cue. Vázquez-Yanes and Orozco-Segovia (1982) showed maximum germination in the pioneer tree *Heliocarpus donnell-smithii* when seeds were exposed to a 15°C daily temperature fluctuation. Vázquez-Yanes and Pérez-García (1976) examined another pioneer, *Ochroma lagopus*, and found that a marked temperature fluctuation made the seed coat permeable; this allowed imbibition and subsequent germination. None of this work has been related to gap environments and microclimatic variation with gap size, gap position, or soil depth.

TABLE 1. Details of the 18 species of pioneer trees studied including seed properties and experimental treatments.

Species and family	Seed mass (mg)	Seed coat thickness† (μm)	Dis-persal‡	Experi-mental treatment§	Seed pretreatments
Piper peltatum, Piperaceae	0.04	9 ± 0.1	A	I, T	...
Miconia argentea, Melastomataceae	0.08	33 ± 1.1	A	I, T, SD	none
Piper dilatatum, Piperaceae	0.10	18 ± 1.5	A	I, T	...
Alseis blackiana, Rubiaceae	0.12	...	W	I	...
Cecropia peltata, Moraceae	0.58	84 ± 4.0	A	I, T	...
Cecropia obtusifolia, Moraceae	0.59	83 ± 4.3	A	I, T	...
Cecropia insignis, Moraceae	0.68	67 ± 4.0	A	I, T, SD	none
Luehea seemannii, Tiliaceae	1.90	83 ± 3.4	W	I, T, SD	hot water (70 °C, 2 min)
Solanum hayesii, Solanaceae	2.40	59 ± 2.8	A	I, T, SD	none
Trichospermum mexicanum, Tiliaceae	2.70	76 ± 3.8	W	I, T, SD	hot water (70 °C, 2 min)
Trema micrantha, Ulmaceae	3.90	...	A	I	...
Guazuma ulmifolia, Sterculiaceae	4.60	105 ± 1.7	A	I, T, SD	hot water (70 °C, 10 min)
Apeiba tibourbou, Tiliaceae	6.10	90 ± 3.4	A	I, T	...
Ochroma pyramidale, Bombacaceae	6.60	160 ± 5.2	W	I, T, SD	water (100 °C, 30 s)
Apeiba membranacea, Tiliaceae	14.20	95 ± 5.9	A	I, T, SD	hot water (70 °C, 2 min)
Cochlospermum vitifolium, Bixaceae	25.40	...	W	I, T	...
Ceiba pentandra, Bombacaceae	70.00	...	W	T	...
Pseudobombax septenatum, Bombacaceae	88.30	202 ± 4.5	W	I	...

† Treatments of 10 seeds per species (mean ± 1 SE).
‡ A, animal dispersed; W, wind dispersed.
§ Abbreviations are: I, germination responses to irradiance; T, germination response to temperature; SD, soil depth and seedling emergence.

Consideration must be given to the capacity of seeds to emerge and the penetration of cues to germination through different soil depths. In the South African fynbos very small-seeded shrubs lack the necessary resources or hydraulic capability to germinate and emerge from more than superficial depths, while large seeds germinate and emerge from greater depths in the soil profile (Bond et al. 1999). Similar data for tropical rain forest plants are not available. However, irradiance is only able to penetrate 4–5 mm into the soil in physiologically significant quantities (Tester and Morris 1987) and is attenuated by leaf litter (Vázquez-Yanes et al. 1990). Therefore we suggest that irradiance is only an appropriate gap cue for very small-seeded species. For larger seeded species additional cues are needed if germination is to occur across the full range of microsites that permit emergence and growth.

Temperature may provide an effective germination cue for larger seeded pioneers with sufficient seed resources to emerge from below more than a few millimeters of soil. In contrast to irradiance, diel variation in temperature in canopy gaps may be manifest at soil depths of several centimeters (Raich and Gong 1990). Consequently, we hypothesize that irradiance should be an appropriate cue for germination of a pioneer only if it has very small seeds, and larger seeded species should germinate in response to an increased magnitude of temperature fluctuation. The few published measurements of soil temperature in tropical forest gaps and understory suggest that the magnitude of temperature fluctuation increases with increasing gap size for an equivalent soil depth (Vázquez-Yanes and Orozco-Segovia 1982, Raich and Gong 1990). Therefore, species that require large gaps for seedling establish-ment should be likely to show a positive germination response to increasing magnitude of temperature fluctuation.

The test species for this research were drawn from the pioneer tree species of Barro Colorado Island (BCI), Panama. On BCI, pioneers comprise a group of 30–40 species varying in seed size over four orders of magnitude (Dalling et al. 1997). We used representative species of pioneers to address the following questions: (1) Does a shift from light-cued to temperature-cued seed germination occur with increasing seed size among pioneer species? (2) Are these results mirrored in seedling emergence from different soil depths? (3) What microsite conditions exist in different sized gaps and therefore in what sites are species with different cues most likely to germinate?

METHODS

Study site and species

Barro Colorado Island (BCI) lies in an area of seasonally moist tropical forest, in the Republic of Panama. The mean annual rainfall is 2700 mm/yr, with a distinct dry season between January and April (Rand and Rand 1982). The flora of BCI is described by Croat (1978) and by Foster and Brokaw (1982); nomenclature follows Croat (1978), except for *Piper peltatum* L. (previously *Pothomorphe peltata* (L.) Miq.). *Ceiba pentandra* did not produce viable seeds on BCI during our study, so collections of seeds from populations of this species in Africa were used instead.

Eighteen species of pioneer trees and shrubs were used (Table 1). They include the most common pioneer species on BCI, both as mature individuals and in the

seed bank (Putz 1983, Dalling et al. 1997). Species selection was based both on prior knowledge of their regeneration ecology (Garwood 1982, Putz 1983, Brokaw 1987, Dalling et al. 1997, 1998*a*, *b*), and their distributions in relation to canopy height on a 50-ha forest dynamics plot on BCI. The sample includes the maximum range of seed size for pioneer trees and was deliberately biased toward common species and those for which large numbers of seeds were available (see Table 1). Generic names are used except for *Apeiba*, *Cecropia*, and *Piper*, for which binomials are used.

Gap microclimates

Irradiance and temperature regimes were characterized in small (~25 m²), medium (~64 m²), and large gaps (~225 m²) and understory sites within 40-yr-old secondary forest (canopy 12–20 m). In mature forest on BCI, Brokaw (1982) found median gap areas to be 57 m² (mean 86 m²) with a range from 26 to 342 m². Gaps were created by clearing all vegetation down to ground level. In each site a pit was dug taking care not to disturb the adjacent soil. Thermistor temperature sensors attached to data loggers (Datahog, Skye Instruments, Powys, UK) were inserted horizontally at 10 cm depth and the pits refilled. Bead thermistors (Skye Instruments, Powys, UK) were also placed on the soil surface covered with a thin (<1 mm) layer of soil to simulate the natural conditions of radiation exchange. Photosynthetically active radiation (PAR) sensors (SKP 215, Skye Instruments, Powys, UK) were placed on the soil surface in the center of each site. Measurements made at 30-s intervals were averaged over 10-min periods. There were two census periods both during the transition from the dry to the wet season (when most germination of pioneers occurs, Garwood 1982). Between 16 and 22 April 2000 a small and a large gap, and an understory site were monitored, and between 1 and 11 May 2000 a different small, two medium sized and a different large gap and understory site were monitored.

Germination responses to irradiance

Seeds were collected from intact fruits on or below trees on BCI, stored in a dark air-conditioned laboratory and shipped within 12 wk, in a polystyrene container, to Aberdeen, UK. All counting of seeds was done under light with a red/far red ratio of <0.01.

Six replicates of 25 seeds of each of 17 pioneer species (Table 1) were placed on the surface of 1% agar in 50 mm diameter petri dishes. Each dish was placed in an open-topped aluminum container (19 × 12 × 3 cm) and arranged at random in a plant growth chamber with a constant 30°C temperature and 8-h day length.

Three replicates per species were assigned at random to a zero irradiance treatment created by placing an inverted aluminum container (as above) on top and surrounding both containers with aluminum foil. The second three replicates were covered by a deep-dyed lexan polycarbonate filter (Chroma green, Supergel Filters, Rosco, UK), which transmitted irradiance with a PAR of 22.3 μmol·m⁻²·s⁻¹ at a red/far red ratio of 1.2. Irradiance in both treatments was measured using PAR (as above) and red/far red sensors (SKR 110, Skye Instruments, Powys, UK). On days 6, 12, 20, 30, and 45 after the start of the experiment, germinated seeds (defined as emergence of the radicle) were removed.

Germination responses to temperature

Seed germination responses to temperature were determined on a two-way thermogradient plate (Model GRD1, Grant Instruments, Cambridge, UK). Seeds were collected and processed as described above. *Ceiba* seeds were collected in Ghana and immediately transported to Aberdeen where they were stored as described above. One batch of 20 (*Ochroma* and *Piper dilatatum*) or 25 (all other species) seeds of each of 15 species (Table 1) was placed in each of 49 germination cells (13 for *Ceiba*) on the plate. This apparatus created independent gradients of day (5 h at 27.5–44.4°C) and night (19 h at 15.3–33.5°C) temperatures, which allowed us to impose a broad range of treatments for the magnitude of diel (day–night) temperature fluctuation across the range −6.0°C to +29.1°C. These conditions encompass the minimum and maximum temperatures that were measured across a variety of gap microhabitats on BCI. Irradiance of 200 μmol·m⁻²·s⁻¹ PAR with a red/far red ratio of 1.8 (sensors as above) was provided for 5 h each day, and was excluded at other times using a 250-mm layer of expanded polystyrene.

Seeds were placed on a double layer of moistened absorbent paper and irrigated by capillary action using a network of lamp wicks connected to a reservoir of deionized water. This arrangement maintained nonlimiting water availability to seeds on the thermogradient plate in preliminary trials. The experiments were scored for germination every 5 d for 60 d, and germinated seeds were removed when first encountered. The 15 species were run in three separate experiments to optimize the space available on the thermogradient plate and minimize the storage time of the seeds.

Soil depth and seedling emergence

Soil, sieved to <1 mm, from an understory site on BCI was used. Subsamples were incubated along with experimental treatments to check for seed contaminants. The remaining soil was compressed into 7 cm deep, 8 cm diameter plastic pots to a bulk density approximately that of forest soil.

Three replicates of 20 seeds of each of eight pioneer species (Table 1) were planted into the soil at seven depths (0, 2.5, 5, 10, 20, 30, and 50 mm). Seeds of all species were collected within 3 mo of the start of the experiment, and in the interim period were stored in a dark air-conditioned laboratory on BCI. Seed pretreatments (Table 1) were used where necessary to break dormancy (Acuna and Garwood 1987). All pretreat-

ments and treatment assignments were carried out under light with a red/far red ratio of 0.05.

For each depth treatment, 0.25 mm mesh-size nylon cloth was laid directly beneath the seeds to prevent them from sinking to a greater soil depth. Soil was then carefully added on top of the mesh to the required depth. Finally, pots were covered with clear polyethylene to conserve moisture, and placed at random within a plant growth chamber on BCI. Both temperature and irradiance were regulated on a 24-h cycle with 12 h at 30°C and 75 μmol·m^{-2}·s^{-1} PAR and a red/far red ratio of 1.65, and 12 h at 24°C in the dark.

Seedling emergence was checked weekly during the day, and pots were watered with a mist sprayer as required. In order not to disturb seedlings that had not yet emerged, emerging seedlings were cut off at the soil surface but not removed. The experiment was terminated for individual species 2 wk after germination ceased. Pots were then checked for seedlings that germinated, but did not emerge.

Data analysis

The null hypothesis of no difference in the probability of germination between irradiance treatments was examined using G tests (Sokal and Rohlf 1995). The relationships between germination and the diel magnitude of temperature fluctuation was examined graphically to determine germination thresholds (after excluding treatments where night temperature exceeded day temperature). Where a clear threshold existed the data were partitioned; relationships between germination and the diel magnitude of temperature fluctuation were obtained, for data points above and below the threshold value, using logistic regression implemented in SPSS version 9.0.0 (SPSS, Chicago, Illinois, USA).

To analyze effects of soil depth on seedling emergence we used generalized linear modeling techniques (McCullagh and Nelder 1989) implemented in the GLIM statistical package (Crawley 1993). To avoid problems of inconstant variance and negative seedling counts that might be predicted with a normal errors linear regression model, we carried out a regression on count data using Poisson errors and a log link function. Hypothesis testing was carried out using the χ^2 test on differences in deviance. The appropriateness of the assumption of Poisson errors was checked by comparing the residual deviance with the residual degrees of freedom after fitting soil depth. To investigate the relationship between emergence potential and seed mass we performed a normal errors regression of the slope values of individual species against ln-transformed seed mass.

Results

Microclimatic variation in relation to canopy openness and burial depth

Microclimatic conditions were sensitive to canopy openness. In both census periods irradiance at ground
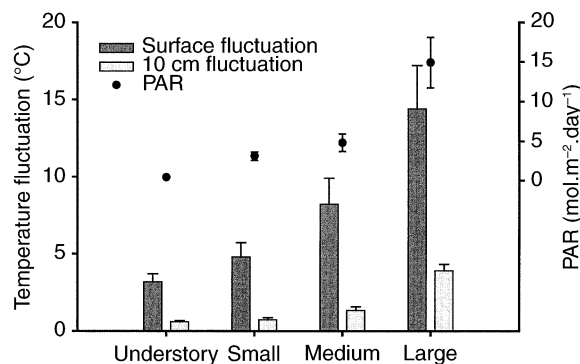

Fig. 1. Daily photosynthetically active radiation (PAR, mol/m^2; mean $\pm$ 1 SE) and daily temperature fluctuation (°C; $\pm$ 1 SE) between 1 and 11 May 2000 for gaps of 25 m^2, 64 m^2, and 200 m^2.

level and mean daily magnitude of temperature fluctuation on the soil surface and at 10 cm increased with gap size (Fig. 1). Minimum night temperature never varied more than ±1.5°C from 25°C, regardless of gap size or soil depth. In contrast the maximum temperature varied markedly dependent on gap size, weather conditions, and soil depth (Fig. 1). For example, on four days maximum temperatures between 45° and 52°C were recorded on the soil surface in the large gap sites, giving temperature fluctuations of >20°C.

Maximum daytime temperature decreased with increasing soil depth, producing smaller magnitudes of diel temperature fluctuation deeper in the profile. However, in the large gaps a magnitude of 5.2°C fluctuation was still recorded at 10 cm depth. In smaller gaps there was very little diel change in temperature at 10 cm depth (Fig. 1).

Effect of irradiance treatments on germination

The study species separated into small-seeded photoblastic species and larger seeded species that are not photoblastic. For eight species that germinated in the light (*Alseis*, *Cecropia insignis*, *C. obtusifolia*, *C. peltata*, *Miconia*, *Piper dilatatum*, *P. peltatum*, and *Solanum*) no germination was recorded in complete darkness (Fig. 2). Six species showed no significant difference in germination between treatments (*Apeiba membranacea*, *Guazuma*, *Luehea*, *Ochroma*, *Pseudobombax*, and *Trichospermum*, Fig. 2b) while the remaining three species showed little or no germination in either treatment. The seed mass of the genera showing a significant positive germination response to irradiance was 0.7 ± 0.4 mg (mean $\pm$ 1 SE), which is more than an order of magnitude less than the mean seed mass of genera containing species that did not respond (22.7 ± 14.8 mg).

Effects of temperature treatments on germination

The species showed a wide variety of germination responses to temperature fluctuation treatments (Fig.

Germination (%)

a

*** (Piper peltatum) *** (Miconia argentea) *** (Piper dilatatum) ** (Alseis blackiana) *** (Cecropia peltata) *** (Cecropia obtusifolia) *** (Cecropia insignis)

Piper peltatum *Miconia argentea* *Piper dilatatum* *Alseis blackiana* *Cecropia peltata* *Cecropia obtusifolia* *Cecropia insignis*

b

NS (Luehea seemannii) *** (Solanum hayesii) NS (Trichospermum mexicanum) NS (Guazuma ulmifolia) NS (Ochroma pyramidale) NS (Apeiba membranacea) NS (Pseudobombax septenatum)

Luehea seemannii *Solanum hayesii* *Trichospermum mexicanum* *Guazuma ulmifolia* *Ochroma pyramidale* *Apeiba membranacea* *Pseudobombax septenatum*
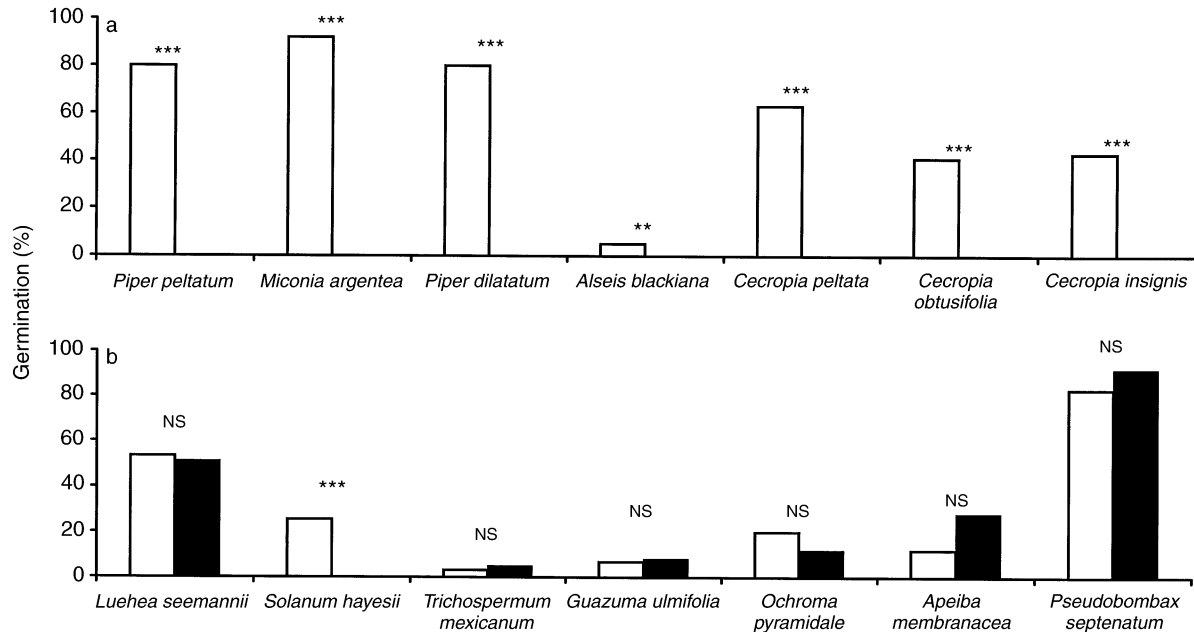
Fig. 2. Final germination percentage in the light (open bars) and dark (closed bars) treatments for (a) seven species with seed mass < 1 mg and (b) eight species with seed mass > 1 mg. Degree of significance (*G* test) is indicated as follows: ** $P < 0.01$; *** $P < 0.001$.

3), although four general classes of response can be identified. Final germination percentages were >20% in at least one treatment for all species (except *A. tibourbou*). The germination responses to day and night temperature are presented in the form of contour diagrams in Appendix A.

The species in the first class displayed consistent high germination until a high threshold temperature fluctuation was exceeded and a steep decline in germination occurred. The seed mass of the three genera in this class was 0.86 ± 0.44 mg (mean $\pm$ 1 SE). For *Luehea*, *Cecropia obtusifolia*, *C. peltata*, and *Miconia* (Fig. 3a–d) the threshold temperature fluctuation was in the range 20–27°C, and above the species-specific threshold, germination declined abruptly to very low values. Below the threshold, germination was high and not significantly related to the magnitude of temperature fluctuation ($P = 0.18$–0.45), although *Miconia* showed an additional negative effect of high daytime temperature (>41.7°C) irrespective of the fluctuation treatment (open symbols on Fig. 3d).

The second group, comprising three species in two genera (*C. insignis*, *Piper peltatum*, and *P. dilatatum*, Fig. 3e–g), had a lower tolerance to large temperature fluctuations and a less distinct threshold effect, with germination declining gradually beyond the threshold. The mean seed mass of the two genera in this class was 0.38 ± 0.22 mg. The *Piper* species had negative linear germination responses to temperature fluctuations of >10°C (*P. peltatum*, Fig. 3f) or 3°C (*P. dilatatum*, Fig. 3g), respectively, and zero or very low germination in response to high night temperatures

(>31.3°C, open symbols on Fig. 3f, g) at any value of temperature fluctuation. *C. insignis* had a negative linear germination response to temperature fluctuation above a value of 6.7°C and an additional negative effect of low night temperatures (<21.7°C, open symbols on Fig. 3e) at intermediate fluctuations.

The third class of germination behavior was a positive response to increasing magnitudes of temperature fluctuation. The mean seed mass of the four species in four genera in this class was 20.90 ± 14.19 mg. *Solanum*, *Guazuma*, and *Ochroma* (Fig. 3h–j) showed a positive linear germination response to temperature fluctuations in the range 0–16.7°C, while *Ceiba* showed a positive response to temperature fluctuation when night temperature was >21.7°C (closed symbols on Fig. 3k). For the first three of these species, germination either declined (*Solanum*) or varied idiosyncratically (*Guazuma*, *Ochroma*) above a temperature fluctuation of 16.7°C (open symbols in Fig. 3h–j).

The remaining species examined (*Trichospermum*, *A. membranacea*, and *Cochlospermum*) did not respond significantly to temperature fluctuations. The mean seed mass of the three species in this fourth group was 12.75 ± 5.45 mg.

Therefore the species that had an abrupt temperature fluctuation threshold for maintenance of high germination (Fig. 3a–d) and those that responded negatively to an increasing magnitude of temperature fluctuation (Fig. 3e–g) all had a seed mass <2 mg. In contrast the species that responded positively to temperature fluctuation across some or all of the treatments used (Fig. 3h–k) and those that showed no response to tempera-
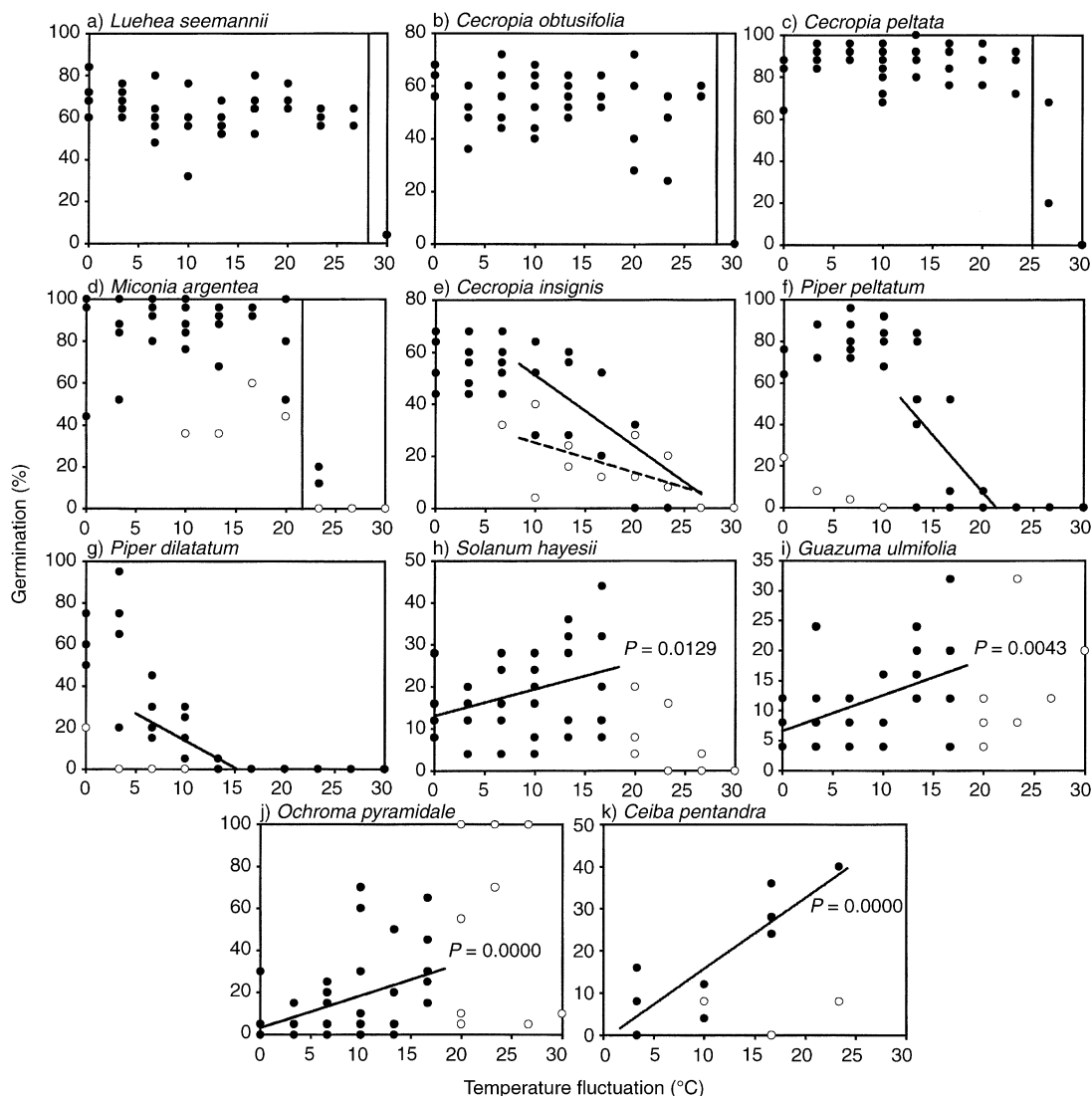
FIG. 3.   Effect of diel temperature fluctuation on final germination percentage for day temperatures (dt) in the range 27.5–44.4°C and night temperatures (nt) in the range 15.3–33.5°C (except where indicated by open symbols as described) in (a) *Luehea*, (b) *Cecropia obtusifolia*, (c) *Cecropia peltata*, (d) *Miconia* (open circles, dt > 41.7°C), (e) *Cecropia insignis* (open circles, nt < 21.7°C), (f) *Piper peltatum* (open circles, nt > 31.3°C), (g) *Piper dilatatum* (open circles, nt > 31.3°C), (h) *Solanum*, (i) *Guazuma*, (j) *Ochroma* (open circles, diel temperature fluctuations >16.7°C), and (k) *Ceiba* (open circles, nt < 21.7°C). Vertical lines in panels (a–d) represent the threshold values (see *Methods: Data analysis* for definition).

ture fluctuation all had a mean seed mass >2 mg (Table 1).

Effects of burial depth on seedling emergence

Seedling emergence was negatively related to burial depth for all species except *A. membranacea* (Fig. 4). Among species, there were large differences in the amount of deviance explained by depth (range r^2 = 0.20 for *Ochroma* to r^2 = 0.97 for *Miconia*). The depth at which 50% of maximum seedling emergence occurred ranged between 1 and 6.5 mm for the small-seeded species *Miconia* and *Cecropia*, and 40 and 82 mm for the larger seeded *Trichospermum* and *Ochroma*.

Seed mass was significantly related to emergence potential, determined as the slope of regressions between emergence success and soil depth (n = 8 species, r^2 = 0.78, F = 21.4, P < 0.01), so that the capacity to emerge from depth increased with increasing seed mass (Appendix B). Excluding the outlier value for *Miconia*, this relationship was still significant (n = 7, r^2 = 0.76, F = 16.0, P < 0.05).

DISCUSSION

Variation in irradiance and temperature conditions in the forest

Temperature and irradiance are both good indicators of canopy openness, but differ in their ability
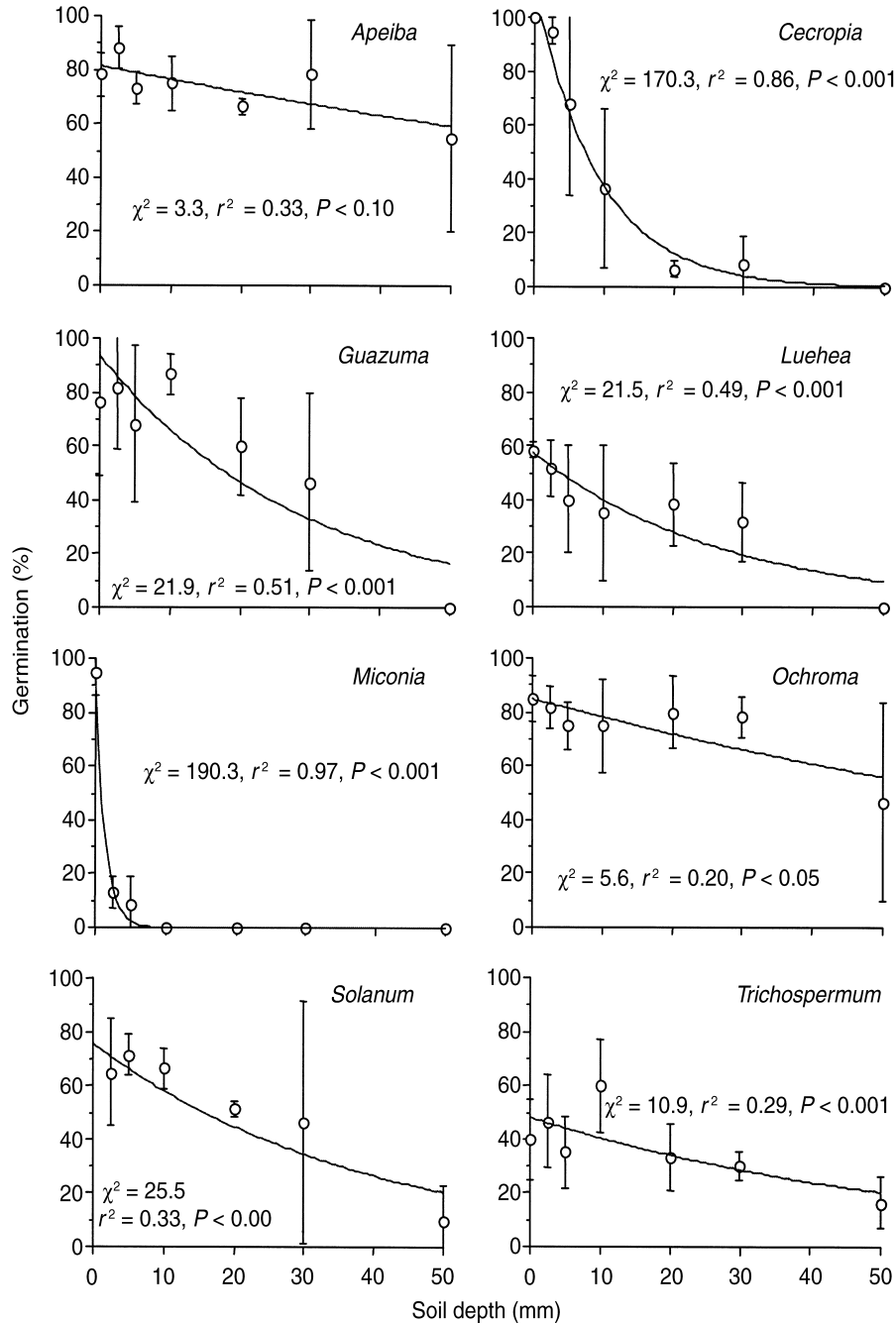
FIG. 4. Mean percentage seedling emergence (± 1 SD) as a function of seed burial depth. Curve-fitting is by regression on emergence count data using Poisson errors and a log link function.

to indicate large and small gaps. Irradiance in tropical forests has been well characterized (Chazdon and Fetcher 1984).There are, however, fewer measurements of soil temperatures in understory and gaps, and these concur broadly with our findings (e.g., Vázquez-Yanes and Orozco-Segovia 1982). Irradiance can act as an index of canopy openness across all spatial scales of disturbance, from a branch fall to a multiple tree-fall gap (Chazdon and Fetcher

1984). In contrast, in the smallest gaps we studied, temperature, especially beneath the soil surface, did not differ greatly from that in the understory. In these gaps, therefore, irradiance would be a more effective cue for the germination of gap-demanding species. Among the BCI pioneer flora, it is noticeable that the photoblastic small-gap specialists (e.g., *Miconia*, *Piper*, and *Alseis*) have the smallest seeds (mostly <0.5 mg dry mass), while the large-gap specialists

(e.g., *Trema* and *Ochroma*) tend to have larger seeds (Brokaw 1987, Dalling et al. 2001).

Effects of irradiance on seed germination

Eight small-seeded pioneer tree species from five genera (mean mass 0.7 mg) were photoblastic. In contrast, the only photoblastic species with a seed mass >1 mg was *Solanum*. While photoblastic germination has been reported in species from some of the genera we studied (e.g., *Cecropia*, *Piper*, and *Solanum* species [Baskin and Baskin 1998]), it has not been reported previously for *C. insignis*, *Miconia*, *P. dilatatum*, *P. peltata*, or *S. hayesii*. The mechanism of the photoblastic response has been studied extensively; phytochrome B is sensitive to the spectral distribution of incident radiation and stimulates germination when the proportion of red wavelengths is high (Smith 2000).

It has been argued that photoblastic germination evolved as a canopy gap detection mechanism in tropical pioneer trees (Frankland 1976, Vázquez-Yanes and Orozco-Segovia 1990). Gap creation leads to a dramatic increase in the red/far red ratio of irradiance at the forest floor, and these shifts are sufficient to initiate germination in photoblastic species (Vázquez-Yanes and Orozco-Segovia 1993). Alternatively, photoblastic germination may act to initiate germination when a seed is close to the soil surface in a litter-free microsite. Litter and soil decrease the quantity and the red/far red ratio of irradiance (Tester and Morris 1987, Vázquez-Yanes et al. 1990) and are barriers to the establishment of small-seeded species (Molofsky and Augspurger 1992, Vázquez-Yanes and Orozco-Segovia 1992, Metcalfe and Grubb 1997) with limited seed reserves for emergence (Bond et al. 1999; Fig. 4 *Cecropia* and *Miconia*). These factors may account for the high density of pioneers in the pits and mounds formed by treefalls on Barro Colorado Island, where high irradiance is combined with an absence of litter (Putz 1983).

Effects of temperature and magnitude of temperature fluctuation on germination

Germination response to increasing magnitudes of temperature fluctuations was negative in the smaller seeded species, but positive in four species with a seed mass >2 mg. Previous studies have demonstrated the positive response in *Ochroma pyramidale* and in the Solanaceae (Baskin and Baskin 1998). The smaller seeded species responded negatively, although responses ranged from broad tolerance to temperature fluctuation in *Luehea* and *Cecropia obtusifolia* to extreme sensitivity even to small temperature fluctuation in *Piper*. Thus, temperature fluctuation acts as a signal to the presence of larger canopy gaps in a wide range of species, but the response to the signal is associated with differences in seed size.

Few previous studies exist on temperature effects on germination although studies of temperate plants support our findings. Temperature has been shown to affect germination of relatively few tropical pioneer tree species (Baskin and Baskin 1998), possibly because most researchers have chosen to work with the more abundant tiny-seeded species that did not respond positively to the magnitude of temperature fluctuation in our experiments. However, among temperate-zone herbs a positive effect of increased temperature fluctuations is widespread among plants that require gaps in vegetation for seedling establishment (Thompson and Grime 1983). The mechanism for an effect of temperature fluctuation on germination of neotropical pioneers and in many temperate species is related to an increase in seed coat permeability induced by alternating temperatures (Baskin and Baskin 1998).

The negative germination response to large temperature fluctuations in small-seeded species and at extreme values for some larger seeded species may represent a waiting strategy to avoid large-gap environments where water shortage would constrain seedling establishment. Small-seeded species are especially susceptible to short periods of drought because of their superficial initial rooting depth (Engelbrecht et al. 2001). Variation among small-seeded species in the critical temperature fluctuation threshold that inhibited germination may reflect differential selection for tolerance of conditions in different irradiance levels linked to early establishment requirements of these species.

Effects of burial depth on seedling emergence

Seedling emergence declined with depth of burial for all species. This may be caused by a lack of seed reserves to elongate the epicotyl sufficiently to reach the soil surface, by buckling of the epicotyl or hypocotyl as a result of insufficient stiffness to emerge, or by the failure of a germination trigger to penetrate the soil. For fynbos shrubs, Bond et al. (1999) found that maximum emergence depth was similarly scaled allometrically with seed mass.

Under natural conditions, emergence from the seed bank might be determined by the detection of dormancy breaking stimuli, rather than limitations imposed by seed reserves. However, it seems implausible that seeds "capable" of emerging from deep in the soil would not have evolved a gap detection mechanism to take advantage of this ability. Thus it is significant that the two species with the lowest emergence potential were photoblastic (*Cecropia* and *Miconia*), while the only species from the large-seeded group that possessed photoblastic germination (*Solanum*), also responded positively to temperature fluctuation.

Limitations and conclusions

Although we included most of the common pioneer species at our study site, not all taxa may show a relationship between germination cues and seed mass (e.g., *Carica papaya* [Paz and Vázquez-Yanes 1998]). Nonetheless, the generality of our model is supported

by research on temperate zone plants demonstrating that dependence on light for germination increases as seed size decreases in interspecific comparisons (Milberg et al. 2000).

One sense in which our sample of species may be biased is that most of the relatively large-seeded species possess thick, hard seed coats that might be opaque. Thus the absence of photoblastism in these species might be confounded by the need for large seeds to be defended against seed predators and pathogens. In our sample of species, mean seed coat thickness (excluding the wax layer) was significantly greater in the larger seeded nonphotoblastic species (116 ± 19 μm) than in the small-seeded photoblastic species (50 ± 12 μm), and ln(seed coat thickness) increases linearly with ln(seed mass) ($r^2 = 0.77$; $P < 0.001$). This implies that larger seeded pioneer species might be better defended against predation and disease than smaller seeded species and provides a mechanistic explanation for the greater persistence of larger seeded species in soil (Dalling et al. 1997). According to this evolutionary scenario, the mechanism of germination response to gap signals has evolved as a consequence of the seed size/seed number trade-off coupled with selection for defense of large-seeded species (Baskin et al. 2000).

Emergence potential may represent an important and previously unrecognized element of the trade-off between seed size and the gap colonizing potential of pioneer species. Larger seeded pioneers have the advantage in probability of establishment and in initial competition. Small-seeded pioneers have a dispersal advantage, since decreased size affords the production of increased seed number, and a consequently higher probability that one or more seeds will arrive at a suitable gap site (Metcalfe and Grubb 1996, Rees and Westoby 1996). The pool of dormant seeds for small-seeded species, however, may be relatively small for two reasons. First, only a small proportion of the germinable seed population in the soil may be physically capable of germination because of their limited emergence potential. Second, seed losses may be greater at the soil surface than deeper in the soil (Dalling et al. 1997, 1998*b*). Thus seed banks of smaller seeded species may be less persistent than those of larger seeded species.

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APPENDIX A

Contour maps of final germination percentages of 15 species across temperature treatments are available in ESA's Electronic Data Archive: *Ecological Archives* E083-054-A1.

APPENDIX B

A figure showing the effect of seed mass on emergence potential is available in ESA's Electronic Data Archive: *Ecological Archives* E083-054-A2.