

LETTER

Does a latitudinal gradient in seedling survival favour larger seeds in the tropics?

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Abstract

The mean size of seeds produced by plants at the equator is two to three orders of magnitude higher than the mean size of seeds produced by plants at 60°. We compiled data from the literature to assess the possibility that this latitudinal gradient in seed size allows species to cope with more difficult seedling establishment conditions in tropical environments. We found no relationship between latitude and seedling survival through 1 week ($P = 0.27$, $n = 112$ species). There was also no evidence that a larger seed mass is required to gain a given level of seedling survival in tropical environments ($P = 0.37$, $n = 112$ species), and no relationship between latitude and the duration of the juvenile period ($P = 0.57$, $n = 132$ species). Thus, our results are not compatible with the idea that seedling establishment is more difficult in the tropics.

Keywords

Latitude, seed mass, seedling establishment, seedling mortality.

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INTRODUCTION

It has long been known that there is a latitudinal gradient in seed mass (Baker 1972; Levin 1974; Lord *et al.* 1997). Recent work suggests that community mean seed mass is 2–3 orders of magnitude greater at the equator than at 60° north or south (Moles & Westoby 2003). The amount of variation in seed mass explained by latitude is surprisingly high. Despite the fact that seed mass ranges over six orders of magnitude within many floras (Leishman *et al.* 2000), latitude explained 21% of the variation in seed mass across 2706 species from around the world (Moles & Westoby 2003).

Latitudinal gradients in habitat shadiness, growth form, dispersal syndrome and the length of the growing period are all likely to contribute to the observed gradient in seed mass. Woody growth forms are more prevalent in the tropics than in the temperate zone, and trees make larger seeds than do shrubs, which make larger seeds than do herbaceous species (Levin 1974; Leishman *et al.* 1995; Lord *et al.* 1997). Similarly, biotic seed dispersal is associated with large-seededness, and is more prevalent in the tropics than at higher latitudes (Leishman *et al.* 1995; Lord *et al.* 1997). In addition, species establishing in shady habitats have larger seeds than species establishing in more open conditions (e.g. Salisbury 1974; Foster & Janson 1985), and tropical

environments tend to have a high leaf area index (Asner *et al.* 2003). Finally, there is some evidence that the length of the growing period might constrain the upper limit of seed mass that can be attained in a given environment (Stebbins 1974; Moles & Westoby 2003). Although all of these factors might contribute to the latitudinal gradient in seed mass, this gradient persists even after growth form, vegetation type, or dispersal syndrome have been controlled for (Levin 1974; Lord *et al.* 1997).

Another possibility is that higher levels of herbivory (Coley & Aide 1991; Swihart *et al.* 1994), greater risk of pathogen attack or greater competition for light (associated with the higher leaf area index, Asner *et al.* 2003) in tropical ecosystems favour large-seeded species whose seedlings are better able to withstand periods of carbon shortage (Leishman *et al.* 2000). In this paper, we provide the first direct test of this hypothesis.

METHODS

Seed mass and seedling survival data for 112 species were taken from a compilation of data from the global literature (Moles & Westoby 2004a). This compilation aimed to collate data on seedling survival through 1 week under natural conditions. Studies in which seedlings were raised in

pots, within enclosures, under shelters, with extra watering, with any kind of pesticide, supplementary fertilization or weeding, or in which seedlings were grown in glasshouses or transplanted were excluded. Studies in which seedlings were not studied from the day they emerged, and studies that did not report their sample size, or that included fewer than 10 individuals of a species, were also excluded. The studies included in this compilation followed seedlings over various amounts of time, mostly much greater than a single week. Here, we use estimates of the proportion of seedlings surviving through the first week (see Moles & Westoby 2004a for details of calculation) to allow comparison of these disparate data. One week should be early enough in seedling development to avoid complications arising from the fact that the advantages of large-seededness dissipate once the seed reserves have been fully deployed (Leishman *et al.* 2000; Moles & Westoby 2004a).

STATISTICS

We analysed the relationship between seedling survival and latitude with random effects logistic regression, which appropriately uses a binomial data structure (seedlings either live or die) within each species, and includes a term for species-to-species variation due to factors other than latitude (see Moles & Westoby 2004a). Analyses were performed with WINBUGS version 1.3 (MRC Biostatistics Unit 2002).

We also performed phylogenetic regression (Grafen 1989) on the relationship between latitude and seedling survival, using the phylogenetic tree presented by Moles & Westoby (2004a). Phylogenetic random effects logistic regression has not been invented yet, so we performed a linear phylogenetic regression with logit-transformed survival data, using PHYLO.GLM version 1.03 (Grafen 1989). In order to avoid computational problems with zero (and 100%) survival values in linear regressions and on graphs, 0.5 was added to (or subtracted from) the number of surviving individuals recorded for these species. This process was not used on data for logistic regressions, which treat 0s and 100s appropriately.

RESULTS

We found no significant relationship between latitude and the proportion of seedlings surviving the first week after emergence either in the cross-species analysis [$P = 0.27$; slope = -0.02 (95 % CI = -0.05 to 0.01); SE of the species random effect = 2.15], or in the phylogenetic regression ($P = 0.26$; d.f. = 1,62; $R^2 = 0.02$).

Species from forests and grasslands are not randomly distributed in relation to latitude (Fig. 1a). In random effects logistic regression with a term for vegetation type included,

vegetation type had significant influence ($P = 0.006$) on the relationship between seedling survival and latitude. In grasslands there was a weak negative relationship between latitude and seedling survival [$P = 0.03$; slope = -0.06 (95% CI = -0.11 to -0.02); SE of the species random effect = 2.11; $n = 43$ species]. In forests there was no significant relationship between latitude and seedling survival [$P = 0.08$; slope = 0.03 (95 % CI = 0.005 – 0.07); SE of the species random effect = 2.75; $n = 69$ species]. The weakness of these within-habitat results indicates that the overall lack of a relationship between latitude and seedling survival is not an artefact generated by pooling results from different habitats.

There was no relationship between latitude and seedling survival. However, there is a strong negative relationship between latitude and seed mass (Levin 1974; Lord *et al.* 1997; Moles & Westoby 2003, Fig. 1b), and a strong positive relationship between seed mass and seedling survival per week (Moles & Westoby 2004a, Fig. 1c). To test whether seeds of a given size lead to different rates of seedling survival at different latitudes, we fitted a random effects logistic regression as previously, but with linear terms for latitude and seed mass. The term for latitude was not significantly different from zero ($P = 0.37$). Thus, seeds of a given size are not associated with significantly different rates of seedling survival at different latitudes. It is therefore not the case that species growing near the tropics need to produce larger seeds to achieve the same levels of seedling survival as species growing farther from the equator.

We found no significant relationship between latitude and seedling survival through 1 week, and no significant relationship between latitude and the seed mass required for a given level of seedling survival. These analyses included 112 species from a wide range of latitudes. Therefore, the lack of significant results is unlikely to be due to a lack of statistical power. The only way our results could be compatible with the idea that seedling establishment is more difficult in tropical environments would be if seedlings growing close to the equator were exposed to a longer period of juvenile mortality. This could possibly arise as a consequence of the greater proportion of large woody species in the tropics, combined with the association between plant size and the length of the juvenile period (Moles *et al.* 2004). To investigate this possibility we combined data on the time taken for 132 species to reach reproductive maturity (from Moles *et al.* 2004, data available at <http://www.blackwell-publishing.com/products/journals/suppmat/JEC/JEC880/JEC880sm.htm>) with information on the latitude at which each species was studied. We found no relationship between latitude and the duration of the juvenile period across species ($P = 0.57$, Fig. 2). This rules out the possibility that tropical species need larger seeds to survive a longer period of exposure to juvenile mortality.

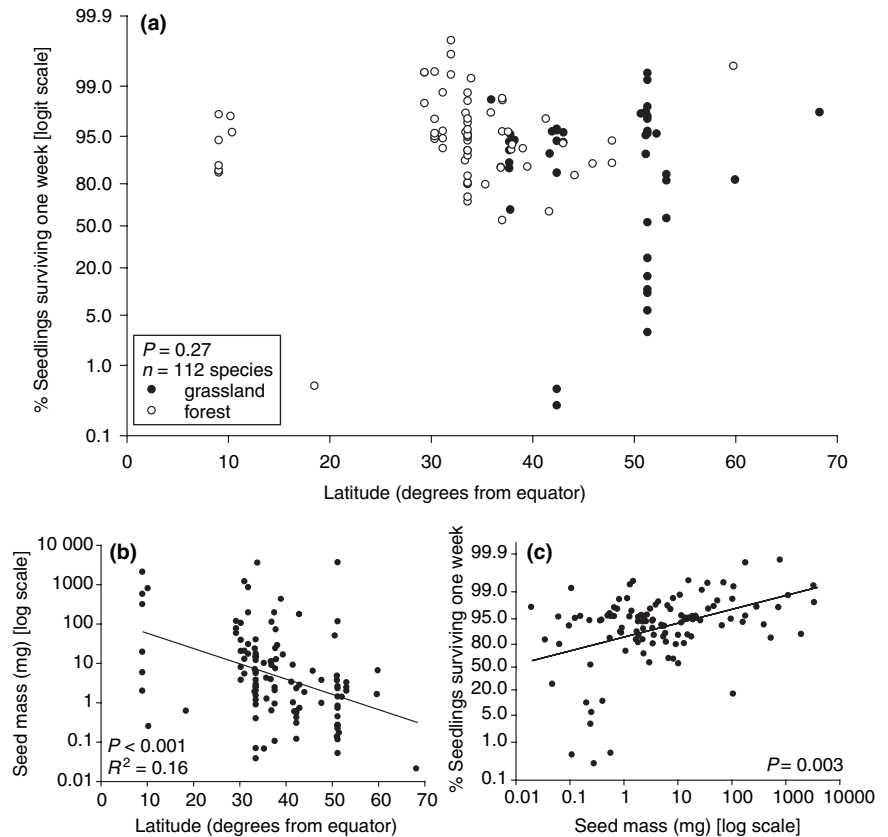


Figure 1 (a) Latitude vs. seedling survival through 1 week. (b) Seed mass vs. latitude. (c) Seed mass vs. seedling survival. Each point represents one species.

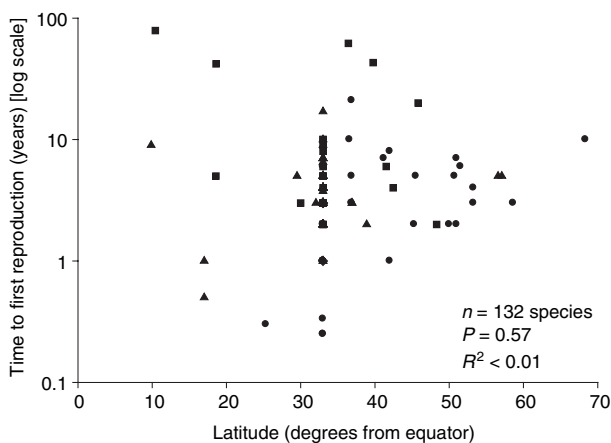


Figure 2 Latitude vs. time to first reproduction. Each point represents one species. Trees are represented by squares, shrubs by triangles, herbs by circles and climbers by diamonds.

DISCUSSION

The data presented here are not compatible with the idea that the larger seeds of tropical species evolved to counter the greater difficulty of establishing seedlings in tropical environments. Thus, we are left with two main questions:

(1) why is there no relationship between latitude and seedling survival, and (2) why is there a latitudinal gradient in seed size?

Perhaps the simplest explanation for the lack of a relationship between latitude and seedling survival is that a latitudinal gradient in mortality due to biotic factors is countered by a latitudinal gradient in mortality due to abiotic factors. We attempted to assess the validity of this hypothesis by combining the available data on seedling mortality under natural conditions (Moles & Westoby 2004b) with data on the latitude at which these data were gathered. We found no significant relationship between latitude and the proportion of seedlings whose deaths were attributed to biotic causes ($P = 0.54$). However, the sparsity of the data (20 species from 11 sites) make it difficult to tell whether this is a genuine null result, or simply an artefact resulting from a lack of power. This would be a worthwhile area for further research, as the (untested) idea that biotic interactions are stronger in the tropics is central to a number of hypotheses regarding the generation of a latitudinal gradient in species richness (Rohde 1992; Willig *et al.* 2003).

Previous studies have demonstrated that neither growth form, vegetation type, nor a combination of growth form and dispersal syndrome can entirely explain the latitudinal gradient in seed mass (Levin 1974; Lord *et al.* 1997).

However, latitudinal gradients in the length of the growing season, habitat shadiness, plant growth form, dispersal syndrome and net primary productivity could all contribute to the observed gradient in seed mass (Moles & Westoby 2003). Further, none of the mechanisms through which these factors might influence seed mass are mutually exclusive. It therefore seems most likely that the latitudinal gradient in seed mass arises through a combination of these factors. We will attempt an assessment of the proportion of variation in the latitudinal gradient in seed mass attributable to each of these variables in future work.

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