Interspecific Variation in Seed Size and Safe Sites in a Temperate Rain Forest

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Interspecific variation in seed size and safe sites in a temperate rain forest

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Summary

- The safe site concept could have utility in community ecology if predictive relationships between plant traits and safe site characteristics could be identified. Here we examine the proposal that the nature and relative abundance of safe sites are systematically related to seed size, in an assemblage of 17 woody species in a temperate forest.
- We compared the degree of association of seedlings of each species with elevated microsites, and examined life-history correlates of this variation.
- Seed size explained 45% of interspecific variation in percentage of seedlings growing on logs and other elevated substrates. Neither specific leaf area nor an index of light requirements gave significant increases in explanatory power. Phylogenetically independent contrasts gave a similar, but weaker, relationship with seed size. Most small-seeded species were overrepresented on elevated microsites, whereas two large-seeded taxa were underrepresented on these substrates. Safe sites of small-seeded species were therefore more spatially restricted than those of large-seeded taxa, as elevated surfaces occupied only 8% of the forest floor.
- Safe site differentiation may help to explain the wide range of seed size present within many communities, as well as species coexistence in forests.

Key words: coexistence, leaf litter, nurse logs, seed mass, shade tolerance.


Introduction

It is generally accepted that the processes of germination, emergence and seedling establishment are critical in determining the fate of individual plants, and hence in shaping community dynamics (Grubb, 1977; Harper, 1977; Fowler, 1988). The microsites that provide favourable conditions for these crucial early processes in a given population are often discontinuous or localised in space and time. Identification of such ‘safe sites’ (Harper et al., 1961) has therefore been a focus in demographic studies (e.g. June & Ogden, 1975; Christy & Mack, 1984; Fowler, 1988).

The utility of the safe site concept will be translatable from demography into community ecology if predictive cross-species relationships between plant functional traits and safe site requirements can be clearly identified. The forest dynamics literature provides abundant evidence that the seedlings of different tree species respond differentially to the mosaic of substrates present on forest floors (Stewart & Veblen, 1982; Putz, 1983; Christy & Mack, 1984; Beatty & Stone, 1986; Nakashizuka, 1989; Lusk & Ogden, 1992; Molofsky & Augspurger, 1992). Seedlings of some species have been reported as largely restricted to fallen logs and other elevated substrates, while others are abundant on undisturbed forest floor microsites covered by deep litter (Stewart & Veblen, 1982; Harmon & Franklin, 1989; Nakashizuka, 1989; Hofgaard, 1993; Lusk, 1995). One of the most striking examples of the ‘nurse log’ syndrome was reported from Picea-Tsuga forests in the Pacific North-west, where 88–97% of seedlings of the dominants are concentrated on logs (McKee et al., 1982), which cover a mere 6–11% of the forest floor (Graham & Cromack, 1982). Thus, safe sites for Picea and Tsuga can be said to occur largely on elevated substrates in these forests, in that the sum of differences in seed arrival, germination, seedling emergence and/or survival consistently gives rise to much higher seedling densities on logs.
Variation in substrate occupancy in forests has been linked to seed size by some authors (Ng, 1978; Putz, 1983). A study of a Chilean temperate forest (Lusk, 1995) found that seedlings of small-seeded species were strongly associated with elevated microsites, whereas large-seeded species were either slightly underrepresented on these substrates or showed no clear preference. One possible explanation for this pattern is that small-seeded species may have difficulty penetrating the litter that accumulates on the forest floor, resulting in a heavy dependence on elevated microsites, which tend to slough litter (Christy & Mack, 1984). Although similar empirical patterns have been reported elsewhere (Nakashizuka, 1989; Lusk & Ogden, 1992; Molofsky & Augspurger, 1992), other mechanistic explanations of the nurse log syndrome have also been explored (e.g. Harmon & Franklin, 1989).

In this paper we show that the nature and relative abundance of species’ safe sites are related to seed size in a Chilean temperate rain forest. We compared the degree of association of seedlings with elevated microsites for a complete assemblage of 17 woody species, and examined life history correlates of interspecific variation in substrate occupancy. The present paper builds on an earlier study at a similar site (Lusk, 1995) by explicitly inserting the nurse log issue of forest ecology into the wider context of the safe site, and provides a stronger test by using a larger assemblage. Furthermore, in order to best infer functional relationships between safe sites and plant traits, we accounted for potential effects of phylogenetic relatedness by applying independent contrasts analyses (Harvey & Pagel, 1991; Kelly, 1995).

### Materials and Methods

#### Study site

Sampling was carried out in low-altitude forests (350–440 m a.s.l.) in Parque Nacional Puyehue (40°39’ S, 72°11’ W) located in the western foothills of the Andes in south-central Chile. The climate is maritime temperate, with an average annual precipitation of around 3500 mm (Almeyda & Saez, 1958). The old-growth rain forest of the lower western slopes of the Andes is composed exclusively of broad-leaved evergreen species (Table 1). Seed size within the assemblage spans 4.4 orders of magnitude.

#### Sampling

Sampling was carried out on a series of transects run throughout a total area of about 125 ha of old-growth forest. At sample points spaced at random intervals (2–10 m apart) along transects, seedlings (10–50 cm tall) were recorded in a circular quadrat of 1-m diameter. A total of 1616 points were sampled, yielding a total of 1321 seedlings, with species representation ranging from 21 to 341 individuals overall. One species represented by only two individuals (Lomatia hirsuta) was discarded, as was Pseudopanax laetevires, which usually establishes as an epiphyte but occasionally appears on the forest floor.

Substrate at each sampling point was classified as ‘elevated’ or ‘forest floor’. Most elevated microsites were fallen logs, with fewer stumps. Uprooting appeared to be less common than

### Table 1 Measured life history traits of study species, and data showing association (+ ve or – ve) with elevated substrates

<table>
<thead>
<tr>
<th>Species</th>
<th>Seed mass (mg)</th>
<th>Light requirements (% canopy openness)</th>
<th>Seedling SLA (cm² g⁻¹)</th>
<th>Total no. of seedlings</th>
<th>% on elevated sites</th>
<th>Association with elevated sites</th>
<th>Density (m⁻²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arbutus unedo</td>
<td>10</td>
<td>26</td>
<td>212</td>
<td>69</td>
<td>8.7</td>
<td>NS</td>
<td>0.037</td>
</tr>
<tr>
<td>Arctostaphylos uva</td>
<td>34.5</td>
<td>8</td>
<td>104</td>
<td>111</td>
<td>9.0</td>
<td>NS</td>
<td>0.061</td>
</tr>
<tr>
<td>Astragalus fasciculatus</td>
<td>120</td>
<td>10</td>
<td>154</td>
<td>68</td>
<td>9.0</td>
<td>– ve (P = 0.002)</td>
<td>0.061</td>
</tr>
<tr>
<td>Azara lanceolata</td>
<td>2.7</td>
<td>10</td>
<td>152</td>
<td>76</td>
<td>30.3</td>
<td>+ ve (P = 0.04)</td>
<td>0.141</td>
</tr>
<tr>
<td>Calceolaria brachypoda</td>
<td>0.06</td>
<td>9</td>
<td>126</td>
<td>63</td>
<td>9.5</td>
<td>NS</td>
<td>0.037</td>
</tr>
<tr>
<td>Emblica officinalis</td>
<td>14</td>
<td>100</td>
<td>175</td>
<td>20</td>
<td>5.0</td>
<td>NS</td>
<td>0.006</td>
</tr>
<tr>
<td>Eucalyptus marginata</td>
<td>1.6</td>
<td>10</td>
<td>132</td>
<td>37</td>
<td>18.9</td>
<td>+ ve (P &lt; 0.03)</td>
<td>0.043</td>
</tr>
<tr>
<td>Fuchsia magellamic</td>
<td>0.4</td>
<td>60</td>
<td>287</td>
<td>23</td>
<td>8.7</td>
<td>NS</td>
<td>0.012</td>
</tr>
<tr>
<td>Gevuina avellana</td>
<td>1950</td>
<td>7</td>
<td>95</td>
<td>41</td>
<td>9.8</td>
<td>NS</td>
<td>0.025</td>
</tr>
<tr>
<td>Luma apiculata</td>
<td>17.4</td>
<td>15</td>
<td>116</td>
<td>72</td>
<td>5.6</td>
<td>NS</td>
<td>0.025</td>
</tr>
<tr>
<td>Lomatia ferruginea</td>
<td>7.8</td>
<td>9</td>
<td>95</td>
<td>57</td>
<td>19.3</td>
<td>+ ve (P = 0.005)</td>
<td>0.067</td>
</tr>
<tr>
<td>Laurelia philippiana</td>
<td>1.7</td>
<td>4</td>
<td>128</td>
<td>47</td>
<td>55.3</td>
<td>+ ve (P &lt; 0.001)</td>
<td>0.159</td>
</tr>
<tr>
<td>Myrtus communis</td>
<td>46</td>
<td>1</td>
<td>111</td>
<td>341</td>
<td>5.0</td>
<td>– ve (P = 0.02)</td>
<td>0.104</td>
</tr>
<tr>
<td>Nandina domestica</td>
<td>1.8</td>
<td>37</td>
<td>124</td>
<td>22</td>
<td>40.9</td>
<td>+ ve (P &lt; 0.001)</td>
<td>0.055</td>
</tr>
<tr>
<td>Rhododendron pachyasperosus</td>
<td>35.7</td>
<td>6</td>
<td>137</td>
<td>58</td>
<td>5.2</td>
<td>NS</td>
<td>0.018</td>
</tr>
<tr>
<td>Weinmannia trichosperma</td>
<td>0.08</td>
<td>13</td>
<td>115</td>
<td>21</td>
<td>42.9</td>
<td>+ ve (P &lt; 0.001)</td>
<td>0.055</td>
</tr>
</tbody>
</table>

Light requirements represent the light environment in which juveniles of each species attain their highest density in the understorey (C. H. Lusk & G. Hofmann, unpublished).
reported in some temperate forests (Beatty & Stone, 1986; Nakashizuka, 1989), with the result that recent tip-up mounds and pits were uncommon. The few mounds that were encountered were classified as 'elevated', and pits were grouped with forest floor microsites.

A pair of LAI-2000 canopy analysers (Li-Cor, Lincoln, Nebraska) was used to quantify light environments at sampling points. One instrument was used to take measurements at each sampling point, while the other, placed at the centre of a 2-ha clearing, was programmed to take readings at 30-section intervals. Integration of data from the two instruments enabled estimation of percentage diffuse nonintercepted irradiance at each sampling point within the forest, equivalent to percentage canopy openness over the quasi-hemispherical (148°) field of view perceived by the LAI-2000 sensors. Measurements with the LAI-2000 are a good surrogate of spatial variation in mean daily photosynthetic photon flux density within a stand (Machado & Reich, 1999). As we explain below, these data were used to quantify species' differences in shade tolerance.

Species traits

We examined three key traits that could potentially influence safe site requirements: seed mass, shade-tolerance, and specific leaf area (SLA). Seed (strictly, diaspore) mass of most species was obtained from Donoso & Cabello (1978). For the remainder, seeds were collected at the study site and weighed.

As logs and other elevated substrates are likely to be associated with well-lit, recently disturbed environments, differences in substrate occupancy could be partly a reflection of shade tolerance variation. To explore this possibility, we also examined the relationship of substrate occupancy with species light requirements, as indexed by the light environment (% canopy openness) in which juveniles of each species attain their highest densities. These modal light environments were estimated with a generalised linear model of variation in density in relation to canopy openness (C. H. Lusk & G. Hofmann, unpublished data), using a β-function (Austin et al., 1994):

\[
\text{density} = a \times (\text{openness})^b \times (1 - \text{openness})^c,
\]

where \(a, b, c, L\) are parameters. The value of \(b\) represents the rate of increase in density with increasing canopy openness, for low light conditions, while \(c/L\) represents the rate of decrease for light ranges beyond the optimum.

As variation in SLA is often correlated with species differences in relative growth rates (Poorter & Remkes, 1990; Cornelissen et al., 1996; Walters & Reich, 1999), it could also potentially influence safe site preferences, through possible effects on the ability of seedlings to avoid burial by litter accumulation. SLA was therefore measured on four individuals of each species, growing in standardised light environments of 10% canopy openness, as measured with the LAI-2000.

Statistical analyses

Randomisation tests were used to determine if each species was more or less common on elevated substrates than would be expected by chance. Multiple regression (JMP Statistical Software, SAS Institute Inc., Cary, NC, USA) was used to explore relationships of seed mass, light requirements and SLA with the degree of dependence on elevated substrates. All of these variables were log-transformed in order to normalise distributions and linearise relationships.

Independent contrasts analyses

In order to best infer functional relationships between safe sites and plant traits, we also accounted for potential effects of phylogenetic relatedness by applying independent contrasts analyses (Harvey & Pagel, 1991; Kelly, 1995). Comparison of results from independent contrasts and cross-species analyses enabled us to identify biases arising from group-specific values of a trait that would confound an inference of functional significance in the context currently under study. That is, if independent contrasts analyses do not show seed size to be correlated with proportion of seedlings on elevated substrates, then, even if cross species analysis does show such a correlation, it would be unwise to infer from the evidence available here that seed size is the functional determinant of safe site use.

The phylogenetic tree used to carry out the independent contrasts analyses for the target species (Fig. 1) was based on Soltis et al. (2000). This tree is resolved only to family level and relationships within the Proteaceae and Myrtaceae, which had multiple members in the data set, followed Johnson & Briggs (1975) and McVaugh (1968), respectively. The recent phylogeny by Soltis et al. (2000) produced only one difference (albeit one of some consequence) from previous phylogenies in the form of the Aextoxicaceae being moved from its previous position within the Celastrales to a dichotomy shared with the rosid clade (Thorne, 1993). While it would be of interest if previous treatments had failed to identify correctly the Aextoxicaceae as a member of a major clade on a par with the rosids, we have an opportunity here to examine directly the change represented by this new arrangement. We investigated the difference between the results assuming the correctness for the Aextoxicaceae of previous classifications based on the complex, multigene character of floral morphology vs the more recent three-gene phylogeny of Soltis et al. (2000).

The data were subjected to independent contrasts analyses for continuous variables (Felsenstein, 1985; Harvey & Pagel, 1991; Pagel, 1992; Kelly, 1995) using the CAIC package (Comparative Analysis using Independent Contrasts; Purvis & Rambaut, 1995). Before analysis, all data were log transformed except for percentage seedlings on logs, for which arcsin √p transformation was applied; arcsin √p produced a normal distribution of contrasts where log or logits transformations (Sokal &
Rohlf, 1995) did not. All regressions were forced through the origin (Grafen, 1989). With seed mass as the predictor variable, in no instance did we find a significant correlation between variable contrast and mean at node (Felsenstein, 1985). Because we performed our analyses on fully resolved phylogenies, it was possible to use multiple regression to determine the independent effects of other variables upon percentage seedlings on logs.

Results

Substrate associations

Elevated sites contributed 128 (8%) of the 1616 sample points. Six species were more common than expected on elevated substrates, a few such as Laurelia philippiana and Weinmannia trichosperma achieving densities as much as 10-fold higher there than on the forest floor (Table 1). Two species, Aextoxicon punctatum and Myrceugenia planipes, were significantly underrepresented on elevated microsites.

Cross-species analysis

Seed mass was strongly negatively correlated with percentage of seedlings on elevated microsites (Fig. 2). When the independent effects of seed mass, SLA and light requirements where examined by multiple regression, the relationship between seed mass and microsite occupancy was strengthened ($P = 0.001$). SLA showed a negative relationship of marginal significance ($P = 0.06$), whereas light requirements had no effect on species' dependence on elevated substrates ($P = 0.61$).

Independent contrasts analyses

When the effects of phylogenetic relatedness were factored out through independent contrasts analyses, seed mass showed a negative relationship with the proportion of a species' seedlings that occurred on logs (Table 2; Fig. 3). Interestingly, the relationship was much stronger when the classification based on the multigene trait of floral morphology was used than in the tree consistent with the more recent three-gene phylogeny (Table 2). Neither light requirements nor specific leaf area (SLA) substantially increased the explanatory power of the model (increases in $R^2 \leq 2.5\%$ in both cases). In no instance did percentage of seedlings on logs show any association with either light requirements or SLA when individual analyses were performed (0.12 $\leq P \leq 0.23$).

Discussion

Cross species analyses showed seed mass to be highly correlated with substrate occupancy patterns. All seven species that were overrepresented on elevated substrates had seed mass $< 10$ mg, whereas both species that were significantly less common than expected on these substrates had seeds $> 40$ mg (Table 1; Fig. 2). The relationship revealed by independent contrasts was not as strong as that found when phylogeny was
Although elevated substrates were on average slightly better with variation in substrate use (Fig. 3). Although only two were not correlated with substrate occupancy. In fact, the proposed causal mechanism (Ng, 1978, Putz, 1983) is closely related taxa for the phylogeny in question.

Table 2 Results of single factor regression analyses for each of the phyllogenies used in our analyses

<table>
<thead>
<tr>
<th>Rosids and Aextoxicaceae (Soltis et al., 2000)</th>
<th>Aextoxicaceae in Celastrales (Thorne, 1993)</th>
</tr>
</thead>
<tbody>
<tr>
<td>F&lt;sub&gt;1,16&lt;/sub&gt;</td>
<td>3.891</td>
</tr>
<tr>
<td>P</td>
<td>0.067</td>
</tr>
<tr>
<td>r&lt;sup&gt;2&lt;/sup&gt;</td>
<td>0.21</td>
</tr>
<tr>
<td>slope</td>
<td>-2.365</td>
</tr>
</tbody>
</table>

Results for the regressions of contrast arcsin√ of seedlings on logs on contrast of log (seed mass). Column titles show the two most closely related taxa for the phylogeny in question.

![Graph](image)

Fig. 3 Regression of contrasts of percentage of seedlings on logs against seed mass. The results displayed here are from the phylogenetic tree in which the Aextoxicaceae is designated as most closely related to the rosids. After accounting for the effect of phylogenetic relationships, only seed mass showed an association with proportion of species’ seedings found on logs vs the forest floor ($F_{1,15} = 3.891; P = 0.067; r^2 = 0.21; \beta = -2.365$).

not accounted for, but seed size still showed an association with variation in substrate use (Fig. 3). Although only two crude substrate categories were distinguished here, if the proposed causal mechanism (Ng, 1978, Putz, 1983) is correct, species of differing seed size should show a continuum of variation in their ability to penetrate forest floor litter (Molofsky & Augspurger, 1992).

The association of some species with elevated substrates did not appear to be attributable to higher light availability there. Although elevated substrates were on average slightly better lit than the rest of the forest floor (geometric mean 4.6 and 3.3% canopy openness, respectively), species light requirements were not correlated with substrate occupancy. In fact, the species with the highest proportion (55%) of its seedlings on elevated substrates was shade-tolerant Laurelia philippiana, confirming a pattern reported elsewhere (Lusk, 1995). This reflects a very weak relationship between light requirements and seed size, as shown elsewhere in studies that have factored out taxonomic relatedness when examining relationships between seed size and successional status (Kelly & Purvis, 1993; Kelly, 1995).

Apart from the effects of litter accumulation, differential retention of seeds on logs and other elevated substrates probably also influenced seedling establishment patterns (Lusk, 1995). Although the limitations of small seed reserves could explain the relative scarcity of species such as Laurelia philippiana and Nothofagus dombeiji on litter-covered forest floor microsites, they do not explain why two large-seeded species (Aextoxicon punctatum and Myrceugenia planipes) were less common than expected on elevated substrates (Table 1). Large seeds are unlikely to lodge in crevices and moss mats on fallen logs, and so would rarely be retained on the convex surfaces presented by most logs and other elevated substrates. In contrast, most of the small-seeded species are anemochorous (Smith-Ramirez & Armesto, 1994), and their dispersal adaptations (hairs or wings) could favour interception of, and adhesion to, elevated substrates.

Elevated substrates can therefore be seen as providing doubly ‘safe’ sites for small-seeded species. In addition to sloughing litter, they confer some degree of protection from competition from seedlings of some of the larger-seeded species, which are likely to have an initial competitive advantage (Turnbull et al., 1999). Safe site partitioning may therefore help explain the wide range of seed sizes present in this and many other communities (Turnbull et al., 1999), despite model predictions of a single optimal seed size for a given environment (Smith & Fretwell, 1974; Lloyd, 1987).

Safe sites for small-seeded species were less common that those apt for larger-seeded associates. Small-seeded species depended strongly upon substrates of limited and discontinuous availability (8% of the forest floor) in a more-or-less continuous matrix suitable for large-seeded species. Several other studies in forests have found similar trends (Putz, 1983; Nakashizuka, 1989; Lusk & Ogden, 1992; Lusk, 1995), supporting the idea of a negative correlation between seed size and safe site abundance in forest habitats. No such consensus emerges from comparable studies in herbaceous vegetation, which have generally focused on relationships of seed size with abundance of adults, rather than juveniles (Rees, 1995; Eriksson & Jakobsson, 1998; Turnbull et al., 1999). A meta-analysis by Xiong & Nilsson (1999) showed that the inhibitory effects of litter on germination and establishment were greater under woody vegetation than in herbaceous communities, giving less reason to expect a strong relationship between seed size and safe site abundance in the latter.

Is safe site differentiation in forests always associated with seed size? Although several other studies have shown this relationship (Nakashizuka, 1989; Molofsky & Augspurger, 1992; Lusk, 1995), other patterns could arise in situations where other selective filters besides litter influence establishment on the forest floor, or when disturbance impedes litter.
accumulation. For example, in a floodplain forest in New Zealand, large-seeded *Prumnopitys ferruginea* was one of several species associated with elevated microsites, whereas small-seeded *Dacrycarpus dacrydioides*, highly tolerant of inundation, grew mainly on the forest floor (Duncan, 1993) where deep litter accumulation may have been prevented by frequent minor floods.

In conclusion, we found that seed size was systematically related to the nature and relative abundance of safe sites for a complete assemblage of woody species in a temperate forest. Although this variety of safe sites is largely a product of disturbance, interspecific variation in responses did not appear to be linked to canopy openness, and leaf litter accumulation patterns seem likely to be the single most important factor mediating the relationship between seed size and safe site availability. This paper builds on earlier work at a similar site (Lusk, 1995), providing stronger evidence by using a more quantitative basis for distinguishing between the effects of light and substrate availabilities, and by factoring out phylogeny in a larger species assemblage. Findings point to a role for safe site differentiation in species coexistence in forests (Grubb, 1977), and in explaining the wide range of seed size present within many communities.

Acknowledgements

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References


Donoso C, Cabello A. 1978. Antecedentes fenológicos y de germinación de *Chile*.


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