Differential seed germination responses to the ratio of red to far-red light in temperate and tropical species

Pimonrat Tiansawat · James W. Dalling

Abstract Variation in vegetation density creates a range of red to far-red ratios of irradiance (R:FR) potentially permitting fine-scale discrimination of light conditions for seed germination. However, remarkably few studies have explored whether R:FR responses of germination vary among species that differ in distribution and life-history traits. In this study, we explored the relationships between R:FR requirements and four species characteristics: seed mass, latitudinal distribution (tropical vs. temperate), seed dormancy (dormant vs. nondormant), and plant growth form (woody vs. nonwoody). We obtained data on germination response to R:FR of 62 species from published literature and added new data for ten species from aseasonal tropical forests in Borneo. First, we analyzed whether species characteristics influenced overall light dependency of germination using phylogenetic logistic regression. We found that seed mass had a strong negative effect on light dependency, but that the seed mass at which tropical taxa had a 50 % probability of light dependency was 40 times that of temperate taxa. For light-dependent species, we found that the threshold R:FR that stimulates 50 % of maximum germination ($R:FR_{50}$) was also related to seed mass and latitudinal distribution. In agreement with an earlier study, we found that for temperate taxa, the $R:FR_{50}$ was significantly negatively correlated with seed mass. In contrast, for 22 tropical taxa, we found a significant positive correlation. These opposing relationships suggest contrasting selection pressures on germination responses of tropical taxa (mostly trees) and temperate herbaceous plants, and which are likely related to differences in seed longevity, seed burial rates, and reproductive output.

Keywords Regeneration niche · Light dependence · Light quality · Seed mass · Lambir Hill National Park

Introduction

Environmental requirements for seed germination constitute a key component of the regeneration niche of many plant species, influencing adult distribution patterns (Grubb 1977). Seed germination is a complex process controlled by both internal properties of seeds and by an array of environmental factors including light quality, soil moisture availability, temperature, and the chemical environment of the soil (Bewley and Black 1994; Baskin and Baskin 1998). For most species, the timing of seed germination is tied to light

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availability (Daws et al. 2002). Although seeds are routinely screened for light sensitivity through germination assays performed in light and dark (e.g. Pons 1991; Baskin et al. 2000), these tests provide only limited information about how light requirements shape the regeneration niche of plants.

Differential germination responses to the ratio of red to far-red light (hereafter R:FR) can provide a sensitive mechanism for detecting the presence of suitable microsites for seed germination. In tropical and temperate forests and grassland habitats, these microsites represent gaps in the vegetation where regeneration can take place (Denslow 1987; Batlla et al. 2000; Dobarro et al. 2010). Gaps differ in size and consequently in the degree to which they receive direct versus transmitted light. Unfiltered daylight contains an approximately equal proportion of R and FR light (R:FR ~ 1.2). Canopy foliage preferentially absorbs R relative to FR. Therefore, R:FR below the canopy may be as low as 0.2–0.3 (Lee 1987; Daws et al. 2002). Moreover, R:FR may be further reduced to 0.1 beneath leaf litter layers (Vásquez-Yanes et al. 1990). As a consequence, R:FR increases with gap size and decreases with foliage or litter density. In addition to delineating gaps, R:FR can also act as a cue for detecting the depth of burial in the soil. Red light can penetrate only few millimeters through the soil, while longer wavelengths penetrate further (Wooley and Stoller 1978; Benvenuti 1995). The wide range in R:FR values associated with spatial variation among microsites therefore provides a gradient potentially allowing fine-scale discrimination by seeds of transient safe sites for germination.

Despite the potential for fine-scale partitioning of light regimes using germination response to R:FR, remarkably few studies have explored whether species with different regeneration requirements vary in the R:FR level necessary to trigger germination. The presence of multiple phytochromes i.e., signal-transducing photoreceptors, in plants might be expected to allow complex responses to R:FR variation (Smith 2000). The few empirical studies conducted to date indicate that the R:FR value required for 50 % of maximum seed germination (hereafter the R:FR$_{50}$) varies markedly among species (e.g. Daws et al. 2002; Pearson et al. 2003; Pereira et al. 2009). Moreover, the magnitude and direction of correlations between R:FR$_{50}$ and seed and whole-plant functional traits do not follow a simple pattern. An example of the complexity embodied in such responses can be found in the relationships among light quality, seed germination, and seed mass.

Light dependency of seed germination has often been linked to seed size (Baskin and Baskin 1998). The germination of "large" seeds (>2 mg) is typically independent of light but may require fluctuations of diurnal temperature as a germination cue (Thompson and Grime 1983; Pearson et al. 2003). Light is unlikely to be an effective indicator of habitat quality for large seeds seedlings of which can emerge successfully from below the depth to which light penetrates into the soil or from beneath layers of surface leaf litter (Molofsky and Augspurger 1992; Pearson et al. 2002; Kostel-Hughes et al. 2005). Since fluctuating temperatures can be detected several centimeters beneath the soil surface (Pearson et al. 2002); temperature can be a more effective signal of environmental conditions for large seeds. No clear consensus has yet been reached on how light dependency varies with latitude, seed dormancy (Pons 1991; Vandelook et al. 2008; Flores et al. 2011), or plant growth form (Bell et al. 1999; Rojas-Aréchiga et al. 1997; De Villiers et al. 2002; Flores et al. 2011).

Although small-seeded species are more likely to use R:FR as a germination cue than large-seeded species, it remains unclear how R:FR$_{50}$ is related to seed mass. One study from a temperate deciduous forest has shown that seed mass is negatively correlated with the R:FR$_{50}$ for germination (Jankowska-Blaszczuk and Daws 2007). However, a single study of nine neotropical species reports the opposite relationship (Pearson et al. 2003). These studies leave unclear whether latitudinal distribution, plant growth form, or even seed dormancy play a role in the interaction between R:FR requirement and seed size.

The aim of this study was to explore the relationship among seed characteristics (seed mass and dormancy traits), species latitudinal distribution (temperate and tropical), species growth form (woody and nonwoody), and R:FR requirement for seed germination. Although a large literature exists on whether or not seed germination is light dependent, our focus was on R:FR$_{50}$ of germination response. To include a range of species with different latitudinal distributions, we combined data from existing literature that includes R:FR germination responses with a new dataset of paleo-tropical species from Borneo. If this expanded dataset reveals consistent relationships between

R:FR$_{50}$ and seed mass across a range of taxa, growth forms, and dormancy types, then it is likely that a single source of selection is primarily responsible for determining R:FR responses. On the other hand, if R:FR$_{50}$ differs among species groups, then this may indicate that multiple contrasting selection pressures generate context-dependent R:FR responses.

Methods

Inclusion of published literature on R:FR responses

Data on species' responses to R:FR were obtained by searching published literature in the SciVerse Scopus database (Elsevier 2012). Two sets of search terms (a) "red far red ratio", and "seed germination"; and (b) "seed germination", and "light quality" were used to capture relevant literature. Candidate literature met criteria for inclusion in this study when (a) the study tested seed germination with at least five levels of R:FR, (b) the response variable in the study was percent germination or germination probability, and (c) the studies included the calculation of the R:FR$_{50}$ (Pearson et al. 2003) and/or included figures that allowed the extraction of R:FR$_{50}$ (i.e., a plot of germination probability against R:FR levels). If the literature did not state seed mass, then seed mass was obtained by searching the Seed Information Database (SID) (Royal Botanic Gardens Kew 2008).

In total, 62 taxa from 11 published studies were included in this analysis (Table 1). We included all species in each literature source, regardless of whether they were light dependent or not. When seed dormancy type was not stated in the literature, it was obtained from Baskin and Baskin (1998), or from other primary literature on dormancy. For 17 species, there was no information on dormancy type; for these species the dormancy type reported for congeners was used (Table 1).

Additional data on seed germination response to R:FR

We also included information for ten species (Table 1) from a germination experiment, conducted over two field seasons at Lambir Hills National Park, Sarawak, Malaysia (NW Borneo) (4°12′ N, 114°02′ E). Lambir

receives rainfall ranging from 2,100 to 3,300 mm per year in all months averaging >100 mm (Kumagai et al. 2009). The mean temperature is 27 °C. There is no clear seasonality in environmental factors such as radiation, temperature, vapor pressure deficits, and precipitation; instead, unpredictable short dry spells (<1 month) often occur throughout the year (Kumagai et al. 2009).

Seeds were separated for individual mother trees and germinated under 30 % full sun in a screened growing house with the mean temperature of 26.7 °C (range of 21.8–37.8 °C). In the first field season (June to October 2009), five levels of R:FR were created using plastic boxes covered with coated polyester filters (LEE Filters, California, USA): 0.01 (filter 322 and 121), 0.09 (filter 322), 0.20 (filter 122), 0.59 (filter 088), and 1.12 (no filter). To better distribute the R:FR range in the experiment, in the second field season (July 2010 to November 2011), there were six levels of R:FR: 0.01 (filter 090), 0.08 (filter 322), 0.20 (filter 122), 0.34 (a double layer of filter 088), 0.67 (filter 088), and 1.11 (no filter). R:FR was measured using R:FR sensor, SKR 110 (Skye Instruments, Powys, UK).

Seeds were collected from three maternal trees, except for *Macaranga bancana*, *Macaranga hullettii* (two trees), and *Macaranga umbrosa* (one tree). Among maternal trees, the number of seeds sown in replicates varied (4–30 seeds) depending on seed availability. Two to three replicates of seeds per maternal tree were sown in Petri dishes lined with two layers of sterile cotton gauze pad, moistened with tap water, and the dishes were covered with the lids. Germination was scored every other day at night under R:FR < 0.01. Seeds were scored as germinated once >1 mm of radicle emerged. Seeds were exposed to R:FR for 8 weeks, and final percent germination was determined.

The relationship between percent germination (y) and R:FR (x) was described by a sigmoidal function (Pearson et al. 2003)

$$y = a/\{1 + \exp[-((x - x_0)/b)]\}$$

where a is a coefficient describing the maximum percent germination, x_0 is a coefficient estimating the R:FR at 50 % of maximum germination (R:FR$_{50}$), and b is a coefficient of the slope of R:FR at 75 and 25 % of maximum germination. The model was fit using nonlinear least-squares estimate (nls) in R (R Core

Table 1 Summary information of 72 species used in this study

S. no.	Species	Clade	Family[a]	Growth form	Region	Seed mass (mg)	R:FR$_{50}$	Dormancy	References
	Light-independent species								
1	Acacia abyssinica	Eudicots	Fabaceae	Tree	Tropical	93.000	–	PD	Yirdaw and Leinonen (2002)
2	Aegopodium podagraria	Eudicots	Apiaceae	Herb	Temperate	2.400	–	MPD	Jankowska-Blaszczuk and Daws (2007)
3	Agrostis castellana	Monocots	Poaceae	Grass	Temperate	0.170	–	PD	Dobarro et al. (2010)
4	Allium ursinum	Monocots	Amaryllidaceae	Herb	Temperate	6.600	–	MPD	Jankowska-Blaszczuk and Daws (2007)
5	Circaea lutetiana	Eudicots	Onagraceae	Herb	Temperate	2.200	–	PD	Jankowska-Blaszczuk and Daws (2007)
6	Corydalis solida	Eudicots	Papaveraceae	Herb	Temperate	3.790	–	MPD	Jankowska-Blaszczuk and Daws (2007)
7	Dactylis glomerata	Monocots	Poaceae	Grass	Temperate	0.900	–	PD	Dobarro et al. (2010)
8	Dillenia suffruticosa	Eudicots	Dilleniaceae	Shrub	Tropical	8.340	–	ND	New data
9	Faidherbia albida	Eudicots	Fabaceae	Tree	Tropical	85.300	–	PD	Yirdaw and Leinonen (2002)
10	Festuca ampla	Monocots	Poaceae	Grass	Temperate	0.910	–	PD	Dobarro et al. (2010)
11	Geum urbanum	Eudicots	Rosaceae	Herb	Temperate	1.900	–	PD[b]	Pons (1983)
12	Holcus setiglumis	Monocots	Poaceae	Grass	Temperate	0.064	–	ND[b]	Dobarro et al. (2010)
13	Lamiastrum galeobdolon	Eudicots	Lamiaceae	Herb	Temperate	2.000	–	PD	Jankowska-Blaszczuk and Daws (2007)
14	Macaranga bancana	Eudicots	Euphorbiaceae	Tree	Tropical	18.730	–	ND	New data
15	Macaranga havilandii	Eudicots	Euphorbiaceae	Treelet	Tropical	33.220	–	ND	New data
16	Macaranga umbrosa	Eudicots	Euphorbiaceae	Tree	Tropical	60.470	–	ND	New data
17	Maianthemum bifolium	Monocots	Asparagaceae	Herb	Temperate	12.800	–	MPD[b]	Jankowska-Blaszczuk and Daws (2007)
18	Melica nutans	Monocots	Poaceae	Grass	Temperate	2.880	–	PD	Jankowska-Blaszczuk and Daws (2007)
19	Paris quadrifolia	Monocots	Melanthiaceae	Herb	Temperate	4.330	–	PD	Jankowska-Blaszczuk and Daws (2007)
20	Picea abies	Gymnosperms	Pinaceae	Tree	Temperate	7.000	–	ND	Ahola and Leinonen (1999)
21	Pinus sylvestris	Gymnosperms	Pinaceae	Tree	Temperate	6.000	–	ND	Ahola and Leinonen (1999)
22	Ranunculus lanuginosus	Eudicots	Ranunculaceae	Herb	Temperate	2.850	–	MPD[b]	Jankowska-Blaszczuk and Daws (2007)
23	Spergularia purpurea	Eudicots	Caryophyllaceae	Herb	Temperate	0.020	–	PD[b]	Dobarro et al. (2010)

Table 1 continued

S. no.	Species	Clade	Family[a]	Growth form	Region	Seed mass (mg)	$R:FR_{50}$	Dormancy	References
24	*Stachys sylvatica*	Eudicots	Lamiaceae	Herb	Temperate	1.460	–	PD	Jankowska-Blaszczuk and Daws (2007)
25	*Stellaria holostea*	Eudicots	Caryophyllaceae	Herb	Temperate	2.810	–	PD	Jankowska-Blaszczuk and Daws (2007)
26	*Vitex pinnata*	Eudicots	Lamiaceae	Tree	Tropical	85.660	–	PY	New data
	Light-independent species								
27	*Ajuga reptans*	Eudicots	Lamiaceae	Herb	Temperate	1.400	0.200	PYPD[b]	Jankowska-Blaszczuk and Daws (2007)
28	*Alcantarea imperialis*	Monocots	Bromeliaceae	Rupicolous	Tropical	1.656	0.095	ND[b]	Pereira et al. (2009)
29	*Anthemis arvensis*	Eudicots	Asteraceae	Herb	Temperate	0.640	0.453	PD	Dobarro et al. (2010)
30	*Betula pendula*	Eudicots	Betulaceae	Tree	Temperate	0.290	0.120	PD	Ahola and Leinonen (1999)
31	*Cecropia insignis*	Eudicots	Urticaceae	Tree	Tropical	0.680	0.205	ND[b]	Pearson et al. (2003)
32	*Cecropia obtusifolia*	Eudicots	Urticaceae	Tree	Tropical	0.590	0.237	ND[b]	Pearson et al. (2003)
33	*Cecropia peltata*	Eudicots	Urticaceae	Tree	Tropical	0.580	0.265	ND[b]	Pearson et al. (2003)
34	*Chrysosplenium alternifolium*	Eudicots	Saxifragaceae	Herb	Temperate	0.058	0.600	ND[b]	Jankowska-Blaszczuk and Daws (2007)
35	*Cirsium palustre*	Eudicots	Asteraceae	Herb	Temperate	1.670	0.320	PD[b]	Pons (1983)
36	*Cordia africana*	Eudicots	Boraginaceae	Tree	Tropical	214.000	0.930	PY	Yirdaw and Leinonen (2002)
37	*Crassula tillaea*	Eudicots	Crassulaceae	Herb	Temperate	0.010	0.311	PD	Dobarro et al. (2010)
38	*Epilobium montanum*	Eudicots	Onagraceae	Herb	Temperate	0.078	0.700	PD	Jankowska-Blaszczuk and Daws (2007)
39	*Geranium robertianum*	Eudicots	Geraniaceae	Herb	Temperate	2.200	0.350	PY	Jankowska-Blaszczuk and Daws (2007)
40	*Hypericum perforatum*	Eudicots	Hypericaceae	Herb	Temperate	0.090	0.900	PD	Jankowska-Blaszczuk and Daws (2007)
41	*Hypochaeris glabra*	Eudicots	Asteraceae	Herb	Temperate	0.778	0.633	ND[b]	Dobarro et al. (2010)
42	*Juncus effusus*	Monocots	Juncaceae	Herb	Temperate	0.015	0.900	ND[b]	Jankowska-Blaszczuk and Daws (2007)
43	*Juniperus procera*	Gymnosperms	Cupressaceae	Tree	Tropical	18.100	0.940	PYPD	Yirdaw and Leinonen (2002)
44	*Lapsana communis*	Eudicots	Asteraceae	Herb	Temperate	0.856	0.500	PD	Jankowska-Blaszczuk and Daws (2007)
45	*Macaranga beccariana*	Eudicots	Euphorbiaceae	Tree	Tropical	12.190	0.110	ND	New data
46	*Macaranga gigantea*	Eudicots	Euphorbiaceae	Tree	Tropical	17.600	0.440	ND	New data

Table 1 continued

S. no.	Species	Clade	Family[a]	Growth form	Region	Seed mass (mg)	R:FR$_{50}$	Dormancy	References
47	*Macaranga hullettii*	Eudicots	Euphorbiaceae	Tree	Tropical	24.720	0.120	ND	New data
48	*Macaranga trachyphylla*	Eudicots	Euphorbiaceae	Tree	Tropical	20.410	0.050	ND	New data
49	*Macaranga winkleri*	Eudicots	Euphorbiaceae	Tree	Tropical	1.720	0.040	ND	New data
50	*Miconia argentea*	Eudicots	Melastomataceae	Tree	Tropical	0.080	0.117	ND	Pearson et al. (2003)
51	*Milium effusum*	Monocots	Poaceae	Grass	Temperate	1.410	0.400	PD	Jankowska-Blaszczuk and Daws (2007)
52	*Moehringia trinervia*	Eudicots	Caryophyllaceae	Herb	Temperate	0.319	0.550	PD	Jankowska-Blaszczuk and Daws (2007)
53	*Mycelis muralis*	Eudicots	Asteraceae	Herb	Temperate	0.306	0.250	ND	Jankowska-Blaszczuk and Daws (2007)
54	*Oxalis acetosella*	Eudicots	Oxalidaceae	Herb	Temperate	1.220	0.250	PD	Jankowska-Blaszczuk and Daws (2007)
55	*Phyteuma spicatum*	Eudicots	Campanulaceae	Herb	Temperate	0.180	0.350	PD	Jankowska-Blaszczuk and Daws (2007)
56	*Pilosocereus arrabidae*	Eudicots	Cactaceae	Succulent	Tropical	20.600	0.247	ND[b]	Martins et al. (2012)
57	*Piper dilatatum*	Magnoliids	Piperaceae	Shrub	Tropical	0.150	0.125	ND	Daws et al. (2002)
58	*Piper hispidum*	Magnoliids	Piperaceae	Shrub	Tropical	0.120	0.090	ND	Daws et al. (2002)
59	*Piper marginatum*	Magnoliids	Piperaceae	Shrub	Tropical	0.150	0.240	ND	Daws et al. (2002)
60	*Piper peltatum*	Magnoliids	Piperaceae	Herb	Tropical	0.040	0.002	ND	Daws et al. (2002)
61	*Pitcairnia albiflos*	Monocots	Bromeliaceae	Epiphyte	Tropical	0.300	0.112	ND[b]	Pereira et al. (2010)
62	*Pitcairnia flammea*	Monocots	Bromeliaceae	Rupicolous	Tropical	0.162	0.122	ND[b]	Pereira et al. (2009)
63	*Plantago coronopus*	Eudicots	Plantaginaceae	Herb	Temperate	0.210	0.629	PD	Dobarro et al. (2010)
64	*Plantago major*	Eudicotss	Plantaginaceae	Herb	Temperate	0.200	0.313	PD	Pons (1986)
65	*Poa nemoralis*	Monocots	Poaceae	Grass	Temperate	0.116	0.550	PD	Jankowska-Blaszczuk and Daws (2007)
66	*Scrophularia nodosa*	Eudicotss	Scrophulariaceae	Herb	Temperate	0.096	0.550	PD	Jankowska-Blaszczuk and Daws (2007)
67	*Silene scabriflora*	Eudicotss	Caryophyllaceae	Herb	Temperate	0.320	0.604	PD	Dobarro et al. (2010)
68	*Solanum hayesii*	Eudicotss	Solanaceae	Tree	Tropical	2.400	0.208	PD	Pearson et al. (2003)
69	*Stellaria nemorum*	Eudicotss	Caryophyllaceae	Herb	Temperate	0.285	0.500	PD	Jankowska-Blaszczuk and Daws (2007)
70	*Urtica dioica*	Eudicotss	Urticaceae	Herb	Temperate	0.170	0.900	PD	Jankowska-Blaszczuk and Daws (2007)

Table 1 continued

S. no.	Species	Clade	Family[a]	Growth form	Region	Seed mass (mg)	R:FR$_{50}$	Dormancy	References
71	*Vriesea heterostachys*	Monocots	Bromeliaceae	Epiphyte	Tropical	0.470	0.013	ND[b]	Pereira et al. (2009)
72	*Vriesea penduliflora*	Monocots	Bromeliaceae	Epiphyte	Tropical	0.470	0.026	ND[b]	Pereira et al. (2009)

[a] Based on the most recent Angiosperm Phylogeny Group classification (APG III 2009)

[b] Dormancy type found in the genus

Dormancy types: *PD* physiological dormancy, *PY* physical dormancy, *PYPD* physical plus physiological dormancy, *MPD* morphophysiological dormancy, and *ND* nondormant

Team 2013). The model was fit separately for maternal trees. Within each species, the mean value of x_0 was obtained.

Data analysis

Unless stated, the data were analyzed with R version 2.15.3 (R Core Team 2013). We were interested in two response variables in the data set, (a) a binary variable of light dependency of seed germination and (b) a continuous variable of R:FR$_{50}$ of each species. For explanatory variables, all species were categorized into two growth forms: woody species and nonwoody species (including herbs, grasses, and epiphytes). Due to the relatively small number of taxa in this study, dormancy types were only classified as nondormant versus dormant, and latitudinal distributions were restricted to tropical versus temperate. Seed mass was log$_e$ transformed before analysis.

Species characteristics, phylogenetic relationship, and light dependence

A phylogenetic tree for species included in this study was generated using Phylomatic (Webb and Donaghue 2005) using the most recent classification (Angiosperm Phylogeny Group 2009; R20091110 megatree). Since the megatree is for angiosperm taxa only, three gymnosperm species were excluded. The branch length was adjusted using age estimates for major nodes from Wikström et al. (2001) (*bladj* algorithm) using Phylocom 4.2 (Webb et al. 2008). There were some polytomies in the phylogenetic tree due to unresolved taxa.

The first response variable, light dependency of seed germination, was modeled as a binomial response. To examine whether light dependence for germination was influenced by seed mass, latitudinal distribution, dormancy, growth form, and phylogenetic relationship, the analysis was performed using a phylogenetic logistic model fitted by generalized estimating equations (GEE; Paradis and Claude 2002) (*compar.gee* in package *ape*). GEE explicitly incorporates the correlation matrix into the framework of a generalized linear model, without assuming a significant phylogenetic signal in the response. Before analysis using GEE, the branch length was transformed using Grafen's computation (Grafen 1989) with the power of 0.1 (*compute.brlen* in package *ape*).

We also analyzed the species data directly using logistic regression with binomial errors and compared the results with the model that controlled for shared evolutionary history.

The relationship of species R:FR$_{50}$ and species characteristics

The second response variable, R:FR$_{50}$, applied only to light-dependent species. The explanatory variables were seed mass, latitudinal distribution, dormancy type, and growth from. To understand the sources of variation in R:FR$_{50}$, data were analyzed using a regression tree (package *tree*). The regression tree was fitted using binary recursive partitioning. The aim is to partition the response variable into homogenous groups which are equivalent to minimizing in the sums of squares about the group means (De'ath and Fabricius 2000). To avoid overfitting by the regression tree, the number of splits that gives the minimum crossvalidated deviance was obtained, and the final regression tree was graphically presented. Linear regression and phylogenetically independent contrasts (Felsenstein 1985), obtained by the analysis of traits module in Phylocom 4.2, were then used to examine univariate relationships identified from the regression tree.

Results

In total, 29 tropical species and 43 temperate species, with 25 woody and 47 nonwoody taxa and 42 dormant and 30 nondormant taxa were included in the analysis (Table 1). Our data set, consisted of 26 light-independent and 46 light-dependent species. Seed size ranged from 0.01 (a temperate herbaceous species, *Crassula tillaea*) to 214 mg (a tropical tree species, *Cordia*

africana). The mean, median, and standard deviation of seed mass were 11.05, 1.06, and 30.96, respectively.

Predictors of light dependence

The phylogenetic logistic model that included all four explanatory variables found no significant effect of seed dormancy, and growth form on the probability that seed germination was light dependent ($P > 0.05$). Model simplification led to the retention of the main effects of log-seed mass and latitudinal distribution as predictors of light dependency. Log-seed mass had a strong negative effect on light dependence, while tropical species were predicted to be light dependent with greater probability than seeds of temperate species (Table 2). The odds of a tropical species, including gymnosperms, having light-dependent seed germination were 25.8 times greater than the odds for a temperate species (Fig. 1). The 50 % probability of a seed being light dependent corresponded to seed mass of 0.9 mg for temperate species, and 37 mg for tropical species. Results were qualitatively similar with and without accounting for phylogeny (Table 2).

Relationship of R:FR$_{50}$ with seed traits and latitudinal distribution

The R:FR required for 50 % of maximum germination varied greatly among species, ranging from 0.013 to 0.94. The variance of R:FR$_{50}$ was the same for tropical and temperate groups ($F = 1.34$, d.f. = 21, 23, $P = 0.49$). The regression tree analysis pointed to an influence of both dormancy and latitudinal distribution on R:FR$_{50}$ values. Nondormant species were associated with a lower R:FR$_{50}$ (mean R:FR$_{50}$ of 0.22) than species with dormant seeds (mean R:FR$_{50}$ of 0.50); however, the model including dormancy explained less

Table 2 Results of phylogenetic and across-species logistic models depicting the main effect of log-seed mass and latitudinal distribution on light dependency for germination.

The phylogenetic logistic model included 69 angiosperm species while there were 72 species for the across-species logistic model

Explanatory variable	Phylogenetic logistic model (GEE)			Across-species logistic model (GLM)		
	Estimate (SE)	t	P	Estimate (SE)	Z	P
Constant	0.11 (0.40)	0.28	0.7830	−0.07 (0.37)	−0.19	0.8483
Log seed mass	−0.84 (0.24)	−3.43	0.0012*	−0.88 (0.23)	−3.82	0.0001*
Latitudinal distribution	2.79 (1.06)	2.62	0.0117*	3.25 (0.99)	3.26	0.0011*

The asterisks show the significance level of $P < 0.05$

variation in R:FR$_{50}$ (pseudo $R^2 = 0.27$) than a parallel model that included latitudinal distribution rather than dormancy (pseudo $R^2 = 0.53$). Both factors were not included in the model because dormancy was strongly associated with latitudinal distribution (Fisher's exact test, $X^2 = 25.78$, d.f. $= 1$, $P < 0.0001$).
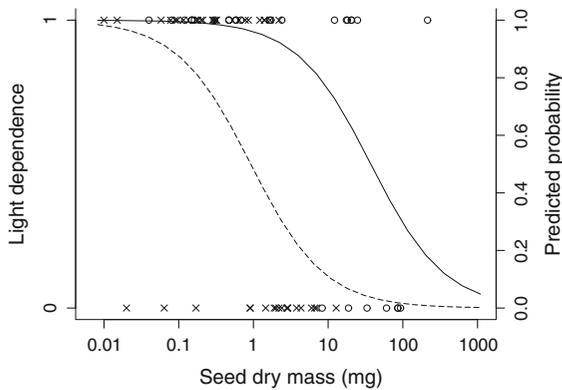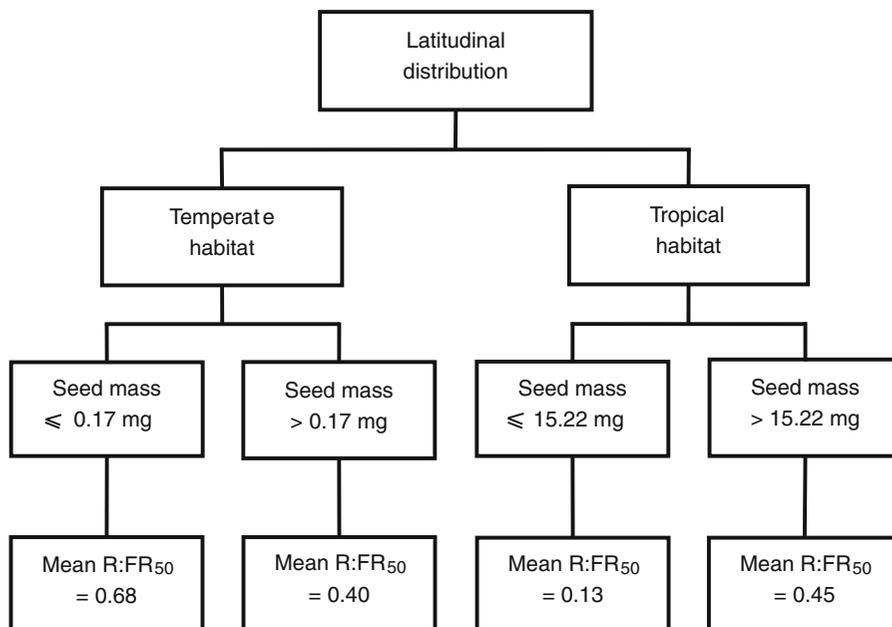

Fig. 1 Relationship between seed mass and light dependency of germination of 29 tropical (*white circle*) and 43 temperate species (*times*). The *y* axis represents light dependency (binary response); a value of *1* indicates light dependence and the value of *0* indicates light independence of germination. The *lines* represent the predicted probability of being light dependent as a function of log-seed mass of tropical (*solid line*) and temperate (*dashed line*) species

In addition to latitudinal distribution, seed mass was also an important explanatory variable in the regression tree (Fig. 2). Temperate species with seed mass <0.17 mg were associated with the highest mean R:FR$_{50}$ at 0.68. The mean R:FR$_{50}$ was 0.40 in temperate species with seed size >0.17 mg. For tropical taxa, species with seed mass >15.22 mg were associated with a higher R:FR$_{50}$ (0.45) than small-seeded tropical species (0.13). Therefore, the regression tree indicated that temperate and tropical species have contrasting relationships between seed mass and R:FR$_{50}$.

For tropical species, there was a positive relationship between log-seed mass and R:FR$_{50}$ ($R^2 = 0.34$, $F = 10.34$, d.f. $= 1$, 20, $P < 0.05$; Fig. 3a). In contrast, for temperate species, there was a negative linear relationship with seed mass ($R^2 = 0.20$, $F = 5.62$, d.f. $= 1$, 22, $P < 0.05$; Fig. 3b). The results accounting for phylogeny were qualitatively similar to the results of the linear regression for both tropical and temperate taxa (Fig. 3).

Discussion

In this study, we explored whether seed mass, latitudinal distribution, growth form, and seed

Fig. 2 Regression tree of R:FR$_{50}$ values for light-dependent species. The two explanatory variables were latitudinal distribution and seed mass. Each terminal node is labeled with mean R:FR$_{50}$ of each group
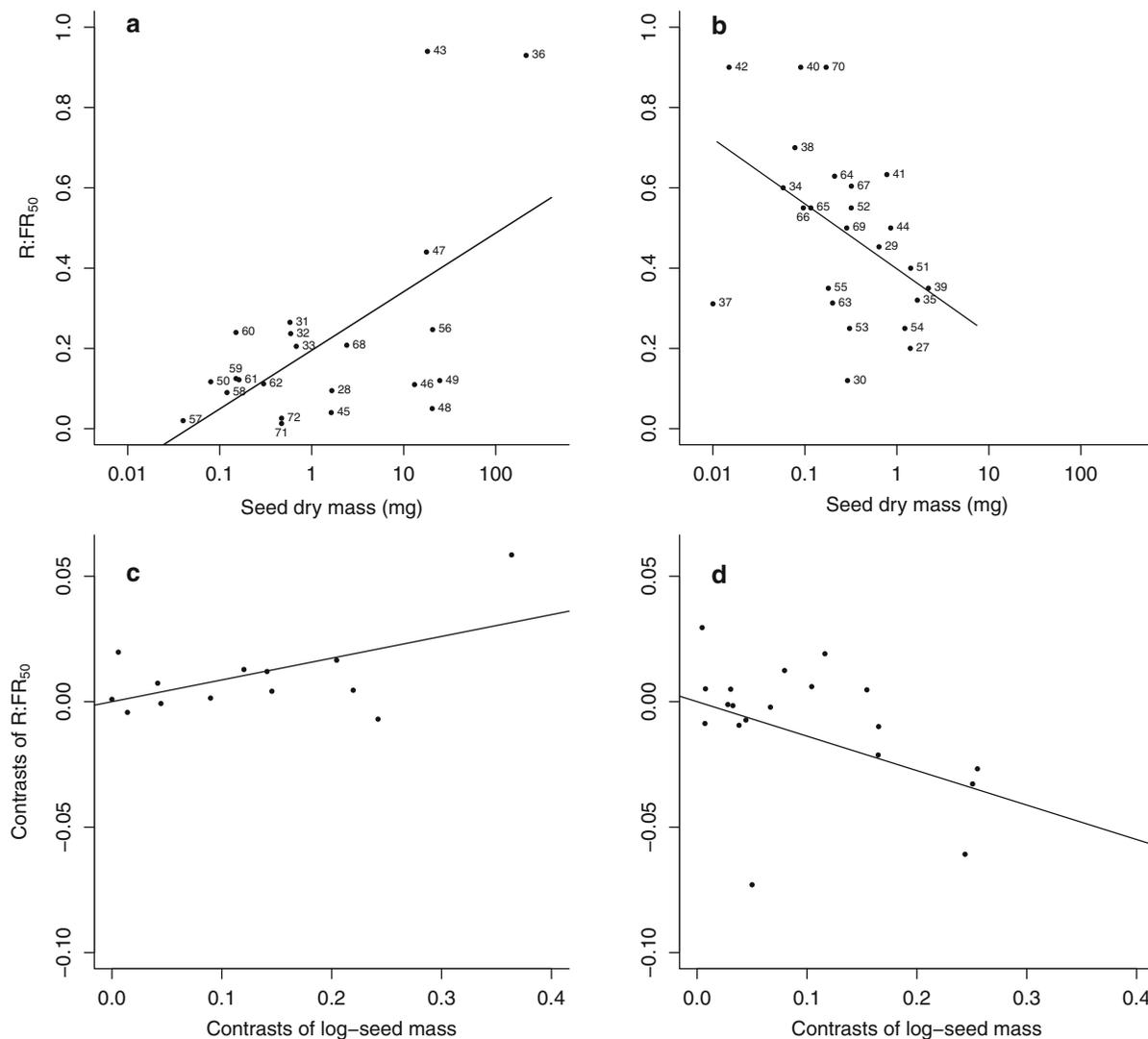
Fig. 3 The relationship between R:FR$_{50}$ and log-seed dry mass for **a** 22 light-dependent tropical species ($Y = 0.06X + 0.20$; $R^2 = 0.34$, $P = 0.004$) and **b** 23 light-dependent temperate species ($Y = -0.07X + 0.40$; $R^2 = 0.20$, $P = 0.03$). The numerical labels corresponding to the species are shown in

Table 1. Linear regression through the origin of phylogenetically independence contrasts of **c** tropical ($n = 13$, $Y = 0.09X$, $R^2 = 0.32$, $P = 0.04$), and **d** temperate taxa ($n = 19$, $Y = -0.14X$, $R^2 = 0.21$, $P = 0.04$)

dormancy are associated with light-dependent seed germination. Of these, we found latitudinal distribution and seed mass influenced the probability that seeds were light dependent, and the sensitivity of germination to R:FR represented by R:FR$_{50}$. Comparing temperate and tropical habitats, we found that R:FR$_{50}$ was positively correlated with seed mass in tropical species, and negatively correlated with seed mass in temperate species. Thus, our data supported the hypothesis that distinct selective forces determine

germination response to R:FR in tropical and temperate species.

Light dependency of seed germination

Logistic regression analysis, implemented while accounting for phylogenetic distance, showed that the smaller seeds were more likely to require light for germination than the larger ones. This finding agreed with previous studies that reported the light

requirement for germination in small-seeded herbaceous and woody species from temperate and tropical habitats (Milberg et al. 2000; Jankowska-Blaszczuk and Daws 2007; Galíndez et al. 2009). In temperate forest, Jankowska-Blaszczuk and Daws (2007) found that a seed dry mass of 1.5 mg was an approximate cutoff between herbaceous species that are light dependent and species that are not. For tropical pioneer tree species, Pearson et al. (2002) found that species with seed size <2 mg require light; larger seeds were more likely to rely on fluctuating temperature as a germination cue. In our compilation of species, the cutoff for light dependency was difficult to determine due to large variation in seed mass in the light-dependent germination group, including the largest seeded species in the study, *C. africana* (214 mg), from tropical forest. On comparison, the largest seeded temperate species with light-dependent germination was *Geranium robertianum* (2.2 mg). However, factors other than light may also contribute to the germination response of *C. africana*. In some species (*Solanum hayesii*, *Holcus lanatus* and *Poa anuua*), temperature fluctuations can trigger germination in the dark, while light may at least partially substitute for fluctuating temperatures (Thompson and Grime 1983; Pearson et al. 2003). Future studies are needed to disentangle temperature and R:FR responses across gradients of seed size.

Seed dormancy and plant growth form did not have significant effects on the light dependency of species. These results were consistent with a previous study of 136 cacti species that found no relation between light-dependent germination and either dormancy or cactus morphology (six physical forms of cacti) (Flores et al. 2011). However, in our study seed dormancy and growth form were also correlated with latitudinal distribution, potentially masking their effects on light requirements.

R:FR$_{50}$ responses of germination

R:FR varies continuously from deep shade to open sky conditions providing a sensitive indicator of canopy vegetation and surface litter conditions. While knowing whether seeds germinate in the absence of light provides some information on the regeneration requirements of plants, vegetation does not consist of a binary patchwork of open sun and full shade (Lieberman et al. 1989). Therefore, understanding how species respond to gradients in R:FR provides insight into the potential for fine-scale partitioning of light gradients akin to the partitioning of gradients in soil moisture availability or soil fertility. For temperate species, the relationship between R:FR$_{50}$ for seed germination and seed mass paralleled that between seed mass and light dependency. The R:FR$_{50}$ for germination is calculated as the R:FR under which 50 % of maximum seed germination is observed. In temperate habitats, smaller-seeded light-dependent species required a higher R:FR$_{50}$ for germination than the larger seeded ones. This suggests that small-seeded temperate species restrict germination to high light environments, or that a high R:FR$_{50}$ prevents small-seeded species from germinating beneath soil depths at which seed reserves would be insufficient to allow successful emergence. This is in accordance with the results of an earlier study (Jankowska-Blaszczuk and Daws 2007), which included 16 of the 24 temperate species in this study.

In contrast to temperate species, a positive relationship was observed between seed mass and R:FR$_{50}$ for tropical species. This indicates that small-seeded species were capable of germinating under a wider range of R:FR values than larger seeded species. This result supported the initial finding of Pearson et al. (2003), based on data for nine species from a seasonally moist tropical forest in Panama, suggesting that the opposing relationship of R:FR$_{50}$ and seed mass between temperate and tropical species is robust.

Jankowska-Blaszczuk and Daws (2007) proposed that a higher risk of lethal desiccation for small-seeded species could explain the positive relationship between seed mass and R:FR$_{50}$ in the tropical species were observed by Pearson et al. (2003). Desiccation tolerance is important for tropical seedlings because surface soil layers in large forest gaps that receive high R:FR dry more quickly than gaps that are partially shaded, or receive direct irradiation for shorter periods during the day (Engelbrecht et al. 2006). The potential for lethal desiccation to impact seedling recruitment is supported by experimental data that shows that dry periods of a few days' duration are sufficient to cause mortality of newly emerging seedlings (Engelbrecht et al. 2006). Furthermore, drought may most strongly impact the smallest seeded species because root extension rate is positively correlated with seed mass (Daws et al. 2007). Finally, consistent with differences in R:FR requirements, Daws et al. (2008) also showed

that large-seeded species are capable of germinating under drier conditions (lower base water potentials) than smaller seeded species.

Here, we question whether desiccation sensitivity is a sufficient explanation for contrasting seed mass–$R:FR_{50}$ relationships in temperate and tropical forests. A key limitation of the desiccation risk hypothesis is that it would predict a unimodal relationship between R:FR and germination success, rather than a threshold response. In other words, if desiccation risk was the primary determinant of germination response, then we would expect small-seeded species to germinate only at low or intermediate R:FR, but not at high R:FR. If desiccation risk drives germination response, then we would also predict that species from tropical forests, which show similar seed mass–$R:FR_{50}$ relationships would also show similar relationships between seed mass and the base water potential under which seeds germinate. Contrary to this expectation, we found that base water potential for the pioneers from our paleotropical site (Lambir) was not significantly correlated with seed mass, and was substantially higher (range from 0.81 to −0.38 MPa; Tiansawat, unpublished data) than those reported for species from seasonal forest in Panama (ranging from −2.02 to −1.07 MPa; Daws et al. 2008). Therefore, species from aseasonal forests in Lambir are restricted to germinating under much higher soil moisture conditions.

A more likely explanation for differing seed mass–R:FR relationships is that small-seeded pioneer species of tropical forests are simply less "choosy" in their germination response to R:FR (Pearson et al. 2003). The differential responses of temperate and tropical taxa may then represent differential selection on germination under low R:FR. Jankowska-Blaszczuk and Daws (2007) rejected the "choosiness hypothesis" on the grounds that small-seeded species form persistent seed banks in a range of habitat types. They argue that greater persistence in small-seeded species increases the probability that seeds will encounter optimal germination conditions during burial, selecting for more selectivity in germination cues.

In contrast, here we argue that small-seeded tropical seeds should be less choosy. Three factors that differ between temperate and tropical taxa are likely to impact risk. First, the temperate taxa included in our analysis were all herbaceous plants, which are expected to have low-reproductive output (relative to

trees). Therefore, recruitment of our temperate herbaceous taxa into suitable regeneration sites may be more strongly dispersal limited than the tropical tree taxa that can produce millions of seeds that accumulate in densities of >9,000 seeds m^{-2} at sites beneath parent crowns, and produce seed shadows that can extend >100 m (Dalling et al. 1998; Dalling et al. 2002; Jones et al. 2005; Corlett 2009). Second, while seed mass is negatively correlated with seed bank persistence in most temperate ecosystems (Thompson et al. 1993; Funes et al. 1999; Cerabolini et al. 2003 but see Leishman and Westoby 1998; Moles et al. 2000 for exceptions), in tropical forests, very small-seeded species appear to have short-lived seed banks (Dalling et al. 1997), while much longer persistence (>30 years) has been demonstrated for relatively large-seeded taxa (Dalling and Brown 2009). In addition, soil perturbation by rainfall and ants in tropical forest rapidly bury small seeds to soil depths below which they are capable of emerging (Pearson et al. 2002; Marthews et al. 2008). Thus, longer persistence and stronger dispersal limitation in larger seeded taxa may select for greater discrimination of the R:FR that stimulates germination in large-seeded tropical taxa.

Our results demonstrate that the difference in the relationship of seed mass and $R:FR_{50}$ between tropical and temperate forests seems to be robust. To better understand how selection operates in each habitat, further studies are needed that incorporate contrasts between herbaceous and woody species, and among species with different seed persistence times.

Our finding also informs a more general hypothesis that trade-offs between fecundity and tolerance to physical and biotic stresses maintain seed size variation in plant communities. Muller-Landau (2010) proposed that in heterogeneous habitats, larger seedlings produced by larger seeded species are more tolerant to stresses such as shade, drought, or defoliation, while smaller seeded species with high fecundity are more likely to occupy and win less stressful sites. Whether small seeded tropical species germinate in less stressful environments is unclear, but higher fecundity presumably allows seeds to risk germinating in microsites with lower R:FR where the probability of encountering favorable conditions for onward growth is lower. In contrast, for the temperate herbaceous species included in this study, small seed size may provide little escape from dispersal limitation relative

to trees. Instead, in accordance with Muller-Landau's hypothesis, large seed mass may be advantageous in surviving shade or litterfall, while small seeded species can await better illuminated microsites through longer persistence in the soil.

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