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Comparative ecology of seed mass in *Psychotria* (Rubiaceae): within- and between-species effects of seed mass on early performance

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Summary

1. Experimental field data and interspecific comparative analyses were used to detect effects of seed mass on seedling performance within and among seven species of *Psychotria* sown in gaps and shaded rainforest sites. In addition we compared the effects of seed mass within and among species to detect concordance between the two ecological scales. We used two comparative methods: phylogenetically independent contrasts and cross-species correlations.

2. Among species, we detected weak evidence of a positive correlation between seed mass and the probability of emergence in the shaded forest, and no effects of seed mass in gaps.

3. Among species, no significant correlations between seed mass and either seedling survival or seedling recruitment were found in any habitat. Other variables specific to each subgenus appear to be more important than seed mass in determining survival in the shaded forest.

4. There was a negative correlation between seed mass and relative growth rate (RGR) in both habitats. In gaps, small-seeded taxa exhibited particularly high RGR, compensating for the initial advantages of higher seed mass.

5. All species studied exhibited recruitment in gaps equal to or higher than that in the shaded forest. However, recruitment success in shaded forest relative to gaps increased with seed mass, indicating a higher affinity for shaded forest among larger-seeded taxa, but this relationship was only detected using PICS analysis.

6. Correlations between seed mass and seedling mass are similar within and among species, indicating a simple principle of mass transference. In contrast, correlations between seed mass and seedling emergence, seedling survival, seedling recruitment and RGR depend on the scale at which they are observed.

Key-words: neotropical forest, phylogenetic independent contrasts, seedling emergence, seedling growth, seedling recruitment, seedling survival

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Introduction

Numerous interspecific studies have found that seed mass (or seed size) commonly plays an important role during seedling recruitment. For example, large-seeded taxa contain a relatively high proportion of uncommitted maternal reserves, presumably contributing to a positive carbon balance under shaded conditions, and they develop into initially larger seedlings than small-seeded

taxa (Green & Juniper 2004a). In turn, seedlings derived from larger-seeded taxa exhibit a higher probability of survival in deep shade (Leishman & Westoby 1995; Osunkoya 1996; Saverimuttu & Westoby 1996; Reich *et al.* 1998; but see Metcalfe & Grubb 1997); higher tolerance to defoliation (Armstrong & Westoby 1993; Green & Juniper 2004b); and lower relative growth rate (RGR) (Marañón & Grubb 1993; Kitajima 1994; Reich *et al.* 1998) than those derived from smaller-seeded taxa.

Other hypotheses for the role of seed mass are not as well studied or validated. For example, large-seeded

taxa often (but not always) produce seedlings with higher probabilities of emergence from beneath the litter layer (Yanful & Maun 1996; but see Molofsky & Augspurger 1992; Eriksson 1995); large-seeded species often have a higher risk of predation (Schupp 1988; Reader 1993; but see Jansen 2003); and large-seeded species may develop into seedlings with higher tolerance to dry spells (Leishman *et al.* 2000). There is, in turn, evidence for an overall positive net effect of seed mass on the probability of seedling recruitment (Seiwa & Kikuzawa 1996; Jakobsson & Eriksson 2000; Moles & Westoby 2002, 2004).

The effects of seed mass observed among species are also often observed within species. Depending on ecological conditions, increased seed mass has been found to be associated with initial seedling biomass, higher probabilities of seedling emergence and survivorship, lower RGR, and a higher risk of seed predation (Gross 1984; Marshall 1986 in herbs; Howe, Schupp & Wesley 1985; Moegenburg 1996; Green 1999; Paz, Mazer & Martínez-Ramos 1999; Paz & Martínez-Ramos 2003 in trees; but see Jansen 2003).

In sum, despite their lower RGR and possible higher risk of seed predation, large seeds and large-seeded taxa appear to exhibit many advantages over their smaller-seeded counterparts, particularly in shaded habitats. The ubiquity of these relationships suggests that there may be intrinsic effects (or correlates) of seed mass on growth and survival that operate consistently across several orders of magnitude in seed mass variation (but see Green & Juniper 2004a). If this is the case, given sufficient variation in seed mass within species, then we predict concordance between the effects of seed mass on performance observed within and among species.

A rigorous test of this prediction would consist of inter- and intraspecific studies of closely related, sympatric species with contrasting seed masses. The rationale behind this approach is that: (i) seed mass variation within a species is part of a wider range of seed sizes found across a group of closely related species; (ii) ecological factors operating on seeds and seedlings are potentially similar across the range of seed mass variation; and (iii) seed mass effects must be explored in species experiencing the same environmental conditions. To assess the predicted concordance, we need the integration of demographic and comparative analysis. Moreover, such observations should be made in the field, providing the opportunity for extrinsic factors that influence successful seedling emergence and performance (such as leaf litter, seed predators or light availability) to exert their natural effects. Ideally, such studies would be conducted across the range of ecological conditions in which the focal species occur. To date, no such study has been performed, although two studies on temperate herbs represent steps in this direction (Gross 1984; Marshall 1986).

In the study reported here, we evaluate the effects of seed mass on seedling performance among seven sym-

patric rainforest species of *Psychotria* experimentally sown in natural forest habitats (gaps and shaded forest).

First, we test the following interspecific hypotheses proposed in the literature by estimating correlations among species means (an 'ahistorical' approach) and among phylogenetically independent contrasts: (i) larger-seeded species develop into larger seedlings with lower RGR than smaller-seeded species; (ii) large-seeded species have a higher probability of emergence, survival and recruitment than small-seeded species, particularly under shaded conditions; (iii) initial advantages to seedlings of large-seeded taxa will diminish over time, especially in light gaps where the higher RGR of small-seeded taxa may compensate for the early advantages enjoyed by large-seeded taxa.

Second, we assess concordance between the intra- and interspecific seed mass effects on seedling performance, by comparing the interspecific effects of seed mass analysed here with those observed within the same species (Paz, Mazer & Martínez-Ramos 1999; Paz & Martínez-Ramos 2003). Both the inter- and intraspecific data were derived from a single field experiment (Paz, Mazer & Martínez-Ramos 1999; Paz & Martínez-Ramos 2003). Relative to previous work, this approach has the advantage that we simultaneously observed the consequences of seed mass variation within and among species in a phylogenetically 'controlled' context, and across the range of environments in which they naturally recruit.

Materials and methods

STUDY SITE AND SPECIES

The experimental work was performed at Los Tuxtlas Biological Station, Veracruz, Mexico, from December 1992 to October 1994. Seven sympatric woody species of *Psychotria* (Rubiaceae) were selected for study: *P. limonensis* K. Krause, *P. graciliflora* Benth, *P. chagrensis* Standley, *P. papantlensis* (Oersted) Hemsley, *P. flava* Oersted formerly Standley, *P. faxlucens* Lorence and Dwyer, and *P. simiarum* Standley. This group was selected for three reasons. First, these congeners represent a wide range of fresh seed mass variation mean individual seed mass ranges from 0.007 g (*P. limonensis*) to 0.381 g (*P. faxlucens*). Second, the group includes species that recruit under different conditions, ranging from gaps to deeply shaded sites. Third, despite these ecological differences the species' fruits, seeds and seedlings are morphologically and phenologically similar, and dispersal agents are shared by all species. A detailed description of these species, including mean values of seedling performance variables per habitat, is given by Paz *et al.* (1999); Paz & Martínez-Ramos (2003).

EXPERIMENTAL SYSTEM

From each species, between November 1992 and January 1993 fruits were collected in the field from

≥20 maternal plants during peak fruiting to give a sample size of 1680 seeds per species. Additional details of seed collection are given by Paz *et al.* (1999).

To evaluate the effects of seed mass and habitat type on seedling performance in each species, seed fates were monitored for 1 year post-emergence. According to the natural time of seed dispersal of each species (from November 1992 to January 1993), seeds were placed in six 20 × 20 m experimental plots, of which three were located in closed canopy forest (hereafter named shaded forest sites), and three were located in 1-year-old tree-fall gaps ≈400 m² in area. Plots were arranged in three pairs, each occupying a gap and a shaded forest site on topographically level zones of the same hillside.

A total of 280 seeds per species were randomly assigned to each plot (see details of experimental design in Paz *et al.* 1999). Across all plots, a total of 11 760 seeds were sown (seven species × six plots × 280 seeds per plot). In order to follow the fate of every seed and seedling while avoiding any physical movements of seeds by abiotic agents, each seed was placed on top of the soil within a 3 cm diameter × 2 cm tall metallic mesh cylinder separated from other such cylinders by 15–20 cm. To avoid potential contamination from *Psychotria* seeds in the seed bank, the 5 cm soil column contained beneath each cylinder was replaced with homogenized soil from a forest site with no *Psychotria* trees nearby (see Paz *et al.* 1999). The transition from seed to seedling and seedling survival were recorded every 4 days during the germination period of each species, and subsequently every 16 days for 2 months, followed by census periods of 56–62 days until 1 year after the first seedling emerged; by this time all seeds had germinated, died or disappeared. The number of surviving seedlings per species per plot 1 year after 50% of emergence varied between 72 and 167 (out of 280), for a total of 7357 seedlings. Each surviving seedling was harvested (including roots and stems), dried for 72 h at 70 °C, and weighed to 0.0001 g. Six variables were obtained for each species–plot combination: (i) probability of seedling emergence (proportion of emerged seedlings from sown seeds); (ii) time to emergence (time to reach 50% of seedlings emerged); (iii) probability of seedling survival (proportion of emerged seedlings that survived until 1 year old); (iv) mean total individual biomass (mean biomass of all emerged seedlings in the plot); (v) mean RGR (log[final seedling dry biomass/seed dry mass without seed coat]); and (vi) probability of recruitment (joint probability of seedling emergence and seedling survival to 1 year). In addition, an index of affinity to forest habitat was calculated as the ratio of the probability of recruitment in shaded forest to the probability of recruitment in gaps. This index was obtained for each pair of gap and shaded forest plots, and a mean value per habitat was then calculated for each species and used as a data point for analysis.

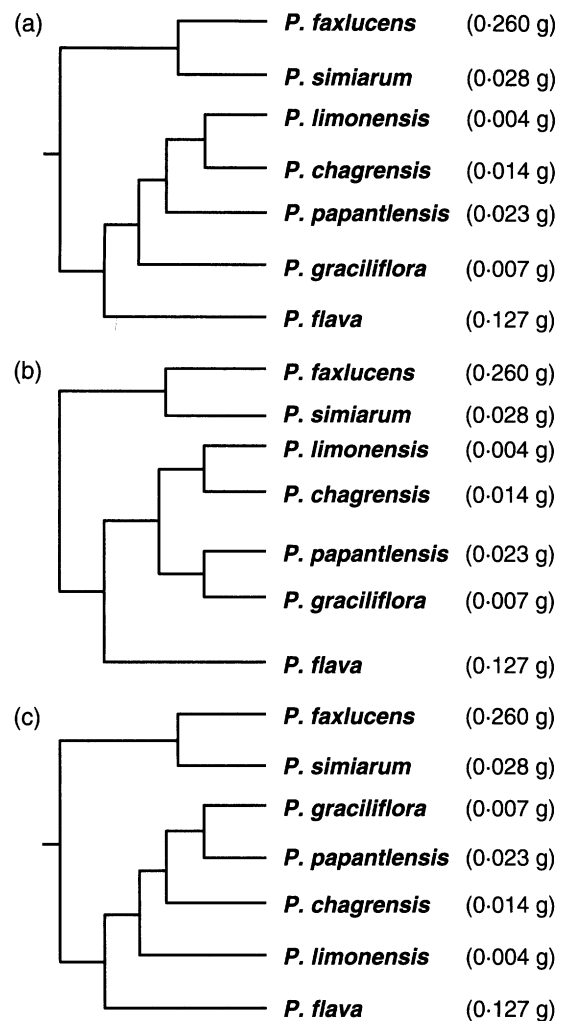


Fig. 1. Phylogenetic relationships among seven species of *Psychotria* co-occurring at Los Tuxtlas Tropical Station, Mexico. Patterns of relatedness were obtained by applying an algorithm of maximum parsimony (PAUP ver. 4.0) on morphological traits. Branch lengths do not reflect phylogenetic distances. These phylogenies were used to test hypotheses concerning the ecological function of seed mass. Species mean seed mass without seed coat (g) in brackets.

PHYLOGENY RECONSTRUCTION

Phylogenetic relationships among the species studied were reconstructed using measures of 41 morphological traits unrelated to seed size (Lorence & Dwyer 1987; Hamilton 1989a, 1989b; H.P., unpublished data). The traits used were reported to be taxonomically informative in extensive taxonomic treatments of the Neotropical species of *Psychotria* (Hamilton 1989a,b). Cladograms were constructed using maximum parsimony (1998), implemented in PAUP ver. 4.0 (Swofford 1998), assuming equal weight of all traits, and rooted using the 'middle rooting procedure' (details of phylogeny reconstruction will be published elsewhere). Three topologies of maximum parsimony were derived. All three topologies were used in the statistical tests to detect the functional relationships considered here (Fig. 1).

STATISTICAL ANALYSES

Two comparative methods were used to assess the functional relationships among species between seed mass and seedling performance traits within each habitat: ahistorical analysis (TIPS); and phylogenetically independent contrasts (PICS), *sensu* Felsenstein (1985). TIPS considers each species to represent an independent data point; this approach tests for correlations between variables by using standard methods of regression or correlation. The assumption that species represent independent data points is appropriate if the target traits may be considered to evolve readily in response to natural selection, independently of the rate or direction of evolution in closely related taxa. In any case, TIPS analyses test the hypothesis that independent variable(s) (here, mean seed mass) reliably predict mean values of the dependent variable. The PICS method estimates correlated evolutionary change between variables while controlling statistically for potential non-independence of species due to their common ancestry (Felsenstein 1985). Standardized PICS are constructed for each trait as the phenotypic difference between sister taxa in the trait of interest divided by the total branch length between the taxa. This model also assumes that traits have evolved under Brownian dynamics (Felsenstein 1985). Here, we used TIPS and PICS analyses as complementary approaches to test the hypothesis that increases in seed mass are associated with increases or decreases in seedling performance traits.

Values of standardized contrasts are sensitive to error in the estimation of branch lengths in the phylogenetic tree (Diaz-Uriarte & Garland 1998). Due to the absence of information concerning the branch lengths in the phylogenetic trees estimated for our focal *Psychotria* species, we assumed equal branch lengths (a punctuational mode of evolution) to obtain acceptable statistical performance when conducting correlations based on PICS (Purvis, Gittleman & Luh 1994). Values of seed mass were log-transformed to ensure the expected variance was independent of the seed mass values compared at each contrast. Standardized independent contrasts were obtained for all traits using CAIC ver. 2.0 (Purvis & Rambaut 1995).

For the TIPS analysis, the mean value of performance in each site (gap or shaded forest) was considered as a data point. To test for correlations between seed mass and seedling performance traits, and to determine whether the correlations differed between habitats (detected as a significant seed mass \times habitat interaction), one regression was conducted per habitat of each performance trait on species mean seed mass. The regression analysis was followed by *t*-tests (assuming heterogeneous variances) to detect slopes significantly different from zero. This approach was preferred over ANCOVA because, for most traits, the within-habitat variance differed between habitats even after several transformations. For the probability of emergence, survival, RGR, recruitment, and the index of affinity

to forest habitat, we tested for significant seed mass effects by using one-tailed *t*-tests, because the expected direction of the qualitative effects of seed mass on performance have been widely accepted. For biomass and time to emergence, we tested the regression slopes against zero using two-tailed *t*-tests because the expected direction of the effects of seed mass on these traits is less clear.

PICS were estimated per trait and habitat combination for each of three alternative phylogenies. PICS of seed mass were always constructed to be positive by subtracting the seed mass of the smaller-seeded taxon from the larger-seeded one; the contrasts of the performance traits were then free to be positive or negative, depending on the phenotypes of the two sister taxa. PICS of performance variables were calculated based on a single value per species per habitat, derived by averaging the values obtained from the three gap sites and the values obtained from the three shaded forest sites. Correlations between seed mass and seedling traits using PICS were explored for each habitat as described above, but the regressions were forced through the origin (Felsenstein 1985). To test for correlations between seed mass and the other traits we assessed variation due to alternative phylogenies, as proposed by Martins (1996). Given *N* alternative phylogenies, this approach consists of estimating a compound variance to test for the significance of the regression coefficient. This compound variance is estimated as the sum of the variance of the empirical distribution of *N* regression coefficients among the alternative phylogenies (Var_p) and the mean residual variance of the three regressions performed (one per phylogeny) (Var_s). In the present study we applied this method to each performance trait considering the three alternative phylogenies.

The parametric requirements of all the regressions performed were evaluated by correlations between residual and predicted values, and by visual inspection. In no case were non-random distributions observed.

Time to emergence could indirectly affect the relationship between seed mass and seedling performance traits if, for example, large-seeded taxa emerged relatively early and experienced a longer period of seedling growth. However, we observed no evidence of a correlation between seed mass and time of seedling emergence among species in either habitat type ($P > 0.703$, $P > 0.641$ for gaps and shaded forest, respectively). Therefore any effects of seed mass on subsequent performance observed here were independent of variation in the time to emergence.

To evaluate whether there is concordance within and among species, for each pair of dependent and independent variables observed in a given habitat, we defined a 'general' effect of seed mass on performance within species as one where a statistically significant (and consistently positive or negative) regression coefficient was observed in five or more of the seven species

(as reported by Paz *et al.* 1999; Paz & Martínez-Ramos 2003). This criterion was used instead of a sign test, which would have been highly restrictive due to the small number of species available for study. For each dependent variable, when we observed such a general effect of seed mass on performance within species and a qualitatively similar and statistically significant relationship among species, we considered the two levels of analysis to be concordant. The two levels of analysis were also defined as concordant when there was no general effect of seed mass on performance detected within species (fewer than five of the species exhibited a significant regression between seed mass and the focal trait), and when the interspecific relationship was not significant. When no general effect was observed within species while a significant effect of seed mass on performance was observed among species (or *vice versa*), we considered the analyses to be discordant.

Results

INTERSPECIFIC CORRELATIONS BETWEEN SEED MASS AND SEEDLING PERFORMANCE TRAITS

Seedling emergence

Large-seeded species had a higher probability of emergence than small-seeded species in the shaded forest, but this effect was detected only when using TIPS. In gaps, seedling emergence was neutral to seed mass when using both TIPS and PICS (Fig. 2a,g; Table 1).

Seedling growth

Large-seeded species grew into larger seedlings than did small-seeded species. According to TIPS, 1 year after sowing, initial seed mass was positively correlated with

Table 1. Interspecific effects of seed mass on seedling performance in gaps and shaded forest sites. Regressions per habitat are shown using TIPS and PICS (three phylogenies)

Dependent variable	Phylogeny	Gap				Shaded forest			
		Slope	SE	<i>T</i>	<i>P</i>	Slope	SE	<i>T</i>	<i>P</i>
Probability of emergence	None	0.039	0.034	1.14	0.270 ^{II}	0.108	0.042	2.61	0.017^{II}
	Ph1	0.030	0.067			0.107	0.056		
	Ph2	0.034	0.060			0.099	0.058		
	Ph3	0.037	0.064			0.122	0.049		
	All	0.034	0.064	0.53	0.623 ^{II}	0.109	0.054	2.02	0.098 ^{II}
Biomass	None	0.369	0.154	2.40	0.028^{II}	0.651	0.066	9.82	0.001^{II}
	Ph1	0.282	0.378			0.638	0.133		
	Ph2	0.338	0.343			0.667	0.114		
	Ph3	0.286	0.352			0.630	0.127		
	All	0.302	0.359	0.84	0.557 ^{II}	0.645	0.126	5.10	0.005^{II}
Relative growth rate	None	-0.649	0.122	5.28	0.001^I	-0.331	0.058	5.74	0.001^I
	Ph1	-0.684	0.293			-0.334	0.073		
	Ph2	-0.634	0.265			-0.309	0.072		
	Ph3	-0.692	0.273			-0.352	0.072		
	All	-0.670	0.279	2.40	0.031^I	-0.332	0.075	4.39	0.004^I
Probability of survival	None	-0.042	0.057	0.75	0.241 ^I	0.044	0.091	0.48	0.318 ^I
	Ph1	0.041	0.106			0.234	0.156		
	Ph2	0.029	0.109			0.227	0.150		
	Ph3	0.056	0.084			0.244	0.138		
	All	0.042	0.101	0.42	0.348 ^I	0.235	0.148	1.58	0.087 ^I
Probability of recruitment	None	-0.001	0.044	0.02	0.986 ^{II}	0.063	0.072	0.89	0.387 ^{II}
	Ph1	0.044	0.095			0.208	0.117		
	Ph2	0.040	0.091			0.196	0.123		
	Ph3	0.057	0.083			0.216	0.110		
	All	0.047	0.090	0.53	0.627 ^{II}	0.207	0.117	1.76	0.137 ^{II}
Shade forest : gap recruitment ratio	None	0.141	0.087	1.62	0.070 ^I				
	Ph1	0.307	0.112						
	Ph2	0.318	0.111						
	Ph3	0.321	0.099						
	All	0.315	0.107	2.93	0.016^I				

'None' indicates regressions using TIPS. Ph1–Ph3 indicate regressions using PICS based on phylogenies 1, 2, 3. Tests based on TIPS were performed taking an experimental error from three replicates. Tests based on PICS were performed taking a compound error due to the three alternative phylogenies (see Materials and methods). Cases of significant correlations ($P < 0.05$) according to *a priori* hypotheses are indicated in bold type.

^{II}, two-tailed *t*-tests; ^I, one-tailed *t*-tests (see Materials and methods). All *t*-tests based on TIPS assumed $df = 18$; all *t*-tests based on PICS assumed $df = 5$.

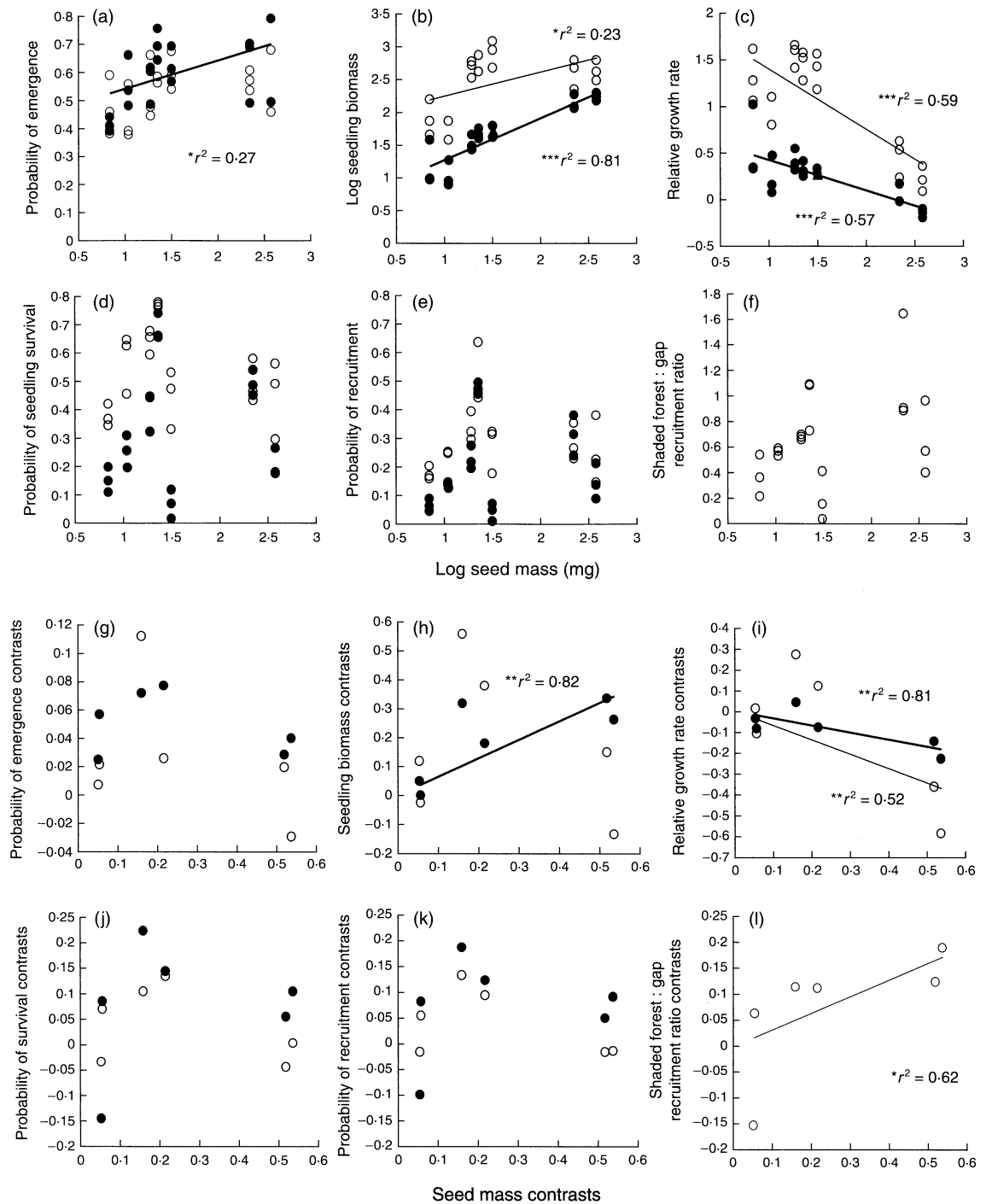


Fig. 2. Interspecific bivariate correlations between seedling performance traits and seed mass in gaps (thin line, ○) and shaded forest (thick line, ●) sites. (a–f) Correlations using each species monitored in each gap or shaded forest site as a data point (TIPS analysis). (g–l) Correlations using phylogenetically independent contrasts as data points (PICS analysis). PICS shown were calculated based on phylogeny # 2 represented in Fig. 1. *, Significant correlations ($P < 0.05$) according to the pre-established hypotheses (one- or two-tailed t -tests; see Introduction).

seedling biomass in both habitats (Fig. 2b,h; Table 1). The relationship detected by TIPS was similar between habitats (slope = $0.37 < 0.65$, $t_{36} = 1.76$, $P < 0.084$ for gaps and shaded forest), although somewhat tighter in the shaded forest ($r^2 = 0.23$ vs 0.80 in gaps vs shaded forest, respectively). PICS analyses detected such a positive correlation between seedling mass and seed mass only in the shaded forest (Fig. 2b,h; Table 1).

Thus, overall, both TIPS and PICS analyses detected a stronger effect of seed mass on seedling biomass (after 1 year) in the shaded forest compared with gaps.

RGR was negatively correlated with seed mass in both habitats according to both TIPS and PICS (Fig. 2c,i; Table 1). This relationship was steeper in the gaps (TIPS-derived slope = -0.49 vs -0.33 for gap vs shaded forest, respectively; one-tailed $t_{36} = 2.34$, $P < 0.024$;

PICS-derived slope = -0.67 vs -0.33 for gap vs shaded forest, respectively; one-tailed $t_{10} = 1.89$, $P < 0.043$). Thus 1 year after emergence the particularly high RGR of smaller-seeded species in gaps compensated for their lower seed mass more than in the shaded forest.

SEEDLING SURVIVORSHIP, PROBABILITY OF RECRUITMENT AND AFFINITY TO FOREST HABITAT

No statistically significant effect of seed mass on 1-year seedling survivorship or seedling recruitment was detected in any analysis performed (Fig. 2d,j,e,k; Table 1). However, seedling recruitment of large-seeded species appeared to be less sensitive to the shaded forest condition than recruitment of small-seeded species. A positive correlation between the ratio of recruitment in shaded forest to recruitment in gaps (the index of affinity to forest habitat) and seed mass was detected using PICS but not TIPS (Fig. 2f,l; Table 1).

CONCORDANCE OF SEED MASS EFFECTS BETWEEN INTRA- AND INTERSPECIFIC LEVELS

Figure 3 illustrates the correlates of seed mass within and among species in each habitat. Following our criterion, we found clear concordance between intra- and interspecific relationships between seed mass and performance traits in five out of 10 comparisons.

We found no evidence of clear concordance within and between species for the relationship between seed mass and the probability of seedling emergence. In the shaded forest only two species exhibited the positive relationship observed at the interspecific level based on TIPS (our less conservative analysis), but not on PICS (our more conservative analysis) (Table 1). In contrast, in gaps the direction of intraspecific seed mass effects exhibited opposing trends, and no significant interspecific relationship was detected.

The relationship between seed mass and 1-year seedling biomass (Fig. 3c,d) showed concordance in the shaded forest, where five species exhibited the positive relationship also detected at the interspecific level based on TIPS or PICS (Table 1; Fig. 2). This clear concordance was absent in gaps where only two species exhibited positive relationships, while a significant positive seed mass effect was detected at the interspecific level, but only when using our less conservative analysis, TIPS (Fig. 3c).

We found no evidence of concordance for the relationship between seed mass and RGR (Fig. 3e,f). Within each habitat, only three of seven species exhibited the significant negative relationship detected among species based on both TIPS and PICS analyses (Table 1).

In the shaded forest, a lack of concordance was detected for the relationship between seed mass and 1-year seedling survival (Fig. 3h). Six out of seven species exhibited positive effects of seed mass on survival,

in contrast to the neutral relationship observed among species. In gaps (with the exception of one species) survival was independent of seed mass at both levels of seed mass variation (Fig. 3g). Finally, concordance was detected for the relationship between seed mass and the probability of seedling recruitment in both shaded forest and gaps (Fig. 3i,j). In shaded forest, only four out of seven species showed positive seed mass effects, and no interspecific relationship was detected (Table 1). In gaps, two species exhibited positive seed mass effects, one species exhibited a negative relationship, and no effect was detected at the interspecific level.

Discussion

INTERSPECIFIC EFFECTS OF SEED MASS ON SEEDLING PERFORMANCE

A vast literature on the effects of seed mass in open vs shaded controlled conditions suggests that species with larger seeds have advantages during emergence, in seedling size and in overall recruitment in shaded forest habitats (Foster & Janson 1985; Foster 1986; Kitajima 1994; Osunkoya 1996; Hewitt 1998; Walters & Reich 2000). The results presented here, obtained in the field (where many mortality risks operate jointly) also support the view that, after 1 year's growth, species' seed mass is a good predictor of seedling size (principally in the shaded forest) and of RGR in both gaps and shaded forest. In addition, mean seed mass is a weak predictor of seedling emergence in the shaded forest, but not in gaps, and does not predict seedling survival or recruitment in either gaps or shaded forest sites.

Probability of emergence

It has been proposed that large seeds develop into large seedlings with a greater ability to emerge from beneath the litter and/or soil layer (Facelli & Pickett 1991; Reader 1993; Bond, Honig & Maze 1999). We found only weak support for this hypothesis. Among species of *Psychotria*, large seeds grew into large seedlings but large seeds did not have a clear advantage with respect to emergence. We found a positive relationship between seed mass and the probability of emergence in the shaded forest, but this relationship disappeared when controlling for phylogenetic relatedness. These results suggest that taxon-specific traits other than seed mass are more important determinants of seedling emergence.

Other studies conducted in tropical and in temperate forests support the view that seedling emergence depends less on seed mass than on species-specific traits such as sensitivity to the litter's microclimate (Vázquez Yanes *et al.* 1990; Molofsky & Augspurger 1992; Eriksson 1995; but see Dalling & Hubell 2002). In our study system, however, the lack of habitat effects on the probability of seedling emergence across species ($F_{1,2} = 0.286$, $P < 0.65$) suggests a lack of sensitivity of germination

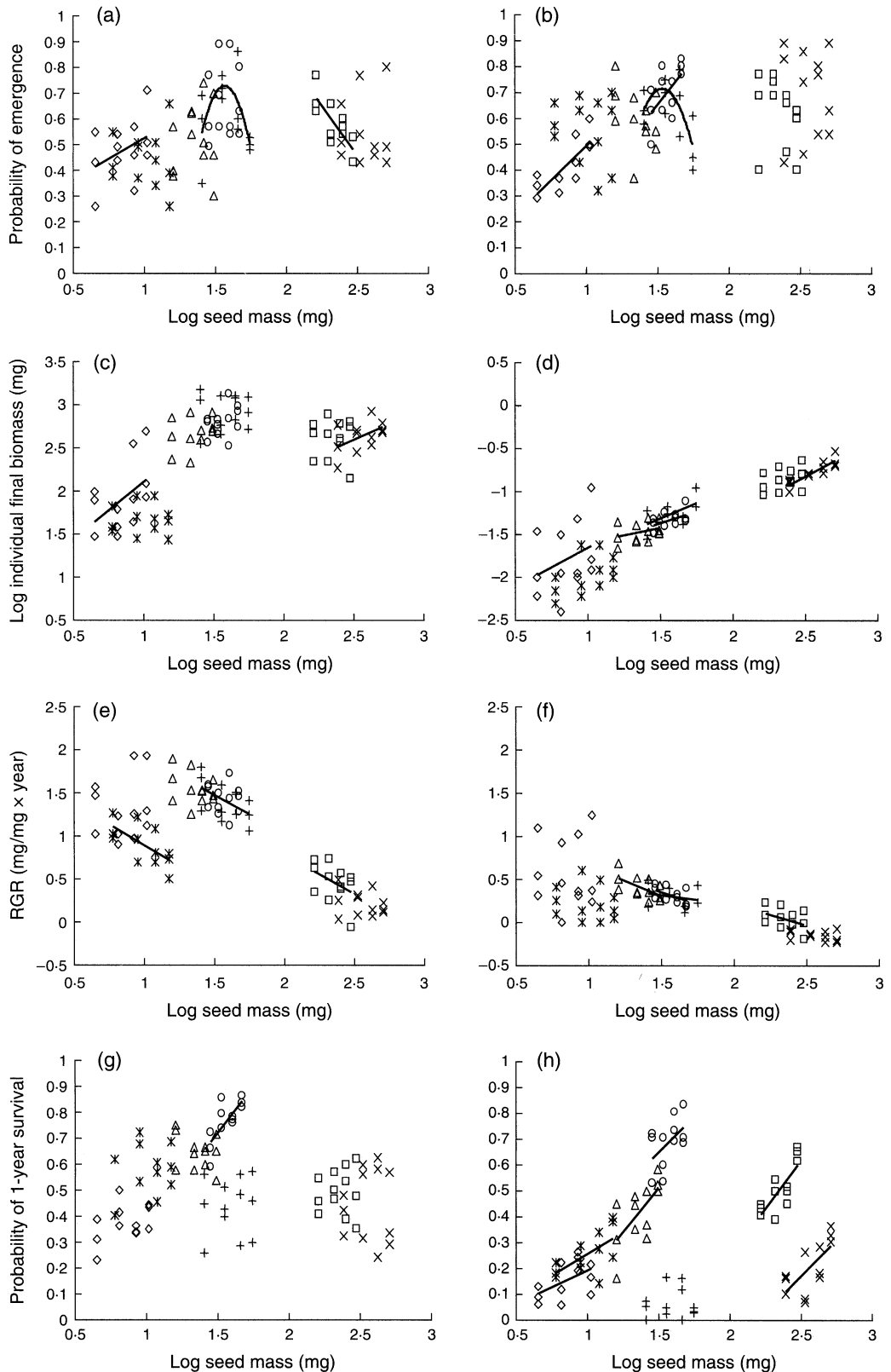


Fig. 3. Intraspecific correlations between seedling performance traits and seed mass in gaps and shaded forest sites. Each graph shows the bivariate plots between one seedling trait and seed mass for seven species analysed. For each dependent variable, left panel indicates observations obtained in light gaps (a,c,e,g,i); right panel indicates shaded forest (b,d,f,h,j). Solid lines, significant intraspecific correlations ($P < 0.05$). $\diamond = P. limonensis$; $*$ = $P. graciliflora$; $\triangle = P. chagrensis$; $\circ = P. papantlensis$; $+$ = $P. simiarum$; $\square = P. flava$; $\times = P. faxlucens$.

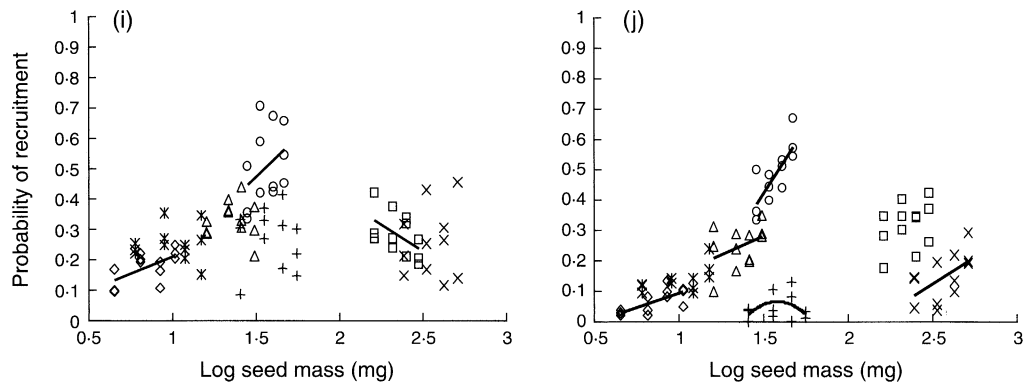


Fig. 3. Continued

to microclimate in these taxa, although more highly controlled experimental studies considering the effects on germination of the microclimate at the soil surface are needed to verify this statement. The net effect of seed mass on emergence may result from opposing factors, with the ability to penetrate the litter layer favouring large seeds, and the preferences of vertebrate seed predators favouring small seeds (Reader 1993). In *Psychotria*, preliminary explorations of the interspecific relationship between seed mass, seed removal and litter cover suggest that, independently of the time to emergence, large seeds have a higher risk of removal by seed predators, especially in gaps; however, if they escape predation, larger seeds have a higher probability of emerging from beneath the litter (unpublished data).

Growth

Many interspecific studies conducted under experimental conditions (Shipley & Parent 1991; Kitajima 1994; Swanborough & Westoby 1996; Reich *et al.* 1998; Wright & Westoby 2001) have detected a negative relationship between seed mass and RGR for young seedlings. This association has been claimed to be an intrinsic feature due to direct or indirect relationships between seed mass and seedling morphology (Kitajima 1996; Leishman *et al.* 2000). For example, larger-seeded species develop into seedlings with a higher proportion of uncommitted resources, resulting in the presence of thick cotyledons with low specific leaf area, and thus low RGR. The negative RGR *vs* seed mass relationship may also result from correlations between seed mass and seedling morphology at the autotrophic phase. For example, seedlings from large-seeded species have a higher allocation to reserves and defence, resulting in low leaf area ratio, low specific leaf area and low RGR (Kitajima 1996; Kidson & Westoby 2000; Leishman *et al.* 2000).

In the present study we found strong support for an intrinsic, negative relationship among species between the seed mass and the RGR of 1-year-old seedlings growing in natural forest habitats. Interestingly, the correlation between seed mass and RGR observed in

both TIPS and PICS analyses suggests that the functional relationship between seed mass and RGR is not affected by other traits that differ among *Psychotria* species (Swanborough & Westoby 1996). The mechanism that causes this correlation among *Psychotria* species has yet to be investigated. As 1-year-old *Psychotria* seedlings exhibit both cotyledons and true leaves, the correlations between seed mass and RGR could result either from direct effects of seed mass on cotyledon morphology, or from correlations between seed mass and patterns of carbon allocation expressed during the autotrophic phase.

Environmental variation can strongly affect the interspecific relationship between seed mass and RGR. One may predict, for example, that in high-light habitats any initial advantages in seedling size provided by large seeds will be counterbalanced by the faster growth rates of small-seeded seedlings. One important consequence of this habitat-specific effect on growth rate is that the effect of seed mass on seedling size should persist longer in shaded than in high light conditions (Boot 1996; Rose & Poorter 2003). We found evidence of such habitat-specific relationships among species. First, the relationship between seed mass and RGR was steeper in gaps than in shaded forest (according to TIPS and PICS), and the relationship between seed mass and seedling biomass was steeper (according to PICS, our most conservative analysis) and tighter (according to both TIPS and PICS) in the shaded forest. Together, these analyses suggest that, after 1 year, differences among species in RGR exhibited in gaps were nearly sufficient to compensate fully for the initial advantages in seedling size due to seed mass, diminishing the relationship between seed mass and seedling biomass. By contrast, in the shaded forest the differences among species in RGR were not sufficient to compensate for the early advantages of large seed mass.

Survival

Several interspecific studies of tropical and non-tropical species conducted in glasshouse conditions predict positive effects of seed mass on seedling survival, particularly under low light (Gross 1984; Leishman &

Westoby 1995; Kitajima 1996 Leishman *et al.* 2000; but see Augspurger 1984 for negative evidence). Similar results were found comparing five species of *Psychotria* under glasshouse low-light conditions (Paz & Martínez-Ramos 2003). In contrast to these studies we found that, in natural habitats, species mean seed mass does not predict seedling survival and recruitment. Together these results suggest that seed mass confers potential survival advantages in the shaded forest, but other traits that differ between the subgenera sampled may also strongly affect survival. The species belonging to the subgenus *Psychotria* (*P. limonensis*, *P. graciliflora*, *P. chagensis*, *P. papantlensis* and *P. flava*) tend to have higher survival in the shaded forest than species belonging to other subgenera (*P. simiarum* and *P. faxlucens*). This may be due to differences between the subgenera in their vulnerability to herbivores, as has been observed in the field (H.P., personal observation). A regression among the five species belonging to the subgenus *Psychotria* indicated that seedling survival increases with seed mass in the shaded forest (slope = 0.216, $t_{13} = 2.35$, $P < 0.035$) but not in gaps (slope = 0.010, $t_{13} = 0.13$, $P < 0.91$). Apparently our analysis based on phylogenetic independent contrasts did not account fully for all potential variables affecting seedling survival.

The lack of a strong interspecific relationship between seed mass and survivorship observed here is unusual relative to other studies of tropical tree species (even those that investigated the relationship among distantly related taxa), and might depend on the range of seed mass variation studied. Field experiments in tropical forests have found that seed mass is a good predictor of 1-year survival in the shaded forest in Mexico (M.M.-R., unpublished data) and in Peru (M.R. Silman, unpublished data), but not in Panama (Augspurger 1984). It appears that a failure to detect a positive correlation between seed mass and survival corresponds to those studies examining a relatively small range of seed mass variation (four and five orders of magnitude in Martínez-Ramos 1991 and Silman 1996, respectively; compared with three and two orders of magnitude in Augspurger 1984 and the present study, respectively).

These results suggest that the two orders of magnitude of seed mass variation among the species of *Psychotria* observed here is not sufficient to reveal a functional relationship between seed mass and survival when other phenotypic differences among taxonomic groups within the genus may affect individual survival. Within subgenera, however, where closely related species share such traits, seed mass can become an important determinant of seedling survival. In addition, it is expected that seed mass effects on performance will decrease as seedlings age (Kitajima 1996). Consequently, failure to detect a strong interspecific correlation between seed mass and survival may also depend on the duration of the study (Leishman *et al.* 2000; Dalling & Hubell 2002). In *Psychotria*, the finding of prevalent positive seed mass effects on 1-year survival within

species (Paz & Martínez-Ramos 2003) suggests that the duration of this study did not limit our ability to detect effects of seed mass on seedling performance, when present.

Recruitment in shaded forest vs gaps

Ultimately, seedling recruitment success depends on the effects of seed mass on the seed-to-seedling transition and on seedling survival. Among species of *Psychotria*, our results suggest that seed mass does not affect net recruitment in either gaps or shaded forest. In gaps, it is clear that seed mass affects neither survival nor emergence of seedlings. However, in the shaded forest the lack of seed mass effects on recruitment is due to the positive effects of seed mass on seedling emergence being diluted by the large species-specific variation in seedling survival. In general, the *Psychotria* species studied recruited as well or better in gaps than in the shaded forest. It is interesting to note, however, that when observing the ratio of recruitment in the forest to recruitment in gaps, PICS analyses detect that the recruitment of large-seeded species is significantly less sensitive than small-seeded species to shaded forest habitat. The detection of this effect of seed mass only when controlling for other ancestor- and species-specific traits confirms the view that seed size is less important than at least some other traits in determining the recruitment success of *Psychotria* in shaded forest relative to gaps.

CONCORDANCE BETWEEN INTRA- AND INTERSPECIFIC CORRELATIONS

Where correlations are examined within and among sympatric species, concordant relationships between levels suggest that either the same functional constraints or similar selective pressures operate at different scales of phenotypic variation. Overall, from our intra- and interspecific studies in *Psychotria* (Paz *et al.* 1999; Paz & Martínez-Ramos 2003; present study), several conclusions emerge. First, seed mass plays a functional role in seedling performance in the shaded forest but not in gaps. Second, we found no general concordance of seed mass effects between intra- and interspecific levels, even in the shaded forest. The only clear exception to this conclusion was the positive effect of seed mass on seedling biomass 1 year after emergence. This case appears to result from a simple mass translation of seed size into seedling size, and from a reduced growth rate under light-limited environments.

An interesting case of discordance was exhibited for the relationship between seed mass and seedling survival; we observed positive relationships within but not among species. In theory, survival advantages of large-seeded seedlings may be an indirect effect of the seedling size vs seed size relationship, because more vigorous seedlings have a greater ability to cope with various mortality factors (Sarukhán *et al.* 1984, Howe

et al. 1985). In addition, large-seeded seedlings may achieve a higher probability of survival by allocating more resources to defences and to reserves with the cost of reduced growth rates (Kitajima 1996). A strong effect of seed mass within (but not among) species of *Psychotria* suggests that other species-specific traits can affect seedling survival more than seed mass itself. The combination of strong seed mass effects on survival within species of the subgenus *Psychotria*, but not among species from the other subgenus (as discussed above), suggests that the role of seed mass across levels of seed mass variation does not change in a simple fashion. Its role may depend on the relative importance of at least two factors, including the magnitude of differences among species in traits other than seed mass, and the absolute range of seed mass variation.

We found no concordance within *vs* among species in the relationship between seed mass and RGR because, at the intraspecific level, only a few species exhibited a negative correlation between these traits in their natural habitats (Paz & Martínez-Ramos 2003). The intraspecific relationships observed in the current field experiment, however, differ from those revealed in an earlier controlled glasshouse study, in which negative correlations between seed mass and RGR appeared under shaded conditions within several species that did not show this relationship in the field (Paz & Martínez-Ramos 2003). We suggest that, in natural habitats, negative relationships between seed mass and RGR within species are often masked by environmental heterogeneity. At the interspecific level, in contrast, the wider range of seed mass variation observed allowed us to discern this negative relationship. Thus in this case, the wide range of phenotypic variation in seed mass overcame variation in RGR associated with ecological or life-history differences among species.

Finally, we found that seed mass does not clearly affect the probability of seedling emergence at any range of seed mass variation. We propose that this is because, prior to emergence, multiple ecological factors may impose opposing selective forces on seed mass (e.g. the physical barrier of the litter layer may favour larger seeds while differential predation may favour smaller seeds).

In principle, the ability to detect concordance in seed mass effects within and among species can be limited by the reduced range of seed mass variation typically found within species, and by differences among species in traits other than seed mass. In this study, when comparing analyses at the two levels, we found that the effects of seed mass are often expressed exclusively either within or among species, depending on the trait observed. This suggests that the relative importance of the absolute range of seed mass variation *vs* the differences among species similarly depends on the focal trait.

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References

- Armstrong, D.P. & Westoby, M. (1993) Seedlings from large seeds tolerate defoliation better: a test using phylogenetically independent contrast. *Ecology* **74**, 1092–1100.
- Augsburger, C.K. (1984) Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* **72**, 77–75.
- Bond, W.J., Honig, M. & Maze, K.E. (1999) Seed size and seedling emergence: an allometric relationship and some ecological implications. *Oecologia* **120**, 132–136.
- Boot, R.G.A. (1996) The significance of seedling size and growth rate of tropical rain forest tree seedlings for regeneration in canopy openings. *The Ecology of Tropical Forest Tree Seedlings* (ed. M.D. Swaine), pp. 267–284. Parthenon, Carnforth, UK.
- Dalling, J.W. & Hubell, S.P. (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology* **90**, 557–568.
- Diaz-Uriarte, R. & Garland, T. (1998) Effects of branch length errors on the performance of phylogenetically independent contrasts. *Systematic Biology* **47**, 654–672.
- Eriksson, O. (1995) Seedling recruitment in deciduous forest herbs: the effects of litter, soil chemistry and seed bank. *Flora* **190**, 65–70.
- Facelli, J.M. & Pickett, S.T.A. (1991) Plant litter: its dynamics and effects on plant community structure. *Botanical Review* **57**, 1–32.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *American Naturalist* **125**, 1–15.
- Foster, S.A. (1986) On the adaptive value of large seeds for tropical moist forest trees: a review and synthesis. *Botanical Review* **52**, 269–299.
- Foster, S.A. & Janson, C.H. (1985) The relationship between seed size and establishment conditions in tropical woody plants. *Ecology* **66**, 773–780.
- Green, P.T. (1999) Seed germination in *Chrysophyllum* sp. nov., a large-seeded rainforest species in north Queensland: effects of seed size, litter depth and seed position. *Australian Journal of Ecology* **24**, 608–613.
- Green, P.T. & Juniper, P.A. (2004a) Seed–seedling allometry in tropical rain forest trees: seed mass-related patterns of resource allocation and the ‘reserve effect’. *Journal of Ecology* **92**, 397–408.
- Green, P.T. & Juniper, P.A. (2004b) Seed mass, seedling herbivory and the reserve effect in tropical rain forest seedlings. *Functional Ecology* **18**, 539–547.
- Gross, K.L. (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *Journal of Ecology* **72**, 369–387.
- Hamilton, C.W. (1989a) A revision of Mesoamerican *Psychotria* (Rubiaceae), Part I. *Annals of the Missouri Botanical Garden* **76**, 67–111.
- Hamilton, C.W. (1989b) A revision of Mesoamerican *Psychotria* (Rubiaceae), Part II. *Annals of the Missouri Botanical Garden* **76**, 386–429.

- Hewitt, N. (1998) Seed size and shade-tolerance: a comparative analysis of North American temperate trees. *Oecologia* **114**, 432–440.
- Howe, H.F., Schupp, E.W. & Wesley, L.C. (1985) Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* **66**, 781–791.
- Jakobsson, A. & Eriksson, O. (2000) A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos* **88**, 494–502.
- Jansen, P.A. (2003) Scatterhoarding and tree regeneration. Ecology of nut dispersal in Neotropical rainforest. PhD thesis, Wageningen University, Wageningen, the Netherlands.
- Kidson, R. & Westoby, M. (2000) Seed mass and seedling dimensions in relation to seedling establishment. *Oecologia* **125**, 11–17.
- Kitajima, K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**, 419–428.
- Kitajima, K. (1996) Ecophysiology of tropical tree seedlings. *The Ecology of Tropical Seedlings* (ed. M.D. Swaine), pp. 559–585. Parthenon, Carnforth, UK.
- Leishman, M.R. & Westoby, M. (1995) The role of large seed size in shaded conditions: experimental evidence. *Functional Ecology* **8**, 205–214.
- Leishman, M.R., Wright, I.J., Moles, A.T. & Westoby, M. (2000) The evolutionary ecology of seed size. *Seeds – The Ecology of Regeneration in Plant Communities* (ed. M. Fenner), pp. 31–57. CAB International, Wallingford, UK.
- Lorence, D.H. & Dwyer, J.D. (1987) New taxa in Mexican *Psychotria* (Rubiaceae, Psychotriaceae). *Boletín de la Sociedad Botánica de México* **47**, 49–64.
- Marañón, T. & Grubb, P.J. (1993) Physiological basis and ecological significance of the seed size and relative growth rate relationships in Mediterranean annuals. *Functional Ecology* **7**, 591–599.
- Marshall, D.L. (1986) Effect of seed size on seedling success in three species of *Sesbania* (Fabaceae). *American Journal of Botany* **73**, 457–464.
- Martínez-Ramos, M. (1991) *Patterns, processes and mechanisms in the seedling community of a Neotropical rain forest*. PhD thesis, National University of Mexico, Mexico.
- Martins, E. (1996) Conducting phylogenetic comparative studies when the phylogeny is not known. *Evolution* **50**, 12–22.
- Metcalf, D.J. & Grubb, P.J. (1997) The response to shade of seedlings of very small-seeded tree and shrub species from tropical rain forests in Singapore. *Functional Ecology* **11**, 215–221.
- Moegenburg (1996) Sabal palmetto seed size: causes of variation, choices of predators, and consequences for seedlings. *Oecologia* **106**, 539–543.
- Moles, A.T. & Westoby, M. (2002) Seed addition experiments are more likely to increase recruitment in large-seeded species. *Oikos* **99**, 241–248.
- Moles, A.T. & Westoby, M. (2004) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology* **92**, 372–383.
- Molofsky, J. & Augspurger, C.K. (1992) The effect of leaf litter on early seedling establishment in a tropical forest. *Ecology* **73**, 68–77.
- Osunkoya, O. (1996) Light requirements for regeneration in tropical forest plants: taxon-level and ecological attribute effects. *Australian Journal of Ecology* **21**, 429–441.
- Paz, H. & Martínez-Ramos, M. (2003) Seed mass and seedling performance within eight species of *Psychotria* (Rubiaceae). *Ecology* **84**, 439–450.
- Paz, H., Mazer, S.J. & Martínez-Ramos, M. (1999) Seed mass, seedling emergence, and environmental factors in seven rain forest *Psychotria* (Rubiaceae). *Ecology* **80**, 1594–1606.
- Purvis, A., Gittleman, J.L. & Luh, H.K. (1994) Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *Journal of Theoretical Biology* **167**, 293–300.
- Purvis, A. & Rambaut, A. (1995) Comparative analysis by independent contrasts (CAIC ver. 2.0): an Apple Macintosh application for analyzing comparative data. *Computer Applications Biosciences* **11**, 247–251.
- Reader, R.J. (1993) Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *Journal of Ecology* **81**, 169–175.
- Reich, P.B., Tjoelker, M.G., Walters, M.B., Vanderklein, D.W. & Buschena, C. (1998) Close association of RGR, leaf and root morphology, seed mass and shade tolerance in seedlings of nine boreal tree species grown in high and low light. *Functional Ecology* **12**, 327–338.
- Rose, S. & Poorter, L. (2003) The importance of seed mass for early regeneration in tropical forest: a review. Long-term changes in tropical tree diversity. *Studies from the Guiana Shield, Africa, Borneo and Melanesia* (ed. H. ter Steege), pp. 19–35. Tropenbos Series 2. Tropenbos International, Wageningen, the Netherlands.
- Sarukhan, J., Matrinez-Ramos, M. & Pinero, D. (1984) The analysis of demographic variability at the individual level and its population consequences. *Perspectives on Plant Population Ecology* (eds R. Dirzo & J. Sarukhan), pp. 141–165. Sinauer Associates, Inc., Sunderland, Mass., USA.
- Saverimuttu, T. & Westoby, M. (1996) Seedling relative growth rate and its components in relation to seed size: phylogenetically independent contrasts. *Functional Ecology* **10**, 176–184.
- Schupp, E. (1988) Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* **76**, 525–530.
- Seiwa, K. & Kikuzawa, K. (1996) Importance of seed size for the establishment of seedlings of five deciduous broad-leaved tree species. *Vegetatio* **123**, 51–64.
- Shiple, B. & Parent, M. (1991) Germination responses of 64 wetland species in relation to seed size, minimum time to reproduction and seedling relative growth rate. *Functional Ecology* **5**, 111–118.
- Silman, M.R. (1996) Regeneration from seed in a Neotropical rain forest. PhD thesis, Duke University, Durham, NC, USA.
- Swanborough, P. & Westoby, M. (1996) Seedling relative growth rate and its components in relation to seed size: phylogenetically independent contrasts. *Functional Ecology* **10**, 176–184.
- Swofford, D.L. (1998) *PAUP Phylogenetic Analysis Using Parsimony (and Other Methods)*. Version 4. Sinauer Associates, Sunderland, MA, USA.
- Vázquez Yanes, C., Orozco-Segovia, A., Rincón E., Sánchez-Coronado M., Huante P., Toledo J.R. & Barradas V.L. (1990) Light beneath the litter in a tropical forest: effect on seed germination. *Ecology* **71**, 1952–1958.
- Walters, M.B. & Reich, P.B. (2000) Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. *Ecology* **81**, 1887–1901.
- Wright, I.J. & Westoby, M. (2001) Understanding seedling growth relationships through specific leaf area and leaf nitrogen concentration: generalizations across growth forms and growth irradiance. *Oecologia* **127**, 21–29.
- Yanful, M. & Maun, M.A. (1996) Effects of burial of seeds and seedlings from different seed sizes on the emergence and growth of *Strophostyles helvola*. *Canadian Journal of Botany* **74**, 1322–1330.

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