Functional significance of photoblastic germination in neotropical pioneer trees: a seed's eye view

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Summary

1. We investigated the relationship between seed mass and the suitability of microsites for germination for five small-seeded (< 2·4 mg fresh mass) photoblastic neotropical pioneer trees. We determined the germination response of these species to the ratio of red to far-red irradiance (r:fr) and compared it to r:fr measured under varying conditions of canopy openness, litter and soil thickness.

2. At a constant temperature the germination percentage of each of the species increased sharply with increasing r:fr above a species-specific threshold r:fr. The smallest-seeded species, *Miconia argentea*, had the lowest r:fr threshold for germination (0·12) while the larger-seeded *Cecropia* species and *Solanum hayesii* possessed higher values (0·21–0·27). The largest seeded species, *Solanum hayesii*, also showed a positive germination response to a 10 °C temperature fluctuation, which was independent of the response to r:fr.

3. The mean r:fr at ground level declined with decreasing gap size but not sufficiently to suppress the germination of these five species. However, a covering of one litter leaf in direct sunlight reduced the r:fr to between 0·18 and 0·83 depending on the species and leaf wetness. The top-soil at our study site was aggregated and irradiance was transmitted or reflected between soil aggregates with little change in r:fr. Light did not penetrate the aggregates.

4. We suggest that photoblastic germination in neotropical pioneers has evolved to inhibit germination in response to conditions most likely to alter within the life of an individual seed (i.e. superficial burial by leaf litter or incorporation into the surface soil), rather than to fine scale variation in canopy openness. Among photoblastic species, the pattern of response to r:fr suggests that smaller-seeded species would germinate in a broader range of microsites than larger-seeded species. This lower degree of discrimination may be associated with their higher risk of mortality and therefore more limited persistence in the soil seed bank.

Key-words: Gap size, litter, r:fr, seed size, tropical forest

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Introduction

Small-seeded species have narrowly defined microsite requirements for successful establishment because of their limited internal resources. This precludes emergence from beneath litter or more than a few millimetres of soil, and survival during droughts that dry the surface soil layer (Metcalfe & Grubb 1996; Engelbrecht *et al.* 2001; Pearson *et al.* 2002). The detection of suitable sites for germination is therefore important for the regeneration of these species. The microsite in which a seed germinates also determines the environment for onward growth of the seedling and therefore plays an important role in defining the habitat distribution of plants (Grubb 1977).

Photoblastic species utilise light to indicate conditions suitable for germination. Gradients in the intensity and spectral quality of light occur at natural germination sites caused by heterogeneity in overhead foliage, litter on the soil surface and burial in soil. Canopy foliage reduces the red to far red ratio (r:fr) of light reaching the ground surface by preferential absorbance of wavelengths of 660 nm (red light) relative to longer wavelengths (far red light) (Stoutjesdijk 1972;

Lee 1987; Smith *et al*. 1990). For the same reason, dead leaves on the forest floor decrease the r:fr of light reaching seeds buried beneath them (Vázquez-Yanes *et al*. 1990; Vázquez-Yanes & Orozco-Segovia 1992). Likewise, total irradiance decreases with soil depth over a scale of millimetres (Wooley & Stoller 1978; Bliss & Smith 1985; Tester & Morris 1987). However, these studies may have limited application to the interpretation of responses of plants in the field because they have used media, such as sand or finely sieved soil, which do not simulate accurately the aggregated nature of most forest soils. With the exception of very sandy soils, soil particles tend to form aggregates under the action of wetting and drying cycles and soil fauna (Marshall *et al*. 1996), and the surface soil structure of most soils under closed canopy forest tends to consist of aggregates typically in the millimetres to a few centimetres size range.

Neotropical pioneer species (*sensu* Swaine & Whitmore 1988) are differentiated in their germination responses to irradiance and temperature in a manner that is predictable from their seed size. Seven small-seeded species with a dry seed mass of less than 1 mg respond to an irradiance cue for germination, whilst only larger-seeded pioneers respond positively to an increasing magnitude of diel temperature fluctuation (Pearson *et al*. 2002). In this paper we test the prediction that the small-seeded group of species are differentiated in the minimum quantity or r:fr of irradiance required to stimulate germination, and that these differences can be interpreted in relation to seed size.

Germination of photoblastic species is stimulated by light with a high r:fr ratio and suppressed by light with a low r:fr ratio (e.g. Vázquez-Yanes & Smith 1982; Orozco-Segovia & Vázquez-Yanes 1989; Vázquez-Yanes & Orozco-Segovia 1990; Vázquez-Yanes *et al*. 1990; Orozco-Segovia *et al*. 1993). However, these studies do not always give a clear indication of the threshold r:fr required for maximum germination. For example, Vázquez-Yanes & Smith (1982) found 80% germination of *Cecropia obtusifolia* seeds exposed to a r:fr ratio of 0·2, but Vázquez-Yanes *et al*. (1990) examined the same species and found that maximum germination was obtained only at a r:fr equivalent to full daylight (1·2). Daws *et al*. (2002) found a range of 0·1–0·3 in the r:fr thresholds to germination among four congeneric *Piper* species.

We previously found only one larger-seeded neotropical pioneer species (*Solanum hayesii*, fresh mass 2·4 mg) that was photoblastic (Pearson *et al*. 2002). While this species also responded positively to an increasing magnitude of diel temperature fluctuation, the pattern of germination response to r:fr and its interaction with temperature fluctuation have not been described and are poorly documented in this genus (Baskin & Baskin 1998).

Seed size affects the resources available to an individual for persistence in a seed bank and for emergence through litter and soil. In this paper we examine how the germination response to r:fr relates to seed size for five species from three families spanning two orders of magnitude in seed mass. We relate our findings to field conditions using measurements of light quality in relation to gap size, litter type and soil depth. We tested the following predictions: (1) germination response to r:fr varies among species; (2) germination response to r:fr correlates with seed mass and hence three congeneric species with similar seed mass have similar germination responses to r:fr; (3) the requirements for light and fluctuating temperature as a cue for germination operate independently.

Methods

STUDY SITE AND SPECIES

We used five neotropical pioneer tree species, from three genera and three families, that occur on Barro Colorado Island (BCI) in the Republic of Panamá (Table 1). BCI is covered by semi-deciduous tropical rain forest and has a mean annual rainfall of 2600 mm (Leigh *et al*. 1982). The flora of BCI is described by Croat (1978) and Foster & Brokaw (1982).

Species selection was based on the availability and information on abundance of adults and of seeds within the soil seed bank on BCI. Seeds were collected from mature intact fruits on or below trees on BCI (at least five spatially separate adults per species) and stored in an air-conditioned laboratory in the dark for less than 12 weeks prior to use in experiments on BCI or until shipping by air (in a polystyrene container) to Aberdeen, UK. All seeds were counted under a green light with a r:fr of < 0·01.

Table 1. Characteristics of the study species, including their seed masses and germination responses to light and fluctuating temperatures (from Pearson *et al*. 2002)

Species	Family	Seed mass (mg)[1]	Light requirement	Temp. requirement
Miconia argentea (Sw.) DC.	Melastomataceae	0·08	Yes	No
Cecropia insignis Liebm.	Cecropiaceae	0·68	Yes	No
Cecropia peltata L.	Cecropiaceae	0·58	Yes	No
Cecropia obtusifolia Bertol.	Cecropiaceae	0·59	Yes	No
Solanum hayesii Fern.	Solanaceae	2·40	Yes	Yes

[1]Variability in seed mass was less than 10% for all species.

R:FR IN RELATION TO GAP SIZE, LITTER TYPE AND SOIL DEPTH

The r:fr of light reaching the soil surface in two artificial gaps was recorded every 10 minutes for 9 days during the 2000 wet season. The gaps measured 5×5 m and 8×8 m on the ground. The r:fr and photosynthetically active radiation (PAR) were measured in the centre of each gap using a two channel sensor (SKR 110), and a PAR sensor (SKP 215), respectively, attached to a data logging device (DataHog); all instrumentation was from Skye Instruments, Powys, UK.

In the laboratory the transmittance of six replicates of the leaves of six different species was measured. The r:fr of the light from a low voltage incandescent bulb (r:fr 0·59) penetrating to the underside of the leaf was measured when the leaf was wet (fresh from the field) and dry (after 48 h in a 60 °C oven). Leaf r:fr values (measured as above) were converted to the r:fr ratios that would have been transmitted under bright sunlight (measured outside as a r:fr of 1·36) by multiplying the measured r:fr by (1·36/0·59). This procedure is derived from the Lambert-Beer Law and was confirmed by measuring the r:fr of irradiance transmitted by *Miconia argentea* leaves in bright sunlight and in the laboratory.

To test the penetration of light through the soil, moist clay loam topsoil from the rain forest on the Buena Vista peninsula (adjacent to BCI) was spread on a glass plate in a closely packed layer about 7 mm in thickness so as to reproduce the soil surface condition observed in the field. Seven millimetres was the thinnest layer that could be recreated without crushing or sieving the natural (0·5–7 mm) soil aggregates that composed the surface of this soil. Since soil disturbance can result in size sorting, in which fine material settles and can accumulate at the bottom of a pile of soil, field-moist soil was sampled and placed directly on to the plate with a minimum of disturbance. The aim was to reproduce as closely as possible the structure and packing of the soil surface. The soil was uniformly illuminated from above by a low voltage incandescent bulb and the underside of the glass was photographed with a Nikon CoolPix900 high resolution (1·4 Mpixel) digital camera (Nikon Inc., NY, USA). The experiment was performed at night in a dark laboratory to avoid extraneous sources of light. The image was thesholded and analysed to determine the percentage of the total area in which light had penetrated.

EFFECTS OF R:FR ON GERMINATION OF MICONIA ARGENTEA AND THREE CECROPIA SPECIES

The r:fr necessary to initiate germination was examined for *Miconia* and the three *Cecropia* species under laboratory conditions in Aberdeen, UK. Twenty-seven replicates of 25 seeds per species were placed on the surface of 1% agar in 50 mm diameter Petri dishes placed in open-topped aluminium containers ($19 \times 12 \times 3$ cm). Three of the replicates per species were assigned at random to a zero irradiance treatment which was created by placing an inverted aluminium container (as above) on top of the first and surrounding both containers with aluminium foil. A separate container was used for each of the replicates, although different species shared the same containers.

The remaining eight light treatments (r:fr from 0·05 to 1·27) were created by placing a layer of deep-dyed lexan polycarbonate filter over the top of the aluminium containers (r:fr properties of light transmitted through the filters are listed in Table 2). Two of the filter treatments were used to test whether germination would be stimulated regardless of irradiance if the r:fr was sufficiently high: filter 72 had a high transmission of irradiance (44%) and produced a relatively high r:fr (0·76), while filter 27 had a similar r:fr (0·70) but a low

Table 2. Red: far-red ratio (r:fr) of light transmitted by different filters in the germination experiments. For the same filter, r:fr differs between environments because of differences in the r:fr of the light source

Manufacturer*	Serial No.	Transmission (%)	r:fr Aberdeen, UK	BCI, Panamá Growing house	BCI, Panamá Growth chamber
Lee	124	29·7	–	0·03	0·02
	327	4·2	0·05	–	–
	115	35·2	0·14	–	–
	322	38·3	0·18	0·12	0·10
	122	51·5	0·39	–	–
	89	29·8	0·62	0·48	0·40
Rosco	72	44·0	0·76	–	–
	389	40·0	1·27	–	–
	27	4·0	0·70	–	–
	86	56	–	0·25	0·18
No Filter	–	100	–	1·17	0·85
Darkness	–	0	–	–	–

*Lee Filters, Andover, U.K., Roscolab Ltd, London, UK.

transmission (4·0%). All treatments were placed at random in plant growth chambers (Fi-totron 600H, Fisons Environmental Equipment, UK) at a constant temperature of 30 °C, and mean PAR fluence rate of 56 µmol m^{-2} s^{-1} with a 12-h photoperiod.

The red: far red of light in all treatments was measured using two channel sensors (as above). On days 6, 12, 20, 30 and 45 after the start of the experiment, germinated seeds (defined as emergence of the radicle) were counted and removed.

EFFECTS OF R:FR AND TEMPERATURE FLUCTUATION ON GERMINATION OF *SOLANUM HAYESII*

Four replicates of 50 *Solanum* seeds were randomly allocated to each of five r:fr treatments and a zero irradiance treatment in a growing house (where they were exposed to diel fluctuation in temperature) or a growth chamber (maintained at a constant 26 °C) on BCI. The filters created different r:fr ratios in the growing house and the growth chamber but in both cases r:fr across the range 0·03–0·85 were obtained (Table 2; monitored by sensor SKR 110). In the growing house, day length was approximately 12 h, PAR (sensor SKP 215) did not exceed 550 µmol m^{-2} s^{-1} and the temperature within Petri-dishes (measured with bead thermistors) did not exceed 36 °C with maximum temperatures lasting less than 1 h. Night temperature did not fall below 23 °C. Mean amplitude of diel temperature fluctuation was > 10 °C in all treatments. Mean PAR, temperature and relative humidity in the growth chamber was 60 µmol m^{-2} s^{-1}, 26 °C and 85% with a 12-h photoperiod.

Seeds were placed on the surface of 1% agar in 100 mm diameter Petri dishes. The lower portion of the Petri dishes were surrounded by two layers of aluminium foil, and the lid was either covered in a further two layers of foil (zero irradiance treatment) or by one layer of deep-dyed lexan polycarbonate filter (Table 2) and sealed with multiple layers of duct tape. Every third day, from day 5 to day 53, germinated seeds (defined as emergence of the radical) were counted and removed.

STATISTICAL ANALYSES

The light transmission of litter was analysed using a general linear model with the species term, the moisture content term and the interaction between species and moisture content as independent variables. Germination is a binary response variable, so the effects of r:fr (and temperature treatment for *Solanum*) were determined using logistic regression (SPSS version 10·0, SPSS Inc., Chicago, USA). The three *Cecropia* species were combined in one analysis, and the species term and interaction between species and r:fr treatment were introduced as additional independent variables. The relationships between germination

percentage (*y*) and r:fr (*x*) were described using a sigmoidal function of the form:

$$y = a/\{1 + \exp - [(x - x_o) b]\} \qquad \text{eqn 1}$$

where *a* is a coefficient describing the maximum (asymptotic) germination percentage, x_o is a coefficient estimating the r:fr at 50% of maximum germination, and *b* is a coefficient of the slope of the germination response calculated from estimates of r:fr at 75% and 25% of maximum germination. There is no prior justification for fitting sigmoidal functions to these data, although they provided good fits ($r^2 > 0.88$) for all seed lots that responded to r:fr. We use the x_o coefficient as a comparative index of the r:fr threshold for germination across species.

The significance of the association between seed mass and threshold r:fr for germination (x_o) was determined using the Pearson correlation coefficient for a combined data-set including the five species in this study and the four *Piper* species from the study of Daws *et al.* (2002) for which the r:fr thresholds for germination were calculated in an identical manner. The comparison necessarily assumes that the nine species could be compared as independent data points. The assumption is unlikely to be strictly valid because the nine species were drawn from only four genera and four families. Therefore, to control for confounding effects of phylogeny similar correlations were conducted on reduced data-sets provided by (a) the four genera represented within this data-set using genus-mean values of seed mass and threshold r:fr for germination, (b) the four species of *Piper*, and (c) the three species of *Cecropia*.

Results

EFFECTS OF GAP SIZE, LITTER TYPE AND SOIL DEPTH ON R:FR

In the smaller gap, mean PAR at ground level was 0·67 (± 0·06) mol m^{-2} day^{-1} over 9 days and mean r:fr was 0·92. In the larger gap where mean PAR was 3·04 (± 0·25) mol m^{-2} day^{-1}, the mean r:fr was 1·18. The minimum r:fr in the smaller gap was 0·69 compared to 0·82 in the larger gap.

The r:fr of light transmitted through leaf litter differed significantly among the six species. The mean ratios ranged from 0·30 to 0·81 in fresh leaves and 0·18–0·83 in dry leaves. There was no consistent trend in the direction of difference in mean r:fr between fresh and dried leaves (Table 3), but many of the dried leaves transmitted so little irradiance that it was close to or below the detection limits of the sensor. Additional leaves further decreased the r:fr, but decreased irradiance below the detection limit of the sensor.

We tested the light transmitted through a 7-mm thick layer of aggregated topsoil. With no enhancement of

Table 3. Mean (± SE) red: far red ratio of the light from bright sunlight (r:fr ratio 1·36) that would be transmitted through fresh and dried litter leaves of six tree species from BCI, Panama. $N = 6$. ANOVA table: variance ratios with degree of significance indicated as follows: NS, not significant; ***, $P = 0.001$: **, $P = 0.01$; and *, $P = 0.05$

Species	Fresh litter	Dried litter
Miconia argentea	0·55 ± 0·07	0·47† ± 0·12
Ochroma pyramidale	0·71 ± 0·04	0·49 ± 0·04
Luehea seemannii	0·35 ± 0·12	0·52† ± 0·08
Solanum hayesii	0·81 ± 0·07	0·79 ± 0·14
Anacardium excelsum	0·30 ± 0·07	0·18† ± 0·02
Cecropia spp.	0·41 ± 0·07	0·83† ± 0·01

	d.f.	*F*	*P*
Species	5	10·4	***
Hydration status	1	0·02	NS
Interaction	5	3·34	**

†Transmitted irradiance close to the detection limits of the sensor.

image brightness, 14 bright spots (each *c.* 1 mm^2 in size) of transmitted white light were visible in an area of about 10×10 cm. Increasing the image brightness without altering the colour balance revealed many more unevenly distributed small white areas as well as more diffuse areas of red light. About 1·4% of the total area was illuminated. Of this area, approximately 70% consisted of white light and the remainder more diffuse red light. This indicates the potential for significant, but patchy, light penetration through the top few mm of structured soil.

EFFECTS OF R:FR ON GERMINATION OF *MICONIA ARGENTEA* AND THE THREE SPECIES OF *CECROPIA*

All species showed a significant effect of r:fr on percentage germination (Table 4). A sigmoidal function provided good fits to the data ($r^2 = 0.88 – 0.98$, Table 5) and showed that germination increased sharply above a threshold r:fr (Fig. 1). The parameter x_o from the sigmoidal regressions is one measure of the value of this threshold and was much lower for *Miconia argentea* (0·12) than the three *Cecropia* species (0·21–0·27). Logistic regression suggested that the germination response to r:fr differed between the three *Cecropia* species (Tables 4 and 5, Fig. 1), but the differences were marginal and possibly not ecologically significant.

Although the flux density of irradiance increased with r:fr in the treatments of this experiment (Table 2), the germination of seeds beneath a filter that transmitted little PAR (2·2 µmol m^{-2} s^{-1}) but at a high r:fr (0·70) was not significantly different from the maximum germination at high PAR and high r:fr in any species. No germination occurred in complete darkness or in the lowest r:fr treatment in any species.

Table 4. Wald values and degrees of significance from analysis by logistic regression of germination response to r:fr in *Miconia*, the difference in response to r:fr among the three *Cecropia* species and the response to r:fr, temperature fluctuation and the interaction between r:fr and temperature fluctuation in *Solanum*. Degree of significance indicated as follows: NS, not significant; ***$P = 0.001$; **$P = 0.01$; and *$P = 0.05$

Species	Factor	Wald	*P*
Miconia	r:fr	72·9	***
Cecropia spp.	r:fr	49·3	***
	species	0·390	NS
	r:fr * spp.	4·65	*
Solanum	r:fr	189	***
	T. fluctuation	292	***
	r:fr * T. fluct.	238	***

Table 5. Coefficients from sigmoidal regression of final germination percent (y) on r:fr (x) derived from the function: $y = a/((1 + \exp − ((x − x_o)b))$. Degree of significance indicated as follows: NS, not significant; ***$P = 0.001$; **$P = 0.01$; *$P = 0.05$

Species	*a*	*b*	x_o	R^2	*P*
Miconia argentea	87·1	0·0183	0·117	0·98	***
Cecropia insignis	36·4	0·0496	0·205	0·88	*
Cecropia obtusifolia	39·7	0·0192	0·237	0·88	*
Cecropia peltata	57·4	0·0488	0·265	0·95	**
Solanum hayesii					
Fluctuation	68·2	0·197	−0·244	0·40	NS
No fluctuation	61·0	0·0225	0·208	0·99	***

EFFECTS OF R:FR AND TEMPERATURE FLUCTUATION ON GERMINATION OF *SOLANUM HAYESII*

The germination of *Solanum hayesii* differed significantly between r:fr treatments, between inferred temperature fluctuation treatments and in response to the interaction between these factors (Table 4). In the growth chamber (where a diel temperature fluctuation was absent) *Solanum* showed a germination response to r:fr that was similar to that of the other species, with a sharp increase in germination centred on a r:fr of 0·21 (Table 5). In contrast, the seeds subjected to fluctuating temperatures in the growing house had a high germination percesntage regardless of r:fr treatment and in complete darkness (Fig. 1e, Table 4).

Effects of seed size

The species-specific threshold r:fr for germination was positively correlated to seed mass for a dataset incorporating the five species used in this study and the four *Piper* species from the study of Daws *et al.* (2002) (Fig. 2, $n = 9$, $r = 0.752$, $P < 0.05$). The equivalent comparisons across the four genera and within *Piper* and *Cecropia* had low statistical power because of the few taxa available for analyses, and none was significant ($r = 0.851, 0.816, −0.926$; $P > 0.05$ in all cases).
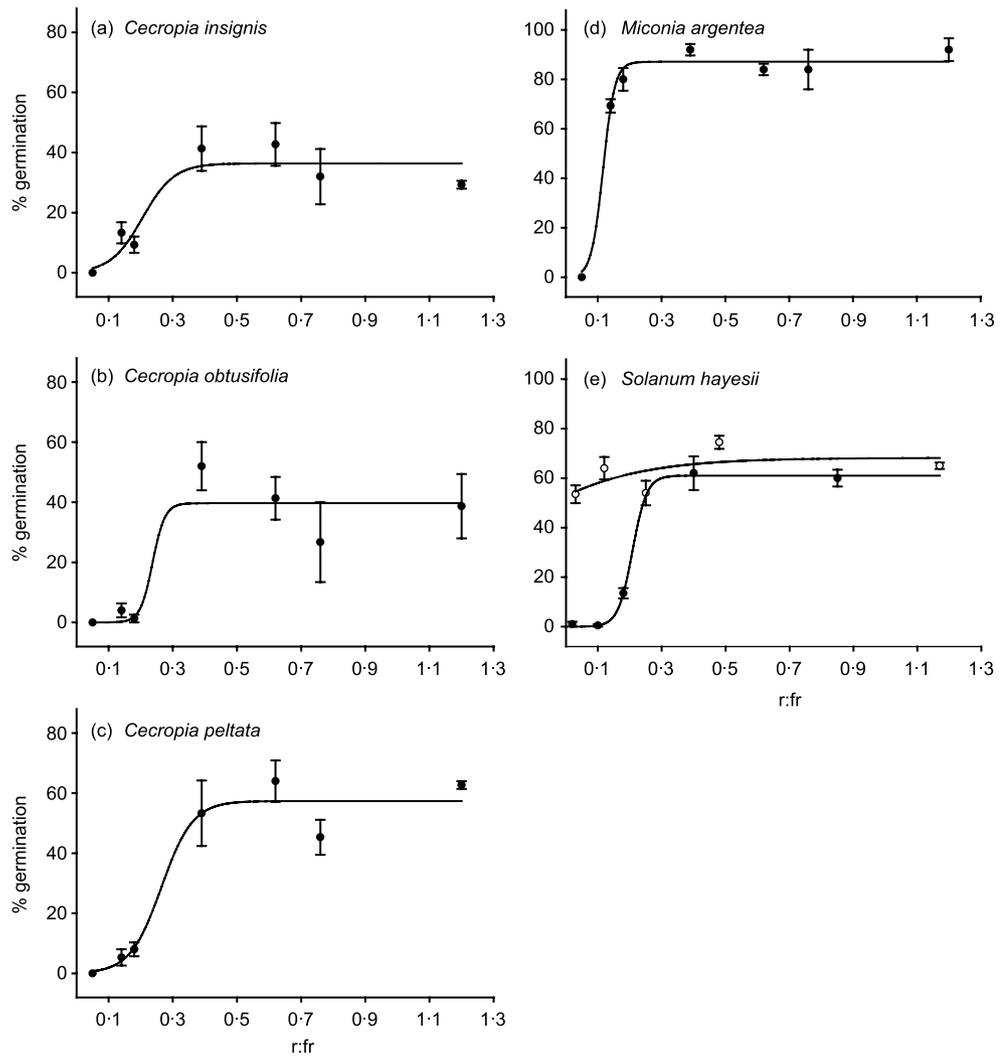
Fig. 1. Sigmoidal regression fit of percentage seed germination against r:fr ratio. For *Solanum*, open symbols indicate the fluctuating temperature treatment, and closed symbols indicate the constant temperature treatment. Germination at zero irradiance was zero for all species (except for *Solanum* in the presence of a temperature fluctuation where mean (± SEM) germination was 72 ± 5%). These values are not plotted as zero irradiance has no value for r:fr.
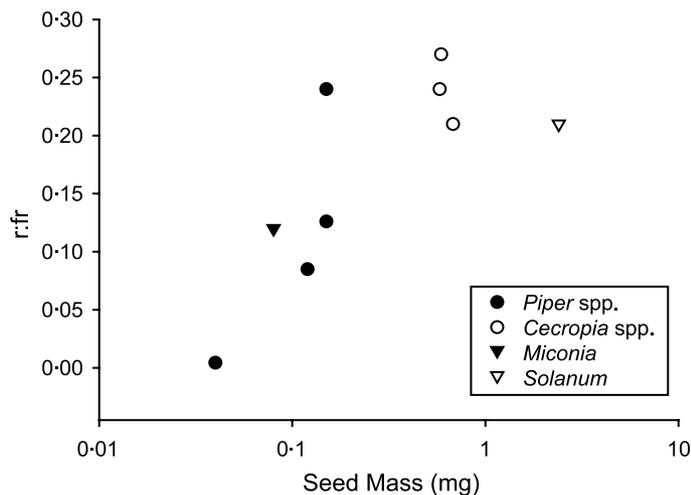
Fig. 2. Log seed mass (mg) against threshold r:fr for germination for the five species used in this study and the four *Piper* species used by Daws *et al.* (2002).

Discussion

RED:FAR RED MEASUREMENTS

The mean values of r:fr in small (*c.* 25 m^2) and medium (*c.* 64 m^2) gaps were only a little less than those in full sunlight and similar to the comprehensive measurements made by Lee (1987) on BCI and at La Selva in Costa Rica. Lee (1987) found a mean r:fr of 1·15 from instantaneous midday measurements in the centres of six gaps (mean PAR 995 µmol m^{-2} s^{-1}) on BCI and a mean r:fr of 0·95 for light flecks in the understorey (*n* = 13). The mean for understorey sites on BCI was 0·35 with a range from 0·13 to 0·67 (Lee 1987). Measurements by Daws *et al.* (2002) concur broadly with those of Lee (1987) and our own.

The r:fr received at the soil surface, however, may exceed that received by seeds in the soil seed bank because most seeds are buried beneath a layer of soil or litter. The r:fr of irradiance was reduced by transmission through leaf litter. This reduction depended on

the species of leaf, the number of leaves present and the water content of the leaves. Vázquez-Yanes *et al.* (1990) worked with two fresh and two dried leaves of each of six species (all different from the species in this study) and found that the dry litter transmitted a greater proportion of far red light than wet leaves. They found a reduction in transmittance from ratios in the range 0·15–0·71 in fresh litter leaves to 0·03–0·48 in dried litter leaves. These results and our own indicate that leaves reduce the r:fr transmitted to the soil surface with dry leaves causing a greater reduction in the irradiance, although the species of leaf in the litter will also determine the ratio and irradiance reduction.

The small body of work on the penetration of light through soil has been reviewed by Tester & Morris (1987). Since it is challenging to obtain thin and undisturbed layers of surface soil through which to measure light transmission, most workers have spread thin layers of sand, or of finely sieved soil on top of a transparent glass plate and have obtained a measurement of the transmitted light that is integrated over a large area. This work has led to the general observations that irradiance is strongly attenuated in passing through thin (< 5 mm) layers of soil and that there is a reduction in the r:fr of irradiance that is transmitted through the soil (Bliss & Smith 1985; Tester & Morris 1987). However, aggregation is the norm for forest soils and, with the exception of very sandy soils, discrete particles or aggregates of less than 0·5 mm diameter are uncommon in natural surface soil except in localised deposits of detached material that have been moved and sorted by surface run-off (Kalpagé 1974; Young 1976). Furthermore, previous methods of measuring transmitted light intensity integrated the intensity over a large area which fails to represent the situation experienced by individual seeds.

In this study, light was shown to pass between and around but not through aggregates, reaching only $1·4 \pm 0·4\%$ of the soil area at a depth of 7 mm. Thus, we might expect only 1·4% of seeds at this depth to be able to germinate (however, a more diffuse light source like sky radiation would be likely to reach a greater proportion of the soil area). Although seeds that are less deeply buried in the soil may have greater opportunities for germination, successful establishment from these seeds is also constrained in gaps by the speed and frequency with which direct sunlight causes drying of the surface of an aggregated soil.

Opportunities for seed germination are also likely to diminish over time. This is because soil invertebrates, soil compression by larger animals, and surface water flow will progressively occlude suitable germination microsites. For seeds below the soil surface, however, these effects may initially increase germination probability (due to the less frequent and severe soil drying and to improved seed soil contact). This highlights an important trade-off between the benefits and costs of photoblasticism and the short-term nature of the photoblastic germination strategy.

EFFECTS OF PHOTON FLUX DENSITY AND R:FR ON GERMINATION

The germination response to r:fr was approximated by a sigmoidal function, which implies stimulation to maximum germination across a narrow range of r:fr values. For all our species, seeds were able to germinate at remarkably low r:fr values. Fifty per cent of maximum germination (x_o) was stimulated by a r:fr of 0·12 in *Miconia*, 0·21–0·27 in *Cecropia* and 0·21 in *Solanum* (in the absence of a temperature fluctuation). A similarly low r:fr (0·20) was necessary for 80% germination of *Cecropia obtusifolia* seeds collected in Mexico (Vázquez-Yanes & Smith 1982). In contrast, Vázquez-Yanes *et al.* (1990) found high germination of *Cecropia obtusifolia* only at a r:fr > 1·2, and 50% of maximum germination (x_o) at a r:fr > 0·9. The discrepancy between these results may have been caused by the short (10 days) light exposure followed by darkness in the latter experiment (Vázquez-Yanes *et al.* 1990) during which production of and reversion to the inactive form of phytochrome would occur (Smith 2000). In our experiments all of the *Cecropia* species germinated over a 45-day period, and germination was slowest in the lowest r:fr treatments (data not shown). Therefore, experiments in which light exposure does not occur over the whole germination period are more likely to yield a higher threshold r:fr for germination.

This study supports and extends the finding of Pearson *et al.* (2002) that light and a fluctuating temperature regime can each cause germination of *Solanum hayesii* independently. In the absence of a temperature fluctuation, *Solanum* responded to r:fr treatments in a similar way to the three *Cecropia* species. Under a very low r:fr, high germination was only observed in the presence of fluctuating temperatures.

The germination of some temperate arable weed species (e.g. *Rumex* spp., Roberts & Totterdell 1981) responds positively to both light and temperature. However, in these species temperature fluctuations have little effect on germination in the absence of light. For example, *Rumex crispus* can be stimulated to germinate by a short exposure to red light and, if light is present, a temperature fluctuation of as little as 2 °C can have a further stimulatory effect. The type of interaction between fluctuating temperature and r:fr that we found for *Solanum hayesii* has not to our knowledge been reported for tropical species, although it does exist in temperate species; for example, Salisbury & Ross (1992) quote the example of Kentucky bluegrass (*Poa pratensis*).

EFFECTS OF SEED SIZE ON GERMINATION RESPONSE TO R:FR

Our data show a lower threshold of r:fr for stimulation of germination in *Miconia* (seed mass 0·08 mg) than the *Cecropia* species (seed mass 0·58–0·68 mg) or *Solanum* (seed mass 2·40 mg). Although the correlation

across species (Fig. 2) has to be interpreted with caution because not all the data points are statistically independent, the comparison across the five species reported in this study plus the four pioneer *Piper* species from Daws *et al.* (2002) showed a significant positive relationship between a species' seed mass and its r:fr threshold for germination (Fig. 2). A non-significant positive relationship was also found in a comparison of the four *Piper* species, but not for the comparison of three *Cecropia* species which had a much narrower range of seed mass than the *Piper* species.

The relationship between seed size and the r:fr germination response may reflect differences in seed survivorship in the soil. For the species used in this study, Dalling *et al.* (1997) found decreases in the density of viable seeds (number per unit volume) in the seed bank of 75% in *Miconia*, 37% in *Cecropia* and 0% in *Solanum* in the 5–6 months after fruiting. These declines were probably caused by fungal pathogens since Dalling *et al.* (1998) showed a significant increase in survival of buried *Miconia argentea* and *Cecropia insignis* seeds if they were pretreated with fungicide. Smaller-seeded species may be more susceptible to these mortality agents because the seed coat is thinner (Pearson *et al.* 2002). Low survival of small-seeded species may have imposed selection for a less discriminating germination physiology. This proposition is supported by the very low r:fr required for germination of the very small-seeded species in this study and for four species of *Piper* studied by Daws *et al.* (2002). They found that *Piper peltatum* has the smallest seeds (0·04 mg) and the lowest threshold r:fr for germination (< 0·01) of the nine species compared in Fig. 2. Plants with a r:fr threshold for germination equivalent to those of *Miconia* or *Piper peltatum* will germinate even in the understorey if the soil is bare (cf. Lee 1987). In the absence of a gap, most of these germinants will die. Li *et al.* (1996) found that *Cecropia* seedlings were the most abundant germinants in the understorey of Costa Rican rain forest, but the unsuitable regeneration site resulted in seedling half-lives that did not exceed 0·8 months. Therefore, very small-seeded species must rely on high seed numbers and effective dispersal to replenish the soil seed bank in sites where tree-fall gaps could appear.

In contrast, photoblastic germination can prevent germination in microsites that are currently adverse for seedling survival but that are likely to become favourable within the lifespan of the seed. The ability to emerge through a covering of litter or soil increases directly with increasing seed mass (Vázquez-Yanes & Orozco-Segovia 1992; Pearson *et al.* 2002). However, a covering of litter or a thin layer of soil sufficient to prevent photoblastic seeds from germinating is likely to be disturbed by animals (Theimer & Gehring 1999), or abiotic factors (e.g. wind or water movement). For example, Theimer & Gehring (1999) found that a medium-sized bird (the Chowcilla, *Orthonyx spaldingii*) in Australia, turned over the whole of the litter-covered area as frequently as every 5 weeks. Thus, the

photoblastic mechanism will prevent germination occurring until conditions suitable for seedling emergence and onward growth have become established.

An alternative explanation for the positive relationship between r:fr germination threshold and seed mass is that the magnitude of the threshold r:fr for germination could be related to relative seed production. The seed size/number trade-off (cf. Smith & Fretwell 1974) predicts that the smallest-seeded species will have a greater density of propagules in potential recruitment sites. This relationship would allow a less discriminating germination behaviour to evolve because the increased risk of post-germination mortality would be balanced by an increased likelihood that at least one seed would be dispersed to each potentially favourable establishment site.

Conclusions

We propose that the smallest-seeded species will face selection for low discrimination in the r:fr required to stimulate germination because they face the greatest risk of mortality, either through high susceptibility to pathogens or through small seed reserves, and because greater seed production decreases the relative cost of low discrimination. A thick covering of soil or litter will prevent the penetration of any light so if light of any spectral composition reaches the seed it might have the potential to emerge. Among these small-seeded photoblastic species, the larger the seed, the greater its potential to persist until a likely further improvement in conditions occurs and also the greater its potential may be for detecting suitable light conditions for germination by integrating the r:fr signal over a larger surface area. Consequently, *Cecropia* had a greater threshold r:fr for germination than *Miconia*. *Solanum* did not have a higher threshold r:fr for germination than *Cecropia*, but its ability to respond positively to fluctuating temperature in the dark will permit it to germinate in gap sites from a depth of soil or litter that receives no transmitted light. Emergence of *Solanum* from beneath a greater depth of litter or soil than *Cecropia* or *Miconia* is possible because its greater seed mass produces a thicker shoot that is better able to displace the obstruction and grow to a greater length before photosynthesis is required (Pearson *et al.* 2002). One outcome of these contrasting responses to r:fr and temperature will be reduced overlap in the types of microsites suitable for the germination and establishment of different species, and an increased potential for coexistence of species within the pioneer functional group.

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