The effect of twig architecture and seed number on seed size variation in subtropical woody species

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Summary

• This study aims to determine the effect of twig (current year shoot) size on seed size variation and to test whether a seed size vs number tradeoff occurs for the twigs of subtropical broad-leaved species.
• Fruit-bearing twigs were sampled for 55 woody species (including 33 evergreen and 22 deciduous dicot species) from a southwest Chinese forest. Twig size, fruit size and number, and seed size and number were measured for each species. The relationships among these functional traits were determined both across species and across correlated phyletic divergences.
• Total fruit mass and total seed mass were positively correlated with twig size. Seed size was positively associated with fruit size, which was, in turn, positively correlated with twig diameter, but negatively correlated with the ratio of twig length to diameter. The effect of twig size on seed size variation was not significant, possibly as a result of the large variation in seed number per fruit. Cross-species and across-phyletic divergence analyses revealed that seed size was negatively and isometrically correlated with seed number per twig mass in both the evergreen and deciduous species groupings, demonstrating the existence of tradeoff between seed size and number.
• A seed size vs number tradeoff is detectable in the twigs of woody species. Comparatively little of the variance in seed size was attributable to twig size variation.

Key words: architecture, fruit size, leaf habit, seed size vs number tradeoff, twig size.

Introduction

Seed size is one of the most important functional traits in the life-history strategy of flowering plants (Harper, 1977; Leishman et al., 2000; Aarssen & Jordan, 2001; Westoby et al., 2002). Numerous workers have examined variation in this functional trait in terms of external abiotic factors, including climate (Murray et al., 2004) and soil conditions (Parolin, 2000), latitudinal gradient (Moles et al., 2007) and habitat quality (Dupre & Ehrlen, 2002), and intrinsic biotic factors, including plant size (Moles et al., 2004), seed number (Mojonnier, 1998) and leaf size (Cornelissen, 1999; Baraloto et al., 2005). Yet, the mechanisms underlying seed size variation are still not fully understood and a theory for seed size evolution remains incomplete (Sadras, 2007).

One hypothesis to explain seed size variation is the effect of twig size constraints (Aarssen, 2005), that is large twigs should be associated with large seeds across species. This hypothesis draws attention to the fact that fruits are usually borne on twigs, rather than on main stems. Therefore, seed size is more likely to be related to twig size than to whole plant size. This perspective is particularly consistent with elementary plant biomechanics, as fruit-bearing twigs are analogous to cantilevered beams that mechanically support either terminal or distributed loads (Niklas, 1992). Assuming that consistent tip deflections are conserved across twigs differing in size and loading conditions, engineering theory predicts that total fruit mass should scale as the square of basal twig diameter and as the ¾ power of twig mass (see Niklas, 1993). Assuming that consistent tip deflections are conserved across twigs differing in size and loading conditions, engineering theory predicts that total fruit mass should scale as the square of basal twig diameter and as the ¾ power of twig mass (see Niklas, 1993). Assuming that fruit size is a conserved feature for each species, these predictions are consistent with previous studies showing that fruit size is positively correlated with twig cross-sectional area or twig diameter (Corner, 1949; Leishman et al., 1995; Ackerley & Donoghue, 1998). Because seed size and fruit size are often positively
associated (Wright et al., 2007), we might also expect seed size to increase with increasing twig diameter as suggested by Westoby & Wright (2003). However, these ‘architectural’ effects on seed size variation have not been examined in sufficient detail to date.

The twig size constraint hypothesis, which predicts that the twig diameter will increase in proportion to the increase in total fruit mass or total seed mass, makes no prediction about the relationship between seed size and number. For this relationship, we must turn to the seed size vs number hypothesis, which argues that seed size variation is attributable to the variation in seed number. This hypothesis rests on the simple fact that total seed mass equals average seed size times seed number. If the total allocation of mass to seed production is somehow constrained by metabolic cost, seed size should, on average, be inversely proportional to seed number. A number of studies have reported a tradeoff between seed size and number across a wide range of species from different ecosystems (Shipley & Dion, 1992; Greene & Johnson, 1994; Turnbull et al., 1999; Jakobsson & Eriksson, 2000), which accounts for the prominence of the fecundity allocation hypothesis in recent theoretical advances in seed size ecology (for example, Westoby et al., 2002; Moles et al., 2004, 2005; Aarssen, 2004, 2005). However, there are alternative, equally viable explanations. For example, as noted by Jakobsson & Eriksson (2000), the body size of the maternal parent plant may directly influence the relationship between seed size and number (Shipley & Dion, 1992; Venable, 1992). Accordingly, several studies have attempted to use leaf mass and basal stem or canopy area as measures of plant size to examine the relationship between seed mass and the number of seeds produced annually among coexisting tree species (Greene & Johnson, 1994; Henery & Westoby, 2001; Moles et al., 2004). However, the measurement of plant ‘size’ remains somewhat problematic when cast in terms of hypotheses attempting to explain reproductive biomass allocation tradeoffs in woody plants. Evidence suggests that fruit and seed development is far more intimately connected with the physiological condition of subtending leafy stems than with the older branches within canopies (Corner, 1949; Watson & Casper, 1984; Westoby & Wright, 2003) and, as noted, reproductive structures are directly mechanically supported by twigs. It is therefore reasonable to suggest that the seed size vs number tradeoff may be more easily detected using twig morphometry as a measure of size.

In this study, we sampled the fruit-bearing twigs of 55 woody species (including 33 evergreen and 22 deciduous species) of a subtropical evergreen broad-leaved forest, and recorded the twig size, fruit size, and seed size and number for each species. The goals of this study were to explore the twig size constraint hypothesis by determining the effect of twig size on seed size variation, and the seed size vs number tradeoff hypothesis by testing whether there is a negative relationship between seed size and number in twigs. As noted, the two hypotheses may be complementary and not mutually exclusive. The scaling relationships among twig and seed size and number were determined using standardized major axis regression analyses. Because phylogenetic affinities can influence comparative analyses of life-history tradeoff patterns (Harvey & Pagel, 1991; Harvey, 1996), we also used phylogenetic independent comparative protocols to remove the effect of phylogeny whilst analysing our data.

Materials and Methods

Study site

This study was conducted in the subtropical evergreen broad-leaved forest of Jinyunshan National Nature Reserve (29°50′N, 106°24′E), southwest China. Elevation within the reserve ranges between 180 and 951.5 m. The climate is mid-subtropical monsoon (warm and moist) and is characterized by a hot, rainy summer from July to August and a warm, dry winter from December to February. The mean annual rainfall is more than 1100 mm; rain occurs mostly in summer. The annual mean temperature is 17°C, reaching a high of 28.6°C in July and a low of 7.5°C in January. The annual effective accumulated temperature (>10°C) is c. 6000°C. The maximum annual frost-free period is 334 d. The mean annual relative humidity is c. 85%. The mean annual sunshine time is c. 1160 h. The soil is mainly of the acid yellow type (Zhong, 1988; Xiong et al., 2005).

The evergreen broad-leaved forest has a clear vertical structure that can be classified into tree, shrub, herb and interlayers. The forest canopy is c. 15–20 m with a few trees taller than 25 m. The tree layer is dominated by species in the Fagaceae and Theaceae (for example, Gordonia szechuanensis, Castanopsis carlesii var. spinulosa and Schima argentea) that average 15 m in height and range between 25 and 35 cm in diameter at breast height. Other species in the canopy range between 7 and 14 m in height and from 10 to 20 cm in diameter at breast height (for example, Neolitsea aurata var. glauca, Elaeocarpus duclouxii, Adinandra bockiana, Liquidambar formosana). The shrub layer is typically less than 3 m in height and dominated by saplings and shrubs (for example, Symplacos setchuenensis, Vaccinium mandarinorum, Maesa japonica and Nothapodytes pittosporoides) (Zhong, 1988).

Plant sampling

Plants were sampled between May 2007 and January 2008, when leaf expansion and shoot growth were complete and fruits were ripe. Species were selected to provide the widest range of taxa and life forms (including tree and shrub species, and deciduous and evergreen species). The only exceptions were species represented by less than three individuals bearing fruit. The total number of sampled species was 55 (representing 48 genera and 32 families), 33 of which were evergreen and 22 were deciduous (Table S1, see Supporting Information).
For each species, three to eight individuals (with an average of five individuals) with mature fruits were randomly selected; at least three fruit-bearing twigs were sampled from branches located close to the outer canopy surface. For the purpose of this study, a ‘twig’ is defined as the terminal (current year) for both evergreen and deciduous species. Therefore, each specimen was always unbranched and consisted of a terminal set of internodes with their leaves and fruits. We note in passing that, for some evergreen species, fruits were sometimes also located on older shoots. These specimens were not included in our study because they are not developmentally homologous with first year shoots. For each twig, 12 traits were recorded: twig length and twig diameter, each measured with digital callipers in the middle of the twig; seed number per fruit; total seed mass; individual fresh or dry fruit mass; total seed mass; individual seed mass; total fruit number; total pericarp mass; and total seed number. Twig mass was the sum of total leaf mass and stem mass (that is the mass of vegetative organs). Fruit intensity was calculated as the total fruit number divided by the twig mass, and seed intensity was calculated as the total seed number divided by the sum of twig mass and total pericarp mass.

Data analysis

The data for each of the 12 functional traits were $\log_{10}$ transformed to achieve a normal distribution. Traits were averaged arithmetically for each individual and subsequently for each species; species averages were $\log_{10}$ transformed for interspecific comparisons. We conducted a hierarchical analysis of variance (ANOVA) for the measured variables. The variance between species was consistently the largest component; the variance among individual plants was always greater than that among twigs or fruits (Table 1).

The relationships between seed size and seed intensity and between fruit size and fruit intensity were analysed using Model type II regression protocols (that is standardized major axes regression; see Warton et al., 2006) to identify allometric (scaling) exponents. The confidence intervals for scaling exponents were calculated following Pitman (1939). We followed the methods of Warton & Weber (2002) to test the heterogeneity of the regression slopes and to calculate the common slopes when homogeneity of the slopes was demonstrated. Scaling equation parameters were determined using (S)MATR Version 2.0 (Falster et al., 2006; http://www.bio.mq.edu.au/ecology/SMATR/).

Phylogenetic independent contrasts (PICs) were performed using the Phylogenetic Comparative Methods of COMPARE, version 4.6b (Martins, 2004). The phylogenetic tree was constructed following Phylogmatic, version 4.01 (http://www.Phylodiversity.Net/phylocom/; Webb et al., 2008). We constructed the phylogenetic tree and conducted PIC for the evergreen and deciduous species, respectively, to determine whether the correlation between different functional traits varied with evolutionary divergence. Differences in the means of the functional traits between life form types were determined using ANOVA for independent variables. The relationships between twig size and fruit size and seed size were analysed using Model type I regression protocols. The relationships among seed number, seed size and twig size were also analysed using multivariable regression methods, in which seed number was a function of seed and twig size. These calculations, as well as the regressive analysis for PIC, were completed with STATISTICA for Windows (StatSoft Inc., 2000).

In order to detect whether there is a particular structural organization among the study variables, we also conducted a confirmatory path analysis using structural equation modelling, as a complement to the regression analyses. Because the twig size effect on seed size variation can be influenced by the tradeoff between seed size and number and between fruit size and number, we set twig mass as the driving variable, seed size as a dependent variable and the other parameters (including total fruit number, individual fruit mass, total seed number and seed number per fruit) as causal variables (see Shipley, 2004). We predicted that twig size (including twig diameter and twig mass) might be the major constraint on fruit production (total fruit number times individual fruit mass), whereas individual seed mass might depend jointly on all the other

<table>
<thead>
<tr>
<th>Component</th>
<th>Species</th>
<th>Individuals within species</th>
<th>Twigs/fruits within individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Twig length</td>
<td>73.04</td>
<td>22.03</td>
<td>4.93</td>
</tr>
<tr>
<td>Twig diameter</td>
<td>94.26</td>
<td>4.86</td>
<td>0.88</td>
</tr>
<tr>
<td>Twig mass</td>
<td>81.58</td>
<td>14.67</td>
<td>3.76</td>
</tr>
<tr>
<td>Total fruit number</td>
<td>68.65</td>
<td>28.35</td>
<td>3.00</td>
</tr>
<tr>
<td>Individual fruit mass</td>
<td>86.38</td>
<td>11.81</td>
<td>1.20</td>
</tr>
<tr>
<td>Total fruit mass</td>
<td>55.01</td>
<td>34.64</td>
<td>10.35</td>
</tr>
<tr>
<td>Seed number per fruit</td>
<td>99.30</td>
<td>0.61</td>
<td>0.01</td>
</tr>
<tr>
<td>Fruit intensity</td>
<td>68.41</td>
<td>23.73</td>
<td>7.86</td>
</tr>
<tr>
<td>Total seed number</td>
<td>68.69</td>
<td>23.76</td>
<td>7.55</td>
</tr>
<tr>
<td>Individual seed mass</td>
<td>83.25</td>
<td>13.77</td>
<td>0.08</td>
</tr>
<tr>
<td>Total seed mass</td>
<td>78.51</td>
<td>21.33</td>
<td>0.16</td>
</tr>
<tr>
<td>Seed intensity</td>
<td>83.20</td>
<td>12.43</td>
<td>4.37</td>
</tr>
</tbody>
</table>
variables. On the one hand, as noted, individual fruit size is physically constrained by twig size from a biomechanical perspective, and individual seed size is physically constrained by individual fruit size. On the other hand, total fruit mass should be proportional to twig size, and hence the total fruit number is expected to be negatively associated with individual fruit mass, but positively associated with total seed number. In addition, the relationship between fruit size and seed size is mediated by seed number per fruit, and so at a given fruit size, the fruits with a greater seed number should have small seeds. Thus, the structural equation model can be hypothesized as shown in Fig. 4.

The path analysis was performed with structural equation modelling using the SEPATH module of STATISTICA (Shipley, 2000). The parameters were estimated using generalized least squares followed by maximum likelihood. The comparative fit index (CFI) and root-mean-square error of approximation (RMSEA) were used to assess the closeness of fit. Good models usually have RMSEA < 0.05 and CFI > 0.95 (for example, Vile et al., 2006).

Results

The effect of twig size on fruit and seed production

In both the evergreen and deciduous species groups, reproductive allocation was significantly correlated with twig size. Total fruit mass scaled positively with twig mass (Fig. 1a), with a common slope of 1.008 (95% CI = 0.835, 1.217), and with twig diameter (Fig. 1b), with a common slope of 2.403 (95% CI = 1.984, 2.935). Although tests for slope heterogeneity indicated that the data from both species groups could be pooled, there was a significant shift along the common slope, indicating that twig diameter and mass were larger for
The result of phylogenetically independent comparative analysis for the relationships between relative traits of the deciduous (D) and evergreen (E) species studied.

<table>
<thead>
<tr>
<th>Correlation</th>
<th>Group</th>
<th>$R^2$</th>
<th>$P$</th>
<th>$a$</th>
<th>$b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total fruit mass–twig mass</td>
<td>D</td>
<td>0.556</td>
<td>$&lt;0.001$</td>
<td>0.733</td>
<td>0.050</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.503</td>
<td>$&lt;0.001$</td>
<td>0.622</td>
<td>0.048</td>
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<tr>
<td>Total fruit mass–twig diameter</td>
<td>D</td>
<td>0.618</td>
<td>$&lt;0.001$</td>
<td>1.498</td>
<td>0.058</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.497</td>
<td>$&lt;0.001$</td>
<td>1.766</td>
<td>0.082</td>
</tr>
<tr>
<td>Total seed mass–twig mass</td>
<td>D</td>
<td>0.477</td>
<td>$&lt;0.001$</td>
<td>0.604</td>
<td>0.037</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.412</td>
<td>$&lt;0.001$</td>
<td>0.675</td>
<td>$-0.010$</td>
</tr>
<tr>
<td>Total seed mass–twig diameter</td>
<td>D</td>
<td>0.429</td>
<td>$&lt;0.001$</td>
<td>1.126</td>
<td>0.053</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.340</td>
<td>$&lt;0.001$</td>
<td>1.641</td>
<td>0.083</td>
</tr>
<tr>
<td>Individual fruit mass–twig length : diameter ratio</td>
<td>D</td>
<td>0.420</td>
<td>$&lt;0.001$</td>
<td>$-1.393$</td>
<td>$-0.065$</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.384</td>
<td>$&lt;0.001$</td>
<td>$-1.175$</td>
<td>0.079</td>
</tr>
<tr>
<td>Individual seed mass–individual fruit mass</td>
<td>D</td>
<td>0.330</td>
<td>0.010</td>
<td>0.524</td>
<td>0.027</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.405</td>
<td>$&lt;0.001$</td>
<td>1.020</td>
<td>$-0.106$</td>
</tr>
<tr>
<td>Individual seed mass–seed number per fruit</td>
<td>D</td>
<td>0.454</td>
<td>0.002</td>
<td>$-0.895$</td>
<td>0.192</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.510</td>
<td>$&lt;0.001$</td>
<td>$-1.179$</td>
<td>0.004</td>
</tr>
<tr>
<td>Individual fruit mass–fruited intensity</td>
<td>D</td>
<td>0.798</td>
<td>$&lt;0.001$</td>
<td>$-1.015$</td>
<td>$-0.024$</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.464</td>
<td>$&lt;0.001$</td>
<td>$-0.825$</td>
<td>0.042</td>
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<tr>
<td>Individual seed mass–seeded intensity</td>
<td>D</td>
<td>0.820</td>
<td>$&lt;0.001$</td>
<td>$-0.896$</td>
<td>$-0.020$</td>
</tr>
<tr>
<td></td>
<td>E</td>
<td>0.766</td>
<td>$&lt;0.001$</td>
<td>$-1.221$</td>
<td>$-0.066$</td>
</tr>
</tbody>
</table>

The simple regression equation of $y = ax + b$ was used; regression coefficients ($a$) and $y$-intercepts ($b$) are provided.

The tradeoffs of individual fruit size vs fruit number and individual seed size vs seed number

Individual fruit mass and individual seed mass varied significantly among species. Individual fruit mass ranged from 3 mg (Clerodendrum bungei) to more than 6000 mg (Vernicia fordii), and thus spanned four orders of magnitude. Average fruit size was approximately 420 mg. However, 53% of all species produced fruits weighing less than 100 mg. Seed size ranged from 0.063 mg (Melastoma normale, a pioneer species) to 2013 mg (Elaeocarpus dulcioculis, a dominant tree species). Average seed size was approximately 100 mg. However, 35% of all species had seeds smaller than 10 mg. Only 13% of all species had seeds exceeding 100 mg in size.

Across both species groups, significant negative correlations were found between total fruit number and individual fruit mass, and between total seed number and individual seed mass (Fig. 3a,b). More than 40% of the variation in individual fruit mass and more than 60% of the variation in individual seed mass could be explained by the variation in total fruit number and total seed number, respectively.

Individual fruit mass was negatively correlated with fruit intensity for both species groups (Fig. 3c) and had a common slope (scaling exponent), denoted here by $\alpha$ (that is $\alpha = -1.205$, 95% CI = $-1.420$, $-1.026$), with no significant difference in the $y$-intercept. However, the scaling relationship for individual seed mass vs seed intensity differed significantly between the two functional species groups (Fig. 3d). The variation in seed intensity accounted for more than 80% of the variation observed for individual seed mass in both species groups. The

deciduous than for evergreen species (Fig. 1a,b). Total seed mass also increased with increasing twig mass and twig diameter (Fig. 1c,d). However, twig size contributed less variance for total seed mass than for total fruit mass (Fig. 1). Cross-species and PIC analyses yielded mutually consistent correlations between twig size and total reproductive allocation (Table 2).

The effect of twig size on individual fruit size and seed size

Twig size had a significant effect on individual fruit size. In the pooled dataset, both fresh and dry individual fruit mass scaled positively with twig diameter ($r^2 > 0.10$, $P < 0.05$ for both), but negatively with respect to twig length ($r^2 \geq 0.15$, $P < 0.01$ for both). Thus, individual fruit mass was negatively correlated with the ratio of twig length to diameter in both the deciduous and evergreen species groups (Fig. 2a). Furthermore, seed size was positively correlated with fruit size in both the deciduous and evergreen species groups (Fig. 2b).

No significant relationship was found between twig size and average seed size, regardless of whether twig size was expressed in terms of diameter, length or mass. The variation in seed number per fruit was high, spanning three orders of magnitude from 1.0 to approximately 1000. Individual seed mass was negatively correlated with seed number per fruit in both species groups (Fig. 2c). The results of PIC for the relationships among twig size, fruit size and seed size were consistent with those of cross-species analyses (Table 2).
scaling exponent for seed mass vs seed intensity was $-1.342$ (95% CI $= -1.549, -1.163$) for evergreens, whereas that for deciduous species was $-0.979$ and indistinguishable from an isometric relationship (95% CI $= -1.181, -0.812$).

Multiple regression analyses showed that total seed number was correlated with twig size and individual seed mass. For deciduous species, total seed number $= 2.409(twig mass)^{0.768}$ (individual seed mass)$^{-0.952}$ ($R^2 = 0.868, P < 0.001$). For evergreen species, total seed number $= 2.118(twig mass)^{0.847}$ (individual seed mass)$^{-0.731}$ ($R^2 = 0.892, P < 0.001$). Total seed number generally scaled isometrically with respect to twig mass for both evergreen (95% CI $= 0.603, 0.998$) and deciduous (95% CI $= 0.418, 1.105$) species groups, but the relationship for seed number vs individual seed number differed significantly. Seed number for deciduous species increased isometrically with decreasing seed size (exponent $=-0.887$; 95% CI $= -1.062, -0.713$), whereas, across evergreen species, the exponent was $-0.691$ and allometric (95% CI $= -0.796, -0.585$). The results of PIC were in accordance with those obtained from the cross-species analyses (Table 2).

Confirmatory path analysis

Our analysis provided a good fit to the hypothesized structural equation model (chi-squared $= 3.292$, df $= 7$, $P = 0.857$, CFI $= 1.0$, RMSEA $< 0.001$). The results were generally consistent with those of regression analyses (Fig. 4). The direct effect of twig size on seed size was not significant as the path from twig mass to individual seed mass was not significantly different from zero ($P > 0.05$). Twig mass indirectly influenced seed size via the path from individual fruit mass to individual seed mass and the path from total fruit number to total seed number per fruit to individual seed mass (Fig. 4). Twig mass had direct effects on fruit production, that is the paths from twig mass to total fruit number and individual fruit mass were positive and significantly different from zero ($P < 0.001$). The path from total fruit number to individual fruit mass was negative and significantly different from zero ($P < 0.001$), whereas the path from total seed number to individual seed mass was not significantly different from zero ($P > 0.05$). Total seed number and individual fruit
Fig. 3 Cross-species bivariate plots for total fruit number vs individual fruit mass \((r^2 = 0.427, P < 0.001)\) and total seed number vs individual seed mass \((r^2 = 0.699, P < 0.001)\) for deciduous and evergreen species, respectively (a), total seed number vs individual seed mass \((r^2 = 0.416, P < 0.001)\) and \((r^2 = 0.645, P < 0.001)\) for deciduous and evergreen species, respectively (b), fruit intensity vs individual fruit mass \((r^2 = 0.680, P < 0.001)\) and \((r^2 = 0.679, P < 0.001)\) for deciduous and evergreen species, respectively (c) and seed intensity vs individual seed mass \((r^2 = 0.836, P < 0.001)\) and \((r^2 = 0.846, P < 0.001)\) for deciduous and evergreen species, respectively (d). The full and broken lines are the regression lines for the deciduous and evergreen species, respectively. Open diamonds, deciduous species; filled circles, evergreen species.

Fig. 4 Diagram of the structural equation model for the effect of twig size on seed size in the 55 subtropical woody dicot species. Chi-squared = 3.292, df = 7, \(P = 0.857\), comparative fit index (CFI) = 1.0, root-mean-square error of approximation (RMSEA) < 0.001. Path coefficients between variables are nonstandardized partial regression coefficients. The path coefficients between variables are shown if they are significantly different from zero. Arrow widths are proportional to the standardized path coefficient. The parts of the variances explained by the model \((r^2)\) are given under the variable names.
size indirectly influenced seed size via the direct effect of seed number per fruit.

Discussion

The effect of twig architecture on fruit size and seed size

As predicted, twig size significantly influences fruit size; thicker twigs support a larger fruit mass and larger individual fruits. The proportionality between total fruit production and twig size is consistent with simple biomechanical treatments of cantilevered beams (Niklas, 1992, 1993). For example, assuming that each twig is a cantilevered beam bearing a terminal load (which equals mass $M$ times the acceleration due to gravity $g$), simple beam theory predicts that the tip deflection of such a cantilever is given by the formula $\delta = gML^3/3EI$, where $E$ is Young's modulus and $I$ is the second moment of area. For a beam with a circular cross-section with uniform radius $r$, $I = (\pi r^4)/4$. Inserting this relationship into the previous formula gives $\delta = (4gML^3)/(3\pi E r^4)$. Assuming elastic self-similarity across beams differing in length $L$, diameter $D$ and $gM$, it follows that $L = k_0 r^{2/3}$, $\delta$ = a constant and $E$ = a constant, such that $\delta = (4gk_0^3)/(3\pi E)(Mr)^2$, where $k_0$ denotes a normalization constant. Rearranging this last expression to relate the terminal load to the beam radius, we see that $M = (3\pi \delta E/(4gk_0^3))r^2$ or, in simple proportional terms, $M \propto r^2$. Thus, the terminal load (total fruit weight) supported by cantilevers (twigs) differing in size should scale as the square of the beam (twig) diameter (that is $M \propto D^2$). Assuming a uniform bulk tissue density across beams differing in size, it also follows that the terminal load will scale as the $\frac{1}{4}$ power of beam mass $m$ (that is $M \propto m^{3/4}$). It should be noted that numerically similar relationships are obtained if we assume that beams are tapered and that loads are unequally distributed along their lengths. The allometry between twig size and total fruit mass (Fig. 1a,b) is consistent with these predictions, although the common slope for the scaling relationship between twig size and total fruit mass is slightly higher than predicted (which may reflect differences in twig tapering or bulk tissue density).

In this regard, it is worth noting that twig length is negatively correlated with fruit size ($r^2 = 0.124, P < 0.01$), such that the quotient of twig length and diameter is negatively correlated with fruit size (see Fig. 2a). These relationships, which may indicate that longer twigs bear more fruits than shorter twigs (see Bowers, 2006), are entirely consistent with elementary beam theory (see Niklas, 1992). Likewise, a positive correlation between twig size and individual fruit size, which is consistent with Corner’s rule as well as with several previous studies (Midgley & Bond, 1989; Niklas, 1993; Wolfe & Denton, 2001), may reflect a hydraulic as well as a mechanical constraint. If twig cross-sectional areas correlate positively with the cross-sectional areas of conducting tissues, we might expect larger twigs to transport nutrients to growing reproductive organs more rapidly or perhaps more efficiently, as suggested by Westoby & Wright (2003) (see also Niklas & Spatz, 2004). Under any circumstances, it is reasonable to argue from purely physical reasons that twig ‘architecture’ (here broadly defined to include mechanical and hydraulic factors) imposes a constraint on total fruit weight.

By contrast, our data do not support the notion that twig size affects individual seed size, regardless of whether twig size is expressed in terms of diameter or mass. Twig size indirectly affects seed size through the negative path of seed number per fruit and a positive path of individual fruit mass to individual seed mass (Fig. 4), which collectively produces an insignificant correlation between twig size and seed size. Although a positive correlation between fruit size and seed size exists for our data (Fig. 3b), it is probably a simple reflection of the fact that fruit size sets an intrinsic limit to maximum seed size and number (Wright et al., 2007). Therefore, we see no evidence to support the twig size constraint hypothesis in terms of the tradeoff between seed number and seed size, which is mediated by seed number per fruit (Fig. 4). A large fruit can contain many small seeds, but a large seed cannot exceed the size of the fruit that bears it, which is clearly shown by the negative scaling relationship between seed number per fruit and seed size (Fig. 2c).

The individual seed size vs number tradeoff

We have shown that individual fruit size is negatively correlated with fruit number and fruit intensity in both the evergreen and deciduous dicot species groups, which is in accordance with the highly negative path from total fruit number to total fruit mass in the structural equation model (Fig. 4). Likewise, individual seed size is negatively correlated with both seed number and seed intensity, although this relationship is apparently mediated by seed number per fruit (Fig. 4). These scaling relationships provide reasonably reassuring evidence for the existence of metabolic (biomass allocation) tradeoffs at the level of current year shoots, particularly when cross-species correlations are juxtaposed with the result of phyletic independent contrast analyses, which indicate that these tradeoffs are ecologically significant.

The tradeoff between seed number and individual seed size is consistent with the results of previous studies addressing the scaling of seed size vs number across species at the whole plant level. Negative correlations between seed size and number have been reported for 57 herbaceous angiosperms from North America (Shipley & Dion, 1992), across seven species of grassland annuals in south Wales (Turnbull et al., 1999), and across 72 grassland species (including 35 phylogenetically independent contrasts) in Sweden (Jakobsson & Eriksson, 2000). Data for tree species are less frequently provided. Greene & Johnson (1994) and Moles et al. (2004) have shown a seed size vs number tradeoff using basal area or leaf mass, or canopy area, as surrogates for plant size. However, such
measurements of plant size appear to be coarse and difficult to integrate into life-history theory, as noted by Kleiman & Aarssen (2007) in their criticisms of studies of the leaf size vs number tradeoff. Regardless of whether this criticism is valid, we have shown for the first time that the morphometry of current year shoots provides a good measure of plant size when exploring fecundity allocation constraints. In this respect, we draw particular attention to the fact that the seed intensity (including variables such as seed number and twig mass) accounts for more than 80% of the variation observed in seed size in both the evergreen and deciduous species groups. The explanatory power of this variable is comparable with that reported using whole plant measurements of herbaceous species (for example, Shipley & Dion, 1992; Aarssen & Jordan, 2001) and significantly higher than that reported for woody species (Greene & Johnson, 1994; Henery & Westoby, 2001; Moles et al., 2004). Therefore, current year shoot characteristics may provide the best metrics for revealing seed size vs number tradeoffs across woody species.

The scaling relationships between seed intensity and size were significantly different between the two species groups, that is they were isometric for deciduous species and allometric for evergreen species. Previous studies have reported a similar phenomenon. For example, the number of seeds produced per unit canopy per year has been reported to increase isometrically with species mean seed mass among coexisting tree species from a sclerophyll shrubland (Henery & Westoby, 2001; Moles et al., 2004), whereas the scaling exponents for seed number vs seed size are between −0.78 and −0.62 for herbaceous species (Shipley & Dion, 1992; Jakobbson & Eriksson, 2000) and even less (−0.58) for tree species (Greene & Johnson, 1994), which suggests that a marginal increase in seed mass leads to a proportionally smaller decrease in seed number, such that plants with larger seeds have an advantage in terms of total seed production compared with plants with smaller seeds. An explanation for these trends remains problematic. However, on the basis of their analyses of 15 monocarpic herbaceous annual or biennial species, Aarssen & Jordan (2001) suggested that the principal selection mechanism of seed number involves a time limitation, and that measurements of lifetime reproduction would produce isometric relationships.

This explanation is consistent with the results presented here. Across deciduous species, fruits are typically borne on current year shoots and usually ripen within 1 yr. However, among evergreen species, reproductive structures can be located on both current year and older shoots. Because the leaf number per unit stem length is often smaller in older shoots than on twigs as defined in this study (S. Sun, pers. obs.), older shoots may provide nutrients and carbohydrates to fruits and seeds from younger shoots, whereas, in some species, young shoots may draw nutrients from older ones when seeds are borne only on young shoots. In addition, there may be an immediate mechanism underlying the difference in the scaling exponents reported for the two species groups. Fruit size scales isometrically with fruit intensity in both the deciduous and evergreen species, whereas the scaling exponents of seed size vs seed intensity differ significantly between the species groups (Fig. 3c,d). This indicates that within-fruit biomass allocation between seed and pericarp could be different in the two species groups. In the present study, seed package (total pericarp mass/seed number per fruit) scales isometrically with seed size in the deciduous species group (α = 1.01, 95% CI = 0.85, 1.17) but allometrically across evergreen species (α = 0.82, 95% CI = 0.70, 0.94). However, it is not clear what contributes to the difference in the within-fruit reproductive allocation.

In summary, we have shown that a highly negative correlation exists between seed size and number for the twigs of woody species, which is consistent with the seed size vs number tradeoff hypothesis explaining seed size variation. By contrast, individual seed size is not detectably correlated with twig size (possibly as a result of the confounding effect of seed number per fruit), which is inconsistent with the twig size constraint hypothesis that predicts that seed size should be primarily determined by twig size. Our analyses further reveal that variations in twig size account for much of the variance observed in reproductive allometry, which holds the potential to provide more rapid (and more accurate) estimates of seed production and primary productivity at the whole stand level (see Ogawa, 2008; Yang et al., 2008).

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Descriptions of the functional traits measured for 55 woody broad-leaved species (Jinyun Mountain, southwestern China)

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