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Allometric relationships between seed mass and seedling characteristics reveal trade-offs for neotropical gap-dependent species

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Abstract A seed size–seed number trade-off exists because smaller seeds are produced in greater number but have a lower probability of establishment. This reduced establishment success of smaller-seeded species may be determined by biophysical constraints imposed by scaling rules. Root and shoot diameter, root growth extension rate (R_{GER}) and shoot length at death for dark-grown seedlings are predicted to scale with the cube root of seed embryo and endosperm mass (m). We confirmed this expectation for ten neotropical gap-dependent tree species with an embryo and endosperm dry mass >1 mg. However, for nine smaller seeded species ($m < 1$ mg) with photoblastic germination, root and shoot diameters were larger than expected, and consequently, R_{GER} was slower than expected. The maximum shoot thrust of seedlings from seeds with masses ≥1 mg was comparable to the estimated force required to displace overlying litter, supporting the hypothesis that photoblastic behaviour only occurs in seeds with insufficient shoot thrust to displace overlying leaves. Using the model soil water, energy and transpiration to predict soil drying in small and large gaps, we showed that: (1) gaps that receive a significant amount of direct sunlight will dry more quickly than small gaps that do not, (2) compared to the wet-season, soil that is already dry at depth (i.e. the dry-season) will dry faster after rainfall (this drying would most likely kill seedlings from small seeds) and (3) even during the wet-season, dry periods of a few days in large gaps can kill shallow-rooted seedlings. We conclude that the smaller the seed, the more vulnerable its seedling would be to both covering by litter and soil drying because it can only emerge from shallow depths and has a slow R_{GER}. Consequently, we suggest that these allometrically related factors contribute to the reduced establishment success of smaller-seeded species that underpins the seed size–seed number trade-off.

Keywords Allometric relationships · Barro Colorado Island · Soil water availability · SWEAT

Introduction

Within many plant communities seed size varies over several orders of magnitude (Coomes and Grubb 2003). In order to explain species coexistence, this implies that there is a trade-off between seed size and seed number. A plant can either produce a large number of small seeds that may be dispersed to a greater number of vacant or patchily distributed micro-sites, but have a low individual probability of establishment, or it can produce a small number of larger seeds that may have a limited dispersal ability, but a high individual probability of establishment (Leishman and Murray 2001).

Once a seed has dispersed, the probability of successful establishment is the product of the probability of emergence and that of the survival of an emerged seedling. Seedlings from larger seeds may have a higher probability

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of survival than those from small seeds because larger seeds result in larger seedlings. These are less prone to physical disturbance, such as soil instability, herbivory and trampling (Armstrong and Westoby 1993; Harms and Dalling 1997), and are able to emerge from greater depths of soil (Bond et al. 1999; Pearson et al. 2002). In addition, there is equivocal evidence that seedlings from larger seeds are more tolerant of low light, nutrients and water availability (Boot 1996; Westoby et al. 1996). Conversely, while the probability of survival is low for small-seeded species, the probability of dispersal to patchily distributed and vacant germination micro-sites is higher.

There are two main physical constraints to successful seedling establishment. First, the shoot must be able to reach the soil surface to obtain light before the seed reserves are exhausted. Secondly, to ensure the survival of seedlings emerging during rain-free periods, the radicle must grow sufficiently fast down the soil profile to keep in advance of the soil drying front. The drying front is the depth to which the soil is at least as dry as the permanent wilting point. For 17 fynbos species, Bond et al. (1999) found that the ability of a shoot to emerge is related to the maximum shoot length that can be produced in the dark and that this length is proportional to the cube root of the seed mass. There is also some evidence that root growth rate may be related to seed mass. Buckley (1982) measured the total root length of 15-day-old seedlings of seven Australian dune species and found that the larger seeded species had longer roots. However, we are unaware of any work which predicts or to tests directly the form of the relationship between seed mass and root growth rate.

Bond et al. (1999) demonstrated an allometric relationship in which shoot diameter scaled in proportion to the linear dimensions of the seed so that it was proportional to the cube root of seed mass. By the same reasoning, we expected that root diameter, d_r would be similarly related to seed (embryo + endosperm) mass, m as:

$$d_r = m^{(1/3)} d_0 \tag{1}$$

where d_0 is a constant.

Furthermore, if (1) this relationship holds, and if the ratio of shoot: root mass is independent of seed size, and large and small seeds have similar metabolic rates, then (2) the root growth extension rate (R_{GER}) should also be related to the cube root of seed mass:

$$R_{\mathrm{GER}} = m^{(1/3)} e_0 \tag{2}$$

where e_0 is a constant.

If, additionally, the fixed proportions of m are converted into shoot and root tissue, then we would expect the maximum shoot l_s (and root) length of seedlings grown in the dark to be proportional to $m^{(1/3)}$:

$$l_s = m^{(1/3)} l_0 \tag{3}$$

where l_0 is a constant.

If, as Eq. 2 predicts, seedlings from small seeds have roots with low extension rates, they will have a reduced probability of successful establishment as a consequence of high mortality following germination in environments where water shortage limits survival. Mortality occurs when the radicle from a seed that germinates before a dry period is overtaken by the drying front, thus killing the seedling. This problem is magnified by the ability of small-seeded species to only emerge from the top few millimetres of soil (Bond et al. 1999; Pearson et al. 2002; Eq. 3) with the consequence that they will be more vulnerable to short dry periods. This assumes that water uptake kinetics do not differ for species with short and long roots. Very small seeds are potentially further disadvantaged because they have insufficient shoot thrust to displace any overlying leaves. Such seeds may exhibit photoblastic germination that requires light of a high red:far red ratio to enable germination, so that seeds receiving light that has passed through an overlying litter leaf are prevented from germinating (Vázquez-Yanes et al. 1990; Pearson et al. 2003a). For example, Pearson et al. (2002) studied 14 tropical pioneer species with seed masses ranging from 0.04–88 mg and found that eight of these, all with seed mass <2.5 mg, had photoblastic germination. None of the remaining six species had seeds sensitive to light, and only one (*Luehea seemannii*, seed mass 1.9 mg) had a seed mass <2.5 mg. However, no comparison has yet been made between shoot thrust and leaf litter weight to test the hypothesis that seeds of forest plants are only photoblastic if their shoot thrust is insufficient to displace a leaf.

Gap-dependent species require canopy gaps or other open areas for successful establishment. In the tropical semi-deciduous forest on Barro Colorado Island, Panama, short dry spells of a few days duration are common during the wet-season (Rand and Rand 1982), and they can result in rapid soil drying in canopy gaps. For example, on bare soil in large canopy gaps, Engelbrecht et al. (2006) reported that the soil water potential close to the soil surface can drop to –4.5 MPa after 4 days without rain. We have used tropical gap-dependent tree species for this study because their seed masses cover almost five orders of magnitude and because the constraint of only being able to regenerate in gaps makes them especially vulnerable to soil drying.

Because allometric relationships reveal the existence of underlying biophysical constraints to seedling growth, they are an important means to investigate seed-size trade-offs. Deviations from the expected relationships may also help to explain how plants partition their resources between competing requirements. In this paper, we define the expected allometric relationships between seed (embryo + endosperm) mass and root diameter, between seed mass and shoot length at death and between seed mass and R_{GER} for 19 gap-dependent neotropical tree species. We use these allometric relationships to test the hypothesis that root growth rate constrains the establishment of small-seeded species. To set these results in context, we model an example of the rate of drying of bare soil in gaps of two sizes at our study site to test the contrasting likelihoods of establishment for species of differing seed mass in the event of short dry spells in the wet-season. We also determine the allometric relationships between seed mass, shoot diameter and maximum shoot length observed by Bond et al. (1999) to confirm whether these relationships also hold for gap-dependent species. Finally, we have estimated and measured the maximum shoot thrust and compared these with the thrust required to displace an overlying leaf to test the hypothesis that photoblastic behaviour only occurs in species with insufficient shoot thrust to displace overlying leaves.

Materials and methods

Seed lot details

Seed lots were collected from an undisturbed semideciduous tropical forest on Barro Colorado Island (BCI) (9°10′N, 79°50′W) and a secondary forest in the adjoining Barro Colorado Nature Monument, Republic of Panama, from a minimum of five individual trees per species. Rainfall on BCI averages 2600 mm year^{-1}, with a pronounced dry season between January and April (Dietrich et al. 1982). However, there may be both periodic rainfall events in the dry-season and dry periods in the wet-season (Rand and Rand 1982; Daws 2002). Table 1 details the 19 species, authorities and oven-dry seed mass. For mass determinations, three replicates of five seeds each were dried at 103°C for 17 h (ISTA 1999) before weighing.

Since the proportion of a seed allocated to seed coat may vary with seed mass (Fenner 1983; Grubb and Burslem 1998), the testa dry mass of all species was determined by removing the testa after germination followed by mass determination, as is the case for whole seeds. All data are presented on an embryo (including endosperm) mass basis rather than whole-seed basis. In discussing allometric relationships, we have concentrated on relationships between embryo plus endosperm mass and seedling characteristics since this represents the resource available to produce shoots and roots.

Root and shoot diameter, maximum shoot length and root growth rate

For all measurements, seeds were sown on the surface of 1% agar in distilled water. This avoided some of the potential problems of using soil, such as difficulties in recovering seedlings of very small-seeded species from soil. Agar was poured into 90-mm petri dishes or sandwich boxes (28 × 18 × 6 cm). After sowing, the containers were held vertically at 25°C in the dark, except for photoblastic species, which were sown in the light and transferred to dark conditions when the first seed germinated. Fifteen seeds of each species were sown across the surface of the agar. Root and shoot diameters were determined 3 days after germination using a microscope and calibrated eyepiece graticule. Measurements were taken approximately midway along the length of the root or shoot.

Average root growth rates were calculated from measurements of the root length of individual seeds (ten per species) over 4 consecutive days. The coefficient of variation for R_{GER} did not exceed 18.9% across the 19 species (range 4.5–18.9%). Maximum root and shoot length were determined in a similar manner to root and shoot diameters: 15 seeds per species were sown on the surface of 1% agar and suspended vertically. As soon as the first seed had germinated, the petri dishes or sandwich boxes were wrapped in aluminium foil to exclude light and held at 25°C for 3 months, after which root and shoot lengths were determined. Depending on seed size, measurements were obtained using either digital callipers (Digimatic Callipers, Mitutoyo, UK) or a microscope and calibrated eye piece graticule.

Root growth rates in soil

To test the accuracy of root growth rates measured on agar, seeds of five species (*Apeiba membranacea*, *A. tibourbou*, *Ochroma pyramidale*, *L. seemannii* and *Cecropia obtusifolia*) were sown in soil. These five species were chosen because they had relatively large seeds and, therefore, their seedlings were comparatively easy to excavate from soil for root length determination. Plastic boxes were filled with a 50-mm-deep layer of Craibstone (sandy loam) soil wetted to field capacity. Seeds were pre-germinated on the surface of agar and transferred to the container as soon as the emerging root tip was visible. They were sown at a depth of 5 (*C. obtusifolia* and *L. seemannii*) or 20 mm (*A. membranacea*, *A. tibourbou* and *O. pyramidale*). After 4 days, ten seedlings per species were exhumed and their root length measured using digital callipers. Across the five species, the coefficient of variation for root length did not exceed 35.5% (range 4.5–35.5%).

Table 1 The study species used in decreasing order of mean (±SEM) embryo + endosperm mass. Mean (±SEM) radicle growth rate (R_{GER}) is also given

Species	Family	Mean oven-dry seed mass ± 1 SE (mg)	Mean oven-dry embryo and endosperm mass ± 1 SE (mg)	Mean R_{GER} ± 1 SE
Clidemia octona[a]	Melastomataceae	0.0160 ± 0.001	0.0120 ± 0.001	0.080 ± 0.004
Tibouchina longifolia[a]	Melastomataceae	0.0403 ± 0.002	0.0294 ± 0.001	0.114 ± 0.007
Piper peltatum[a]	Piperaceae	0.0370 ± 0.002	0.0316 ± 0.002	0.240 ± 0.012
Leandra dichotoma[a]	Melastomataceae	0.0553 ± 0.0071	0.0402 ± 0.0063	0.341 ± 0.016
Miconia argentea[a]	Melastomataceae	0.076 ± 0.007	0.0552 ± 0.007	0.108 ± 0.005
Cecropia obtusifolia[a]	Moraceae	0.74 ± 0.03	0.09 ± 0.02	0.90 ± 0.04
Solanum hayesii[a]	Solanaceae	0.57 ± 0.03	0.11 ± 0.02	0.72 ± 0.03
Piper marginatum[a]	Piperaceae	0.157 ± 0.011	0.1243 ± 0.008	0.37 ± 0.01
C. insignis[a]	Moraceae	0.61 ± 0.05	0.18 ± 0.03	0.96 ± 0.05
Ochroma pyramidale	Malvaceae	5.20 ± 0.17	0.310 ± 0.18	2.50 ± 0.13
Luehea seemannii	Malvaceae	1.51 ± 0.17	0.326 ± 0.11	2.12 ± 0.09
Trema micrantha	Ulmaceae	3.53 ± 0.22	1.20 ± 0.13	0.85 ± 0.04
Guazama ulmifolia	Malvaceae	4.51 ± 0.32	2.31 ± 0.25	4.51 ± 0.07
Apeiba tibourbou	Malvaceae	5.57 ± 0.66	2.32 ± 0.47	1.68 ± 0.13
A. membranaceae	Malvaceae	12.1 ± 0.55	2.71 ± 0.24	3.1 ± 0.1
Carica papaya	Caricaceae	14.01 ± 2.3	7.58 ± 1.90	2.10 ± 0.06
Platypodium elegans	Fabaceae	477 ± 24	51.7 ± 9.1	4.8 ± 0.1
Ceiba pentandra	Malvaceae	121.4 ± 5.3	83.9 ± 4.3	8.5 ± 0.4
Swietenia macrophylla	Meliaceae	412 ± 41	292 ± 26	7.8 ± 0.4

SEM, Standard error of the mean

[a] Photoblastic spp

Maximum shoot thrust and mass of litter leaves

For *Trema micrantha* and *C. insignis*, the maximum force that could be exerted by a shoot was measured on ten shoots of each. Shoots were grown to approximately a length of 10 mm and their diameters measured. They were subsequently pushed slowly, tip downwards, against a top-pan balance, with the shoot held by tweezers only at the seed end; the aim of this manipulation was observe the maximum force that the shoot could exert before buckling. These two species were selected because their shoot diameters were large enough to obtain reliable estimates of shoot thrust using this technique and because seeds of other larger seeded species were not available when the work was conducted. The fresh weight of individual leaves and leaf fragments intercepted by a 10-m line transect during the dry-season was also determined for the primary forest on BCI.

Modelling movement of the soil drying front using SWEAT

We used the soil water, energy and transpiration (SWEAT) model of simultaneous heat and water flow through the soil, which includes both vapour flow and mass flow of water (Daamen and Simmonds 1994, 1996; Burke et al. 1997; Daamen 1997), to model the variation of soil temperature and water availability (matric potential) as a function of depth and time during rain-free periods. The soil parameters necessary for modelling (including soil texture and the water release characteristic) were measured on soil samples from BCI, or estimated (Daws et al. 2002). SWEAT is driven by meteorological variables (net radiation, relative humidity, wind speed, air temperature and rainfall). These variables were measured in small and large gaps in April 2001, and predicted and measured values of soil temperature and matric potential were compared for the large gap in order to calibrate the model by choosing the value of soil-saturated hydraulic conductivity that gave the best fit. For the purpose of simplicity and because we did not have the necessary root density data, we ignored any possible water loss through soil water extraction by the roots of trees surrounding the gap in our modelling. Consequently, although the model gave predictions for soil drying in the small gap that were comparable to measured values of matric potential over a period of a few days, we did not have measurements over longer rain-free periods, and our predictions for small gaps may underestimate the rate of soil drying over longer periods.

Conditions were modelled for the centre of a large and small square gap with tree height:gap width ratios of 1:6 and 1:1 in the dry- and wet-seasons; these sizes are typical of large and small gaps on BCI, respectively (Yavitt et al. 1995). It was assumed that the soil profile started at wilting point (–1.5 MPa matric potential) or field capacity (–0.01 MPa) for the dry- and wet-season, respectively. In the dry-season, simulated rainfall events of 10 or 40 mm were added to the profile to provide the opportunity for seed germination. The depth of the drying front was taken as the maximum soil depth to which the soil was dryer than the permanent wilting point, a matric potential of –1.5 MPa (Marshall et al. 1996), which we assumed here to be the threshold value for seedling survival.

Statistical analysis

Reduced major axis regression implemented in RMA (Bohonak 2004) was used to fit lines to log-log plots of shoot and root dimensions and growth rates against seed embryo and endosperm mass. The slopes of regression lines were compared to null lines of slope 0.333 (root and shoot diameter and R_{GER}) using the following *t* test:

$$t = (b - H)/S \tag{4}$$

where b is the slope of the fitted regression line, H is the slope of the null line, S is the standard error of b and t has (n - 2) *df*, where n is the number of replicate data points sampled (Underwood 1997).

In a number of the allometric plots there appeared to be a discontinuity in the data at approximately 0.1 mg (i.e. the small seeds responded differently than larger seeds), which corresponds to the transition from photoblastic to non-photoblastic species. Consequently, separate regression lines were fitted to the data above and below this threshold and the slope of each line compared with the expected slope.

Results

The seed coat constituted 21–94% of the total seed mass (Table 1). There was no relationship between this percentage and seed mass. The seed coat of both small and large seeds could account for a large (e.g. in *C. obtusifolia* and *Platypodium*) or small (e.g. in *Clidemia* and *Swietenia*) percentage of the total seed mass.

For the ten larger seeded (non-photoblastic) seeds, there was a highly significant relationship between log(shoot diameter) and log(embryo + endosperm mass) (Fig. 1a; $r^2 = 0.96$, $df = 8$, $P < 0.001$). In addition, the slope of this allometric relationship was not significantly different from the expected relationship with the cube root of embryo + endosperm mass (RMA slope = 0.29, *t* test $t = 2.17$, $df = 8$, $P > 0.05$). Similarly, for the larger seeded species, there was a highly significant relationship between log(root diameter) and log(embryo + endosperm mass) (Fig. 1b; $r^2 = 0.91$, $df = 8$, $P < 0.001$), the slope of which did not differ significantly from the expected relationship (RMA slope = 0.30, *t* test, $t = 1.09$, $df = 8$, $P > 0.05$).

For the nine photoblastic (small-seeded) species, the relationship between log(shoot diameter) and log(embryo + endosperm mass) was not significant (Fig. 1a; $r^2 = 0.241$, $df = 7$, $P > 0.05$), and the slope of the fitted regression line differed significantly from the expected relationship (RMA slope = 0.13, *t* test $t = 5.03$, $P < 0.01$). For root diameter, there was a significant relationship with embryo + endosperm mass (Fig. 1b; $r^2 = 0.633$, $df = 7$, $P < 0.05$), and the slope of this line differed significantly from the expected slope (RMA slope = 0.14, *t* test $t = 6.10$, $P < 0.001$).

The *y*-axis on the right side of Fig. 1 gives theoretical estimates of the maximum shoot thrust based on the shoot diameter and an assumed extension pressure of 1 MPa

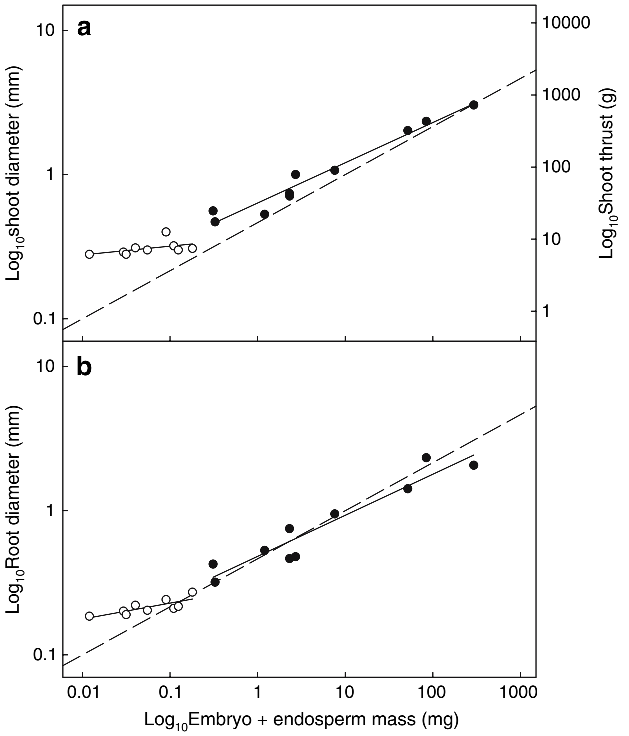

Fig. 1 Allometric relationships between embryo plus endosperm mass (*Log*$_{10}$*embryo + embryo mass*) and shoot diameter (**a**) and root diameter (**b**) for nine species of photoblastic (*open symbols*) and ten species of non-photoblastic (*closed symbols*) gap-dependent neotropical trees. The *dashed line* represents the expected allometric ratio:shoot or root diameter α (mass of embryo + endosperm)$^{1/3}$. The theoretical shoot thrust corresponding to the measured shoot diameters (Weaich et al. 1992) is presented on the *y*-axis on the right side of **a**

(Weaich et al. 1992). Our measured values of 2.26 ± 0.24 and 3.91 ± 0.54 g for *C. insignis* and *T. micrantha*, respectively (mean ± SE), are considerably less than the theoretical estimates of 6.36 ± 1.31, and 42.8 ± 6.0 g because the shoots buckled well before they were able to exert their maximum thrust.

Along the line transect we determined the fresh mass of 151 leaves and intact leaf fragments. Of these, 80% had a fresh weight of between 0.1 and 1.0 g, although the heaviest 10% of the leaves, which covered a substantial proportion of the area, weighed 2.4–10 g. More importantly, most of the smaller leaves and partially decayed leaves and leaf fragments were quite firmly attached to the underlying soil surface. Additionally, most leaves formed a partially interlocking network of more than one leaf thick that was also held in place by long pieces of decaying twig. Consequently, we estimate that the weight range of 0.1–1.0 g is likely to be an underestimation of the force required to displace the smaller leaves and partially decomposed leaf fragments.

Across all 19 species there was a significant relationship between both log(shoot length) and log(embryo + endosperm mass) ($r^2 = 0.764$, $df = 17$, $P < 0.001$) and log(root length) and log(embryo + endosperm mass) ($r^2 = 0.884$, $df = 17$, $P < 0.001$) for seedlings grown in the dark (Fig. 2a). For shoot length, the slope of the relationship was significantly less than the expected slope of 1/3 (RMA slope = 0.28, t test $t = 2.19$, $P < 0.05$), while the slope of the relationship with root length was significantly greater than expected (RMA slope = 0.52, t test $t = 4.36$, $P < 0.001$). These deviations in slope from the expected relationship are reflected in the ratio of root length:shoot length (Fig. 2b), with the ratio increasing significantly with increasing seed mass ($r^2 = 0.70$, $df = 17$, $P < 0.001$): the small-seeded species produced seedlings with proportionately shorter roots than their larger seeded counterparts studied here.

For each of the five species that were tested, root growth rates (R_{GER}) measured in soil were not significantly different to those measured on agar (Fig. 3; t test t values < 2.1, $df = 18$, $P > 0.05$). We have therefore assumed that the results from the agar technique are representative of root growth rate in loose, moist forest soil for all of the species studied. Although there was an overall tendency for R_{GER} to follow the allometric relationship given by Eq. 2, there are two contrasting trends apparent in Fig. 4. For the nine smallest seeds, although there was a significant relationship between log(R_{GER}) and log(embryo mass) ($r^2 = 0.67$, $df = 7$, $P < 0.01$), the slope of this relationship was significantly greater than $m^{(1/3)}$ (RMA slope = 1.11, t test, $t = 3.25$, $P < 0.02$). There was also a significant relationship for the ten largest seeded species ($r^2 = 0.55$, $df = 8$, $P < 0.05$), although the slope of this line did not differ significantly from the expected relationship (RMA slope = 0.31, t test $t = 1.10$, $P > 0.05$).

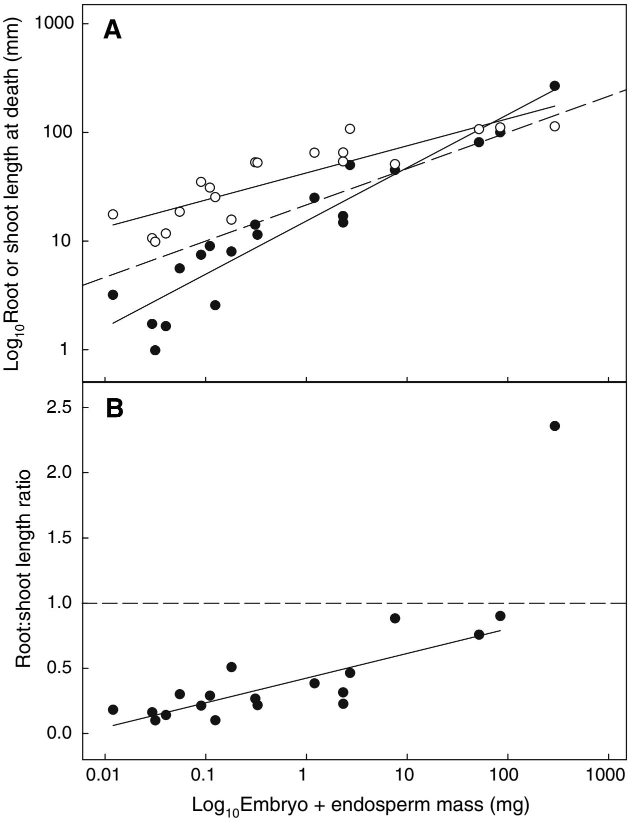

Fig. 2 The relationship between: **a** embryo + endosperm mass and root (*closed symbols*) and shoot (*open symbols*) length at death, and **b** the ratio of root:shoot length. The *dashed line* on **a** represents the expected allometric ratio:shoot or root length α (mass of seed or embryo + endosperm)$^{1/3}$ while the *horizontal line* on **b** refers to a root:shoot length ratio of 1

Figure 5 shows the progress of the soil drying front during rain-free periods under a range of conditions. In the top 5 mm especially, capillary recharge overnight partially rewets the profile. However, these rewetting excursions have been omitted from Fig. 5 for clarity because we have assumed that seedlings with roots that have been overtaken by the drying front during the period of maximum evapotranspirative demand will be killed. In all scenarios, with the exception of the small gap in the wet-season, soil drying in the top 6 mm of soil progressed rapidly, with the matric potential reaching the permanent wilting point (–1.5 MPa) within 2–10 days, although drying occurred most rapidly in the large gap and dry-season scenarios (Fig. 5).

Discussion

For the gap-dependent tree species studied, there were allometric relationships between root and shoot diameter

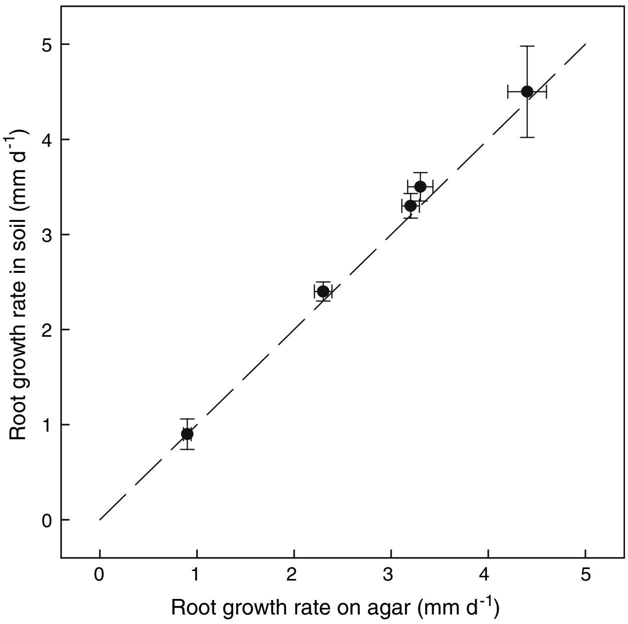

Fig. 3 The relationship between root growth extension rate in soil and on agar. The *dashed line* represents the expected 1:1 correspondence. *Error bars* are ±1 SE of the mean

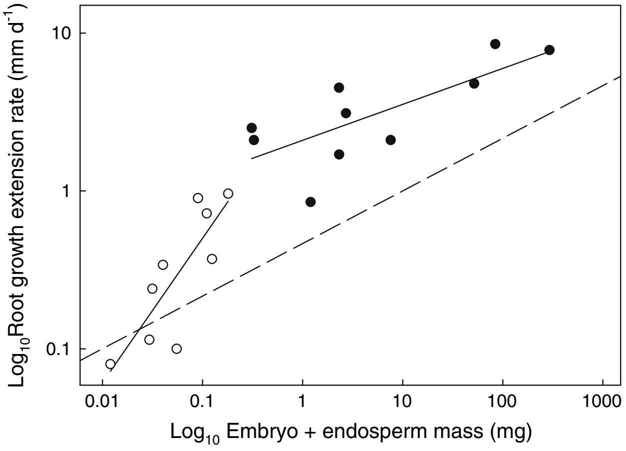

Fig. 4 The relationship between embryo + endosperm mass and root growth extension rate (R_{GER}) on agar for nine species of photoblastic (*open symbols*) and ten species of non-photoblastic (*closed symbols*) gap-dependent neotropical trees. The *dashed line* represents the expected allometric ratio: $R_{\mathrm{GER}} \propto$ (mass of embryo + endosperm)$^{1/3}$

and seed embryo and endosperm mass, as well as R_{GER}, maximum root and shoot length at death and embryo and endosperm mass. For the small-seeded species (photoblastic), these relationships suggest that a minimum threshold for root and shoot diameter and, consequently, extremely low root growth rates and the inability to emerge from anything but superficial soil may impact negatively on seedling emergence and survival.

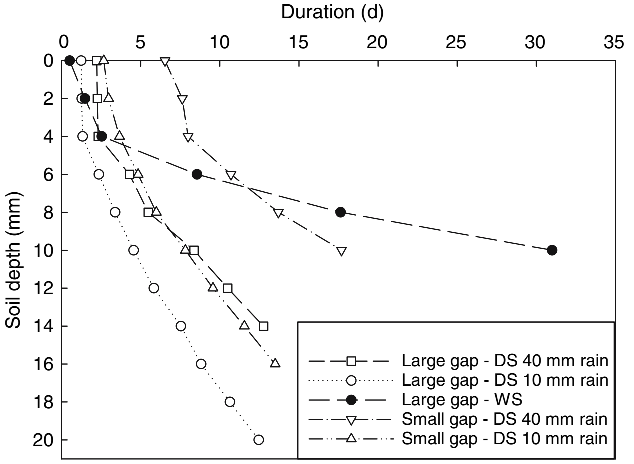

Fig. 5 The time predicted by the soil, water, energy and transpiration (*SWEAT*) model at which the soil drying front [when the soil first reaches the wilting point (a matric potential of –1.5 MPa)] reaches different depths beneath a bare soil in a large or small gap during the dry-season (*DS*) after a single rainfall of 10 or 40 mm in a semideciduous tropical forest on Barro Colorado Island, Panama. Also presented is the time taken for the soil matric potential to reach the wilting point in a large gap during the wet-season (*WS*), assuming the soil profile is initially fully hydrated (–0.01 MPa). The small gap scenario in the wet-season is excluded since the soil matric potential failed to reach the wilting point over the 35 days of the model run

Can emerging shoots displace leaf litter?

We estimated that small seeds would be unable to generate sufficient shoot thrust to displace leaf litter on the forest floor of Barro Colorado Island, Panama. This conclusion is supported by evidence that litter greatly reduces seedling emergence at the same site although for small-seeded species the production of large numbers of seeds may increase the probability of emergence in the few suitable germination micro-sites (e.g. litter gaps). In various experiments, cumulative seedling emergence was observed to nearly treble when litter was removed weekly (Dalling and Hubbell 2002; Daws et al. 2005); however, since even then less than 7% of germinable seeds emerged, more frequent removal might have had an even greater effect (Dalling and Hubbell 2002). However, such experiments may combine at least four physical effects: (1) seeds that land on litter cannot imbibe sufficiently to germinate, (2) for small seeds on the surface of litter that can germinate, root penetration through the litter is likely to be a problem, (3) for small seeds buried beneath litter that can germinate, shoot penetration through the litter is likely to be a problem and (4) litter cover prevents the germination of photoblastic seeds.

Since the soil is frequently covered nearly or completely with litter (Daws et al. 2005), the first two effects (1 and 2) might be considered to be the most serious for newly dispersed seeds. However, the high frequency of raindrop impact, which can move soil particles weighing up to approximately 40 mg (corresponding to 3 mm; Morgan 1995), will regularly move seeds about until they lodge, most likely in a patch of bare soil. Since median raindrop size in tropical rainfall is 2.3 mm (Hudson 1971), small seeds may be impacted about 6.5 times in a 40-mm rainfall. Using photography before and after a single 40-mm rainfall, we have observed that most small seeds and small pieces of litter were moved, the seeds tending to become embedded in bare soil patches or moved sideways to become occluded under litter ©. Mullins, unpublished data). Thus, for seeds less than approximately 40 mg (all but three of our study species), the presence of litter before dispersal probably does not greatly reduce emergence due to effects (1) and (2). However, subsequent displacement beneath existing litter means that the longer the time to germination, the greater the relative importance of (3) and (4) will become.

The measured shoot thrusts of 2.26 and 3.91 g for *C. insignis* and *T. micrantha*, which were the largest of the photoblastic and one of the smallest of the non-photoblastic species, respectively, were probably sufficient to displace most litter (mass of the heaviest 10% of leaves 2.4–10 g). Photoblastic behaviour may have several functions, including ensuring germination does not occur when seeds are buried too deeply or when shaded by other seedlings or taller plants (Pearson et al. 2002, 2003a). Our data provide support for the complementary hypothesis that photoblastic behaviour only occurs in species with insufficient shoot thrust to displace most overlying leaves. The clear distinction in both shoot diameter and seed mass between species that are and are not photoblastic gives further support to our hypothesis. No species with a shoot diameter >0.40 mm was photoblastic, and none of the remaining species had a shoot diameter <0.56 mm. Similarly, the largest seed mass of the photoblastic species was 0.74 mg, while the smallest of the remaining species was 1.51 mg (Table 1). In West Africa, Kyereh et al. (1999) also found that of 19 species of tropical forest trees, only the three species with a seed mass <3 mg were photoblastic.

The large variation of shoot thrust with shoot diameter probably provides the main explanation for the sharpness of the divide between photoblastic and non-photoblastic species. The shoots that we measured failed by buckling well before they could exert the theoretical maximum thrust due to cell turgor pressure shown in Fig.1. The Euler buckling load of a cylindrical column is proportional to Er^4/l^2 (Gordon 1978), whereas shoot thrust is proportional only to r^2 (where E is the shoot's Young's modulus or stiffness, r its radius and l the unsupported shoot length). Thus, starting with small shoots that fail by buckling, as shoot diameter increases we expect thrust to increase in proportion to r^4 until it matches the maximum thrust due to turgor – if other factors remain constant. This means that shoots with diameters of between roughly two- and threefold or more than the diameter of *C. insignis* and *T. micrantha* (0.28 and 0.72 mm, respectively) should be able to exert their maximum thrust due to turgor, corresponding to diameters of between about 0.5 and 2.4 mm and above. The contrast between *C. insignis* and *T. micrantha* must be due to differences in shoot stiffness as well as diameter. Additionally, because the maximum buckling load depends on the unsupported shoot length (i.e. between the seed and any overlying leaf if the surrounding soil does not limit bucking) and also on whether either end of the shoot is rigidly fixed, free to swivel, or free to move sideways (Gordon 1978), the boundary between shoots that buckle before they can reach their maximum thrust and those that do not will not only be dependent on shoot diameter. Nevertheless, shoot diameter and stiffness are the only seed-specific factors controlling shoot thrust, with diameter being the dominant factor. In addition, this study highlights the need for further comparisons of shoot thrust across species.

There was also a general relationship between the maximum root and shoot length of seedlings grown in the dark and embryo and endosperm mass (Fig. 2a). However, neither relationship had the expected slope of 1/3. Part of the explanation for the deviations in slope is that both shoots and roots of the smallest seeds had disproportionately large diameters (Fig. 1). There is also a clear indication that smaller seeds devoted more of their resources into producing shoot rather than root length (Fig. 2b; the root:shoot length ratio varied from 0.1 to 0.3 for the 14 smaller seeded species), while the largest seeds did the reverse (0.8–2.4). Thus, the implication is that shoot length is a survival priority for small seeds in order to emerge from the maximum possible soil depth from beneath litter and establish photosynthesis. In contrast, root length becomes relatively more important for the larger seeds because maximum shoot length ceases to be a serious constraint to emergence. It is likely that the benefit gained from deeper rooting continues to provide an advantage in terms of greater dry-season survival (Poorter and Hayashida-Oliver 2000).

Does root growth rate constrain seedling establishment?

Our simulations suggest that drying proceeds faster down the profile after rainfall in the dry- than in the wet-season (Fig. 5). This is mainly because in the dry-season, the soil is much drier at depth so that the zone wetted by rainfall dries both by evapotranspiration and downward movement, whereas during the wet-season capillary recharge slows the rate of surface drying. Engelbrecht et al. (2006) observed the drying of bare soil in large gaps during the middle of the wet-season on the Barro Colorado Nature Monument adjacent to BCI. After only 4 days of rainfall exclusion by a plastic roof, the matric potential of soil from a depth of 5–10 mm had fallen to –4.5 MPa. This is an even faster rate of drying than that indicated by Fig. 5, which is to be expected since the soil did not start as wet as field capacity and because we ignored root water extraction. However, the important point is that both the experimental observations and our modelling indicate that bare soil in a large gap can experience sufficient drying to kill shallow rooted seedlings. This was confirmed by Engelbrecht et al. (2006) who observed up to 20% mortality of 3.5-month-old seedlings of pioneer species after 4 days of rainfall exclusion, rising to up to 40% after 11 days, in comparison to a control treatment.

Soil drying is not always faster in the centre of large gaps than in the understorey, presumably because there may be no tree roots that reach that far (Veenendaal et al. 1996). Since our simulations ignore any soil drying caused by the roots of surrounding trees, the curves for the large gap are likely to be realistic, while the curves for small gaps may underestimate the rate of soil drying and can only be considered as a lower limit to the actual rate of soil drying. In addition, the results are specific to a particular soil and do not take account of the reduction in drying rate that can be caused by a litter layer (Marshall et al. 1996). Nevertheless, we can expect that actual soil drying in gaps and its effect on seedlings will be characterized by the following features on a wide range of soil types:

1. Gaps that receive direct sunlight on the ground will dry more quickly than small gaps that receive no direct sunlight on the ground other than occasional sun flecks.
2. Soil that has already dried during the dry-season will dry faster after rainfall than in a dry spell in the wet-season. Therefore, the germination of small seeds and those buried to only shallow depths after rainfall in the dry-season is very likely to result in seedling death.
3. Dry spells in gaps that receive direct sunlight during the wet-season can kill shallow rooted seedlings, especially if they have a low R_{GER}.

Among other factors, differential responses to light, disturbance and natural enemies may impact on seedling establishment (Harms et al. 2000; Dalling and Burslem 2005; Poorter 2005). Our R_{GER} data (Fig. 4) suggest that in conjunction with shallow emergence depths, a low R_{GER} is a further constraint to establishment, particularly for small-seeded species. Not only was there an allometric relationship between R_{GER} and embryo and endosperm mass, such that larger seeds have a faster R_{GER}, but for the smallest seeded (and photoblastic) species the slope of this relationship was >0.333; the smallest seeded species had proportionately slower R_{GER} than expected, which will further exacerbate this constraint. We suggest that the greater than predicted increase in R_{GER} with embryo and endosperm mass for the photoblastic species (Fig. 4) is a consequence of the correspondingly slower than expected increase in root diameter with embryo and endosperm mass (Fig. 1b). This relationship, as well as the similar relationship for shoot diameter, suggests that there is a biophysical limit to the minimum diameter of roots and shoots which may be an important factor that sets a lower limit to seed size. A lower limit to shoot diameter and hence seed size has been proposed before on theoretical grounds (Raven 1999). However, this appears to be the first experimental demonstration of a possible minimum limit on root and shoot diameter. Consequently, our R_{GER} data suggest that in the event of dry periods, particularly in large gaps, small-seeded species are likely to be killed because the elongating radicle is overtaken by the soil drying front. Thus, except in prolonged wet periods, small-seeded species may be limited to successful emergence only in small gaps (Daws 2002). In further support of this proposition, on BCI the small-seeded pioneer species *Miconia argentea* is most frequently found in small gaps, while the larger seeded species *T. micrantha* is found most frequently in large gaps (Brokaw 1987). Experiments have confirmed that their contrasting germination and emergence responses to gap size contribute to the observed gap size partitioning (Pearson et al. 2003b).

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