Evolutionary Ecology Research, 2003, **5**: 79–88

An allometric model for seed plant reproduction

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ABSTRACT

An allometric framework is used to construct a model for seed plant annual reproductive biomass based on standing leaf, stem and root biomass. According to this model, the scaling of reproduction is governed by numerous taxon-specific scaling exponents and constants that reflect the allometry of vegetative biomass partitioning. Although this allometry cannot be predicted *a priori*, the model accurately predicts all observed inter- and intraspecific reproductive biomass trends based on the exponents and constants determined for a worldwide database representative of herbaceous and tree-sized dicot, monocot and conifer species growing in diverse habitats. The model also identifies the body proportions for which reproduction is energetically untenable. The limits for seed plant reproductive biomass are thus established, providing a conceptual and quantitative basis for understanding the scaling of reproductive capacity across and within ecologically and evolutionarily diverse spermatophytes.

Keywords: allometry, plants, reproductive biomass, scaling, vegetative biomass.

INTRODUCTION

Sexual reproduction is important for most plants, since it introduces genomic variation within populations (Begon *et al.*, 1990). It also helps in the expansion of seed plant geographic ranges via propagule dispersal (Bazazz and Grace, 1997). However, reproductive effort also requires an expenditure of resources that might otherwise be used for vegetative growth. Therefore, a trade-off exists for the annual allocation of metabolic production to the construction of either new vegetative or reproductive organs (Ramirez, 1993; Mole, 1994; Zhang, 1998). The impressive variation in reproductive capacity across plant species indicates that this trade-off has been resolved in manifold ways. For example, an annual grass may produce 10^2 seeds, whereas a tree may produce 10^{9-10} seeds in its lifetime. Identifying the mechanisms responsible for this variation is of central importance to life-history and evolutionary theory. Yet, there is no generally agreed upon analytically quantitative description for these mechanisms (Klinkhamer *et al.*, 1992; Iwasa, 2000; Aarssen and Jordan, 2001).

Recently, however, an allometric approach to biology based on ‘first principles’ has identified canonical scaling relations for the vegetative body parts of seed plants (Niklas,

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1994a; Enquist *et al.*, 1999; Enquist and Niklas, 2001, 2002; Niklas and Enquist, 2001, 2002; for a different mechanistic treatment, see West *et al.*, 1999a,b). This approach has provided two important theoretical and empirically supported insights relevant to the formulation of models for plant reproductive capacity. First, standing leaf biomass M_L is shown to scale as the 3/4-power of standing stem M_S (and root M_R) biomass (Enquist and Niklas, 2002). Second, total annual growth in vegetative biomass G_T and annual leaf, stem and root tissue growth (G_L, G_S and G_R, respectively) are shown to each scale isometrically with respect to the light harvesting capacity of the individual plant, which for most seed plants correlates with M_L (Niklas and Enquist, 2001).

In this paper, we use these relations to derive a model for the scaling of annual reproductive biomass M_P with respect to M_L, M_S and M_R. This model is also tested (and found to have strong statistical support) by comparing its predictions against the trends in plant reproduction observed for a large, worldwide database of standing organ biomass spanning a broad spectrum of annual and perennial dicot, monocot and conifer species (Enquist and Niklas, 2002; Niklas and Enquist, 2002).

MATERIALS AND METHODS

Data sets and analyses

Data for tree-sized monocot, dicot and conifer species differing in size and age were collected from the primary literature to compute standing reproductive, leaf, stem and root biomass (in units of kg of dry weight per plant) and the annual growth rate of each type of organ (kg of dry weight per plant per year) (Enquist *et al.*, 1999; Enquist and Niklas, 2001, 2002; Niklas and Enquist, 2001, 2002). Additional data were gathered from the primary literature for non-woody or small species published between 1990 and 2001 for naturally growing or experimentally manipulated plants (Enquist and Niklas, 2002; Niklas and Enquist, 2002). Only two criteria were used to select these latter publications: the data had to have small variance (as gauged by the reported standard error) and they had to be reported in units of kg of dry weight per plant. Intraspecific data for *Pinus rigida*, *Capsella bursa-pastoris* and *Dolicus lablab* were taken from previously published work of Niklas (1993, 1994b, 1998). The complete database reflects the properties of 356 species and 549 individual plants. Importantly, none of the data accumulated to determine the scaling relations for vegetative body parts are estimated on the basis of standing (annual) reproductive biomass.

Model Type II (reduced major axis) regression analysis was used to determine empirically the scaling exponents and allometric constants (regression slope and y-intercept, α_{RMA} and β_{RMA}, respectively) of pairwise comparisons of $\log_{10}$-transformed data. This protocol is recommended when functional rather than predictive relationships are sought among variables that are biologically interdependent and subject to unknown measurement error (Sokal and Rohlf, 1981; Niklas, 1994a). All statistical analyses used the formulas $\log y_2 = \log \beta_{RMA} + \alpha_{RMA} \log y_1$, where y_2 and y_1 are interdependent variables (e.g. reproductive and standing leaf biomass per plant), $\alpha_{RMA} = \alpha_{OLS} / r$, where α_{OLS} and r are the slope and correlation coefficient determined from ordinary least squares (Model Type I) regression analysis, and $\log \beta_{RMA} = \log (\hat{y}_2) - \alpha_{RMA} \log (\hat{y}_1)$, where $(\hat{y})$ denotes the mean of variable y. The 95% confidence intervals for β_{RMA} values were computed based on the corresponding 95% confidence intervals of α_{RMA} (Sokal and Rohlf, 1981). Comparisons between predicted

α_{RMA} and β_{RMA} values and those obtained by Model Type I regression analyses failed to detect statistically significant differences; that is, the choice of Model Type I or II analyses did not affect the conclusions presented here. Sample sizes vary among comparisons because some authors failed to report the biomass of all organ types.

Importantly, none of the y_1 variables used in the regression analyses reported here is based on calculations involving reproductive biomass. Similarly, none of the derivations used to theoretically relate reproductive biomass to leaf, stem or root biomass is based on the allometry of reproductive biomass with respect to leaf, stem or root biomass (see below).

Extension of previous work

Previous allometric derivations and analyses of data sets for unicellular and multicellular plant species show that total annual vegetative growth rate G_T scales as the 3/4-power of total vegetative body mass M_T (Niklas, 1994a; Niklas and Enquist, 2001). Thus, for most seed plants, $G_T = \beta_1 M_T^{3/4} = \beta_1 \, (M_L + M_S + M_R)^{3/4}$, where β_1 is a taxon-specific (allometric) constant. With the exception of very small or annual species, we assume that M_P does not contribute significantly to M_T, because reproductive body parts, even for many conifer species, are typically shed in less than 1 year. However, G_T is taken as the sum of G_L, G_S, G_R and G_P because G_P requires expenditures of annual metabolic production.

Therefore, across seed plant species, $G_L + G_S + G_R + G_P = \beta_1 \, (M_L + M_S + M_R)^{3/4}$. As noted, M_S and M_R each scale as the 4/3-power of M_L, whereas G_L, G_S and G_R scale isometrically with respect to each other: $M_S = \beta_2 M_L^{4/3}$, $M_R = \beta_3 M_L^{4/3}$, $G_S = \beta_4 G_L$, and $G_R = \beta_5 G_L$ (Enquist and Niklas, 2002; Niklas and Enquist, 2002). Analyses also show that $G_L = \beta_6 M_L$, where β_6 includes units of year^{-1} (Niklas and Enquist, 2002). Therefore, $G_P = \beta_1 \, (M_L + M_S + M_R)^{3/4} - (1 + \beta_4 + \beta_5) \, \beta_6 M_L$. Assuming that the relation between reproductive growth and biomass scales as $G_P = \beta_7 M_P$, where β_7 includes units of year^{-1}, the predicted relations among M_P and M_L, M_S and M_R are:

$$M_P = \beta_8 \, (M_L + \beta_9 M_L^{4/3})^{3/4} - \beta_{10} M_L \tag{1}$$

$$M_P = \beta_8[(M_S/\beta_2)^{3/4} + (\beta_9/\beta_2) \, M_S]^{3/4} - \beta_{10} \, (M_S/\beta_2)^{3/4} \tag{2}$$

$$M_P = \beta_8[(M_R/\beta_3)^{3/4} + (\beta_9/\beta_3) \, M_R]^{3/4} - \beta_{10}(M_R/\beta_3)^{3/4} \tag{3}$$

where $\beta_8 = \beta_1/\beta_7$, $\beta_9 = \beta_2 + \beta_3$, and $\beta_{10} = (1 + \beta_4 + \beta_5) \, (\beta_6/\beta_7)$. Each of these equations predicts a slightly non-linear log–log (concave) relation for M_P versus M_L, M_S or M_R. However, the trend predicted by each equation is approximated well by linear regression of log-transformed data (see Figs 1 and 2).

As noted, none of the scaling relations used to derive equations (1–3) directly or indirectly relates M_P to M_L, M_S or M_R. Therefore, no mathematical ‘circularity’ exists if M_P is predicted based on the values of M_L, M_S or M_R reported in the literature for plants (regardless of their reproductive status). The α_{RMA} and β_{RMA} of the scaling relations for M_P versus M_L, M_S or M_R depend exclusively on the numerical values of β_{8-10}, which, in turn, emerge from taxon-specific vegetative biomass partitioning patterns. Although the model cannot predict the numerical values of β_{8-10} *a priori*, its validity can be tested directly by evaluating whether predicted α_{RMA} and β_{RMA} values agree with those observed for inter- and intraspecific reproductive trends (Niklas, 1994b).

Equations (1–3) will not hold true if M_P contributes substantially to total plant biomass – that is, $M_T = \beta_1\ (M_L + M_S + M_R + M_P)^{3/4}$ – which is true for many annual species and not unusual for small perennial species. Under these circumstances,

$$M_P = \beta_8\ (M_L + \beta_9 M_L^{4/3} + M_P)^{3/4} - \beta_{10} M_L \tag{4}$$

$$M_P = \beta_8\ [(M_S/\beta_2)^{3/4} + (\beta_9/\beta_2)\ M_S + M_P]^{3/4} - \beta_{10}\ (M_S/\beta_2)^{3/4} \tag{5}$$

$$M_P = \beta_8\ [(M_R/\beta_3)^{3/4} + (\beta_9/\beta_3)\ M_R + M_P]^{3/4} - \beta_{10}\ (M_R/\beta_3)^{3/4} \tag{6}$$

These recursive equations cannot be evaluated in the same way as equations (1–3) because of autocorrelation, although they can be solved with MATHEMATICA as quadratics, which gives four roots, one of which is positive. However, equations (4–6) can be rejected if they obtain numerical inequalities – that is, if the slope of the regression curve for predicted M_P versus observed M_P deviates significantly from unity.

RESULTS AND DISCUSSION

Analyses of our worldwide database for seed plant biomass relations provided robust statistical support for equations (1–3) (Table 1). Across all species, $\beta_8 = 0.027$, $\beta_9 = 4.22$ and $\beta_{10} = 0.018$. Using these values, equation (1) predicts M_P will scale as the 0.861-power of M_L with a regression y-intercept of $\beta_{RMA} = 0.067$ (Fig. 1A). This scaling relationship was statistically indistinguishable from that observed: $\alpha_{RMA} = 0.841$ and $\beta_{RMA} = 0.064$ (Table 1). Similarly, the scaling relations predicted for M_P based on observed values of M_S or M_R and equations (2) and (3) (Fig. 1B,C) were statistically indistinguishable from those observed statistically (Table 1).

The accuracy of equations (1–3) was also comparable to that of direct regression analysis of the raw (non-transformed) data (Fig. 2). For both methods, the smallest difference between predicted and observed M_P values was obtained when M_L was used as the predictive variable. Both methods underestimated M_P for some of the largest tree species, possibly because the published values of M_P for these species were measured by some authors after leaf- or fruit-fall or herbivory. Nonetheless, the model was strikingly accurate for most plants in our database, even within the size range of small annual species (Fig. 2).

Significant numerical differences in $\beta_{8\text{–}10}$ were observed among clades (angiosperms and conifers) and individual species. As predicted by equations (1–3), these differences accounted for most of the 'data-spread' observed in bivariant plots because, in each case, the equations accurately predicted all observed inter- and intraspecific M_P trends (Table 1). For example, across all angiosperms, $\beta_8 = 0.023$, $\beta_9 = 7.77$ and $\beta_{10} = 0.015$ such that equation (1) predicted that M_P will scale as the 0.918-power of M_L with $\beta_{RMA} = 0.101$. This scaling relation was statistically indistinguishable from that observed. Similarly accurate results were obtained for conifers (Table 1).

The reproductive trends of phyletically and ecologically disparate species for which $\beta_{8\text{–}10}$ values could be determined were also accurately predicted by equations (1–3) (Fig. 3). For example, in the case of *Pinus rigida*, M_P was predicted to scale as the 0.909-power of M_S with $\beta_{RMA} = 1.66$, whereas $\alpha_{RMA} = 0.909 \pm 0.015$ and $\beta_{RMA} = 1.66 \pm 0.021$ were observed (Table 1). Similarly, for the large annual monocot species *Pennisetum glaucum*, M_P was predicted to scale as the 0.775-power of M_S with $\beta_{RMA} = 0.235$, whereas $\alpha_{RMA} = 0.776 \pm 0.017$ and $\beta_{RMA} = 0.232 \pm 0.008$ were observed. Finally, using equations (4–6), isometric

Table 1. Representative statistical comparisons between predicted and observed scaling exponents (α_{RMA}) and taxon-specific (allometric) constants (β_{RMA}) for inter- and intraspecific relations of reproductive, leaf, stem and root biomass (M_{P}, M_{L}, M_{S} and M_{R}, respectively) based on reduced major axis regression of $\log_{10}$-transformed data (original units in kg of dry weight per plant)

	α_{RMA} ± s.e.	95% CI	antilog β_{RMA} ± s.e.	95% CI	n	r^2	F
Across all species ($\beta_8 = 0.027$, $\beta_9 = 4.22$, $\beta_{10} = 0.018$)							
M_{P} versus M_{L}							
predicted	0.861 ± 0.002	0.856–0.865	0.067 ± 0.004	0.068–0.069	279	—	—
observed	0.841 ± 0.025	0.784–0.898	0.064 ± 0.046	0.057–0.072	279	0.754	851.1
M_{P} versus M_{S}							
predicted	0.657 ± 0.001	0.655–0.659	0.059 ± 0.003	0.048–0.049	418	—	—
observed	0.674 ± 0.016	0.637–0.709	0.051 ± 0.039	0.047–0.055	418	0.754	1331
M_{P} versus M_{R}							
predicted	0.654 ± 0.001	0.652–0.656	0.049 ± 0.003	0.048–0.050	204	—	—
observed	0.700 ± 0.020	0.656–0.745	0.044 ± 0.046	0.040–0.048	204	0.827	967.0
Across angiosperms ($\beta_8 = 0.023$, $\beta_9 = 7.77$, $\beta_{10} = 0.015$)							
M_{P} versus M_{L}							
predicted	0.918 ± 0.003	0.912–0.923	0.101 ± 0.006	0.098–0.104	195	—	—
observed	0.924 ± 0.035	0.858–0.990	0.115 ± 0.065	0.092–0.143	195	0.799	768.2
Across conifers ($\beta_8 = 0.036$, $\beta_9 = 9.87$, $\beta_{10} = 0.056$)							
M_{P} versus M_{L}							
predicted	0.961 ± 0.001	0.958–0.963	0.161 ± 0.001	0.159–0.160	84	—	—
observed	0.778 ± 0.072	0.515–1.042	0.167 ± 0.066	0.167–0.259	84	0.296	34.5
Within species							
M_{P} versus M_{S}							
Pinus rigida (conifer) ($\beta_8 = 0.142$, $\beta_9 = 25.6$, $\beta_{10} = 0.001$)							
predicted	0.909 ± 0.002	0.905–0.909	1.66 ± 0.002	1.58–1.60	16	—	—
observed	0.909 ± 0.015	0.876–0.942	1.66 ± 0.021	1.49–1.84	16	0.996	3556
Dolicus lablab (dicot) ($\beta_8 = 0.090$, $\beta_9 = 10.2$, $\beta_{10} = 0.002$)							
predicted	1.24 ± 0.002	1.23–1.24	21.9 ± 0.002	21.7–22.1	44	—	—
observed	1.25 ± 0.081	1.06–1.42	22.1 ± 0.291	5.71–85.5	44	0.822	193.7
Pennisetum glaucum (monocot) ($\beta_8 = 0.024$, $\beta_9 = 5.61$, $\beta_{10} = 0.017$)							
predicted	0.775 ± 0.002	0.774–0.776	0.235 ± 0.002	0.233–0.237	50	—	—
observed	0.776 ± 0.017	0.739–0.810	0.232 ± 0.008	0.227–0.237	50	0.976	1920

Note: In all cases, $P < 0.0001$. F- and r-values for predicted relations ≥85,000 and ≥0.998, respectively. s.e. = standard error.

scaling relations were observed between the predicted and observed M_{P} of small annual dicot and monocot species for which $M_{\mathrm{P}} \geq 35\%\ M_{\mathrm{T}}$; for example, regression of observed M_{P} versus predicted M_{P} using equation (4) gave $\alpha_{\mathrm{RMA}} = 0.982$ for *Capsella bursa-pastoris* ($n = 53$, $r^2 = 0.862$).

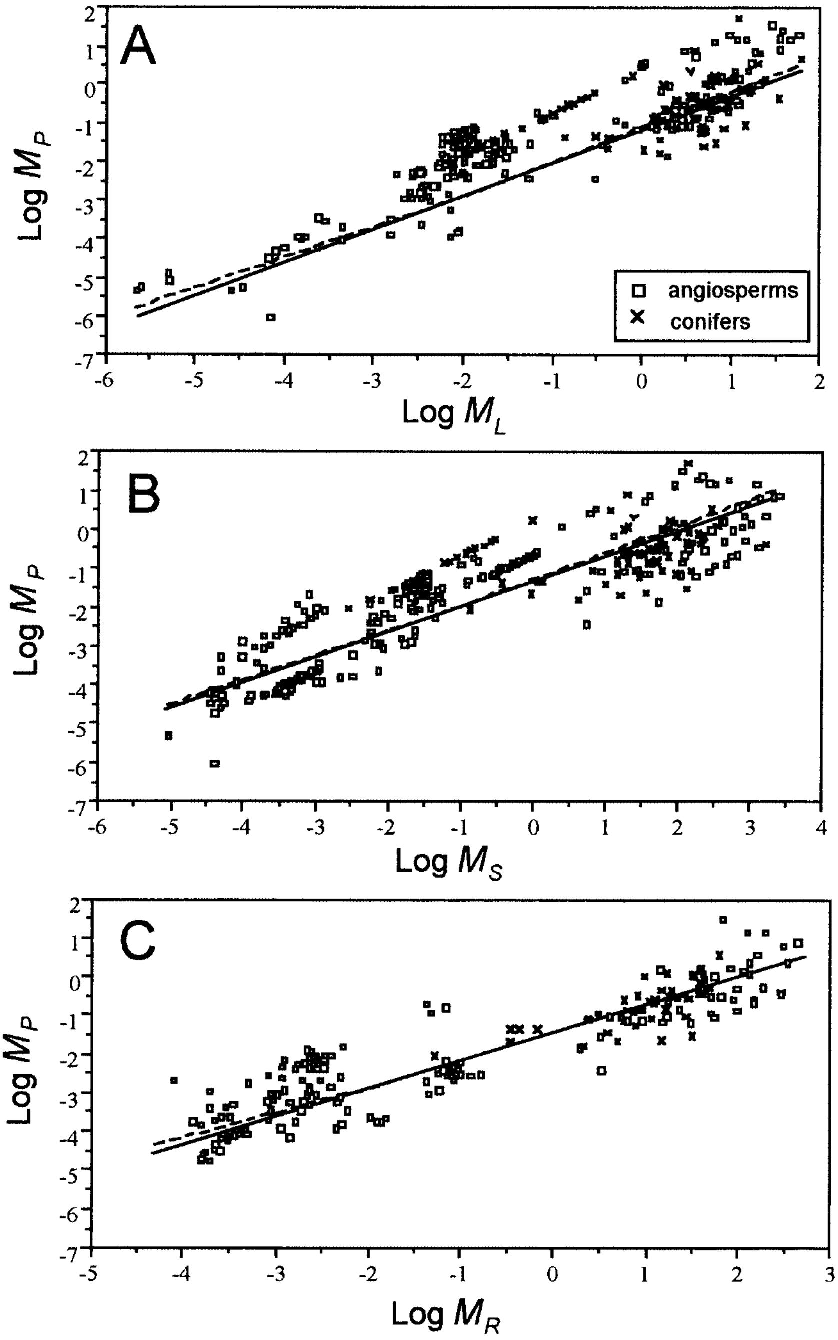

Fig. 1. Statistically observed and predicted relations among annual standing reproductive biomass M_P and leaf M_L (A), stem M_S (B) and root M_R (C) biomass per plant (original units in kg of dry weight per plant). Observed and predicted relations shown by solid and dashed (slightly log–log concave) RMA regression lines, respectively. The relevant statistical parameters are given in Table 1.

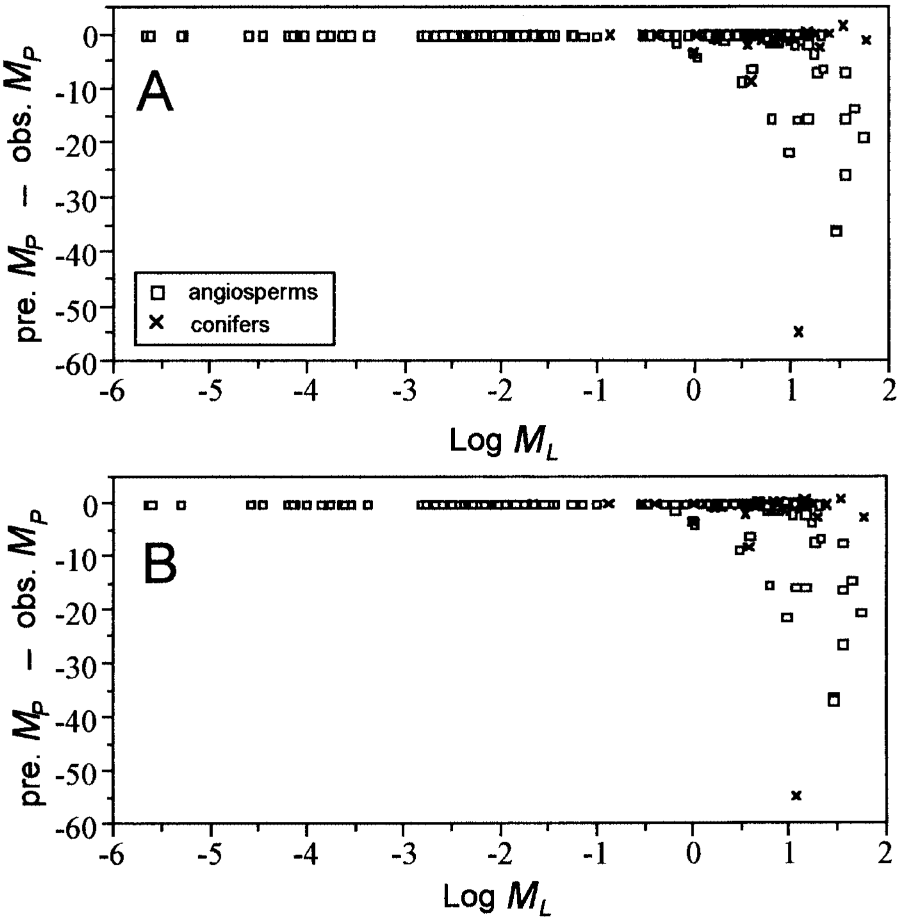

Fig. 2. Comparisons between the accuracy of predicted and observed reproductive biomass (pre. M_P and obs. M_P, respectively) relative to standing leaf biomass M_L across all species. Predicted values for M_P using equation (1) are based on raw (non-transformed) data for leaf biomass M_L to avoid artifacts of back-transforming log-transformed data. (A) Predicted M_P minus observed M_P plotted against M_L. (B) M_P predicted by RMA regression analysis (M_P versus M_L) minus observed M_P plotted against M_L. All units are in kg of dry weight per plant.

Unlike regression analyses, the theoretical framework of our model explains as well as describes M_P trends. This framework shows that trade-offs are required for the annual partitioning of a finite amount of M_T among two or more organ types (Enquist and Niklas, 2002; Niklas and Enquist, 2002). In turn, the model shows that these trade-offs are resolved in varying ways reflected by $\beta_{8\text{–}10}$ values, which, in turn, distinguish among different (taxon-specific) vegetative biomass partitioning patterns. Accordingly, taxa with dissimilar partitioning patterns will have different reproductive trends, whereas those with the same or very similar vegetative partitioning patterns will share similar $\beta_{8\text{–}10}$ values and thus similar M_P scaling relations.

An additional insight provided by the model is that reproduction is predicted to be energetically untenable below a species-specific threshold of vegetative biomass. For

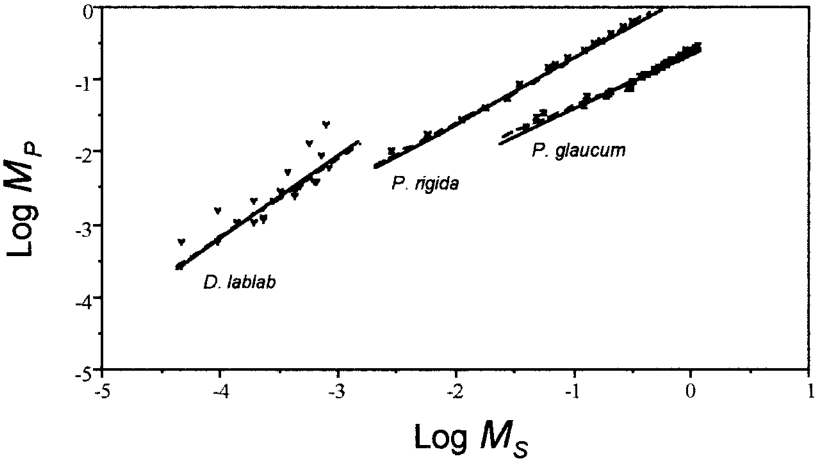

Fig. 3. Statistically observed and predicted relations between standing reproductive biomass M_P and leaf biomass M_L per plant for three species. Observed and predicted relations shown by solid and dashed (slightly log–log concave) RMA lines, respectively. The relevant statistical parameters are given in Table 1.

example, equations (1–3) obtain zero or negative M_P values when M_L, M_S or M_R values drop below specific thresholds for each species. Above these thresholds, M_P is predicted (and observed) to increase with increasing body size. In this sense, standing vegetative biomass 'drives' an individual's reproductive capacity such that reproductive biomass may increase or decrease relative to total vegetative body mass depending on the allocation of biomass to the three different vegetative organ types. This aspect of the model is consistent with the broad spectrum of reproductive patterns reported for different species in the literature (Reekie and Bazzaz, 1987; Klinkhamer *et al.*, 1992).

An important caveat regarding our database and the derivation of our model is that the reproductive capacities of perennial plants can vary from year to year depending on past or current growth conditions. The data collected from the primary literature to test our model reflect this variation, but in each case pertain to plants that produced at least some reproductive organs in the particular year the data were collected. Another caveat is that reproductive effort has been measured and reported in different ways by different authors (Doust, 1992; Ramirez, 1993; Mole, 1994; McLachlan *et al.*, 1995; Zhang, 1998; Eppley and Wenk, 2001). Our database reflects this heterogeneity, since it contains most M_P 'currencies' (e.g. total flower, seed or fruit biomass per plant). Our model also explicitly assumes that leaves are the primary photosynthetic organ, which is violated when other photosynthetic organs, such as stems, contribute significantly to total metabolic production (see Pfanz *et al.*, 2002). We also speculate that monocarpic species metabolically 'self-sacrifice' by reapportioning their vegetative resources to seeds towards the closure of their life spans. These and other features possibly contribute to the residual data-scatter seen in our bivariant plots (Fig. 1).

Nonetheless, our model accurately describes all observed inter- and intraspecific trends in reproductive biomass, while offering an analytical and quantitative rationale for each trend. It also identifies the minimum body mass (and vegetative organ proportionalities) required for reproductive effort, and it explicitly links the mechanisms dictating reproductive effort to vegetative biomass partitioning patterns. The numerical accuracy of the model also indirectly validates its theoretical underpinnings, since the model would predict inaccurate trends otherwise (Enquist and Niklas, 2001, 2002; Niklas and Enquist, 2001, 2002). A robust analytical and conceptual framework is thus rapidly emerging that can shed light on some of the most important aspects of plant biology, such as the intrinsic mechanisms underpinning reproductive capacity.

ACKNOWLEDGEMENTS

This work is an outgrowth of discussions from the Body Size in Ecology and Evolution Working Group (F.A. Smith, Principle Investigator) sponsored by the National Center for Ecological Analysis and Synthesis (NCEAS). We thank J. Brown, M. Christianson, T. Owens and D. Raup for comments on an early version of this paper. K.J.N. was supported by NYS Hatch Grant and CALS funds. B.J.E. was supported by NSF.

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