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LETTER

# Nitrogen/phosphorus leaf stoichiometry and the scaling of plant growth

**Karl J. Niklas,[1]* Thomas Owens,[1] Peter B. Reich[2] and Edward D. Cobb[1]**
[1]*Department of Plant Biology, Cornell University, Ithaca, NY 14853, USA*
[2]*Department of Forest Resources, University of Minnesota, St Paul, MN 55108, USA*
**Correspondence: E-mail: kjn2@cornell.edu*

## Abstract

We adopted previous N : P stoichiometric models for zooplankton relative growth to predict the relative growth rates of the leaves $\mu_L$ of vascular plants assuming that annual leaf growth in dry mass is dictated by how leaf nitrogen $N_L$ is allocated to leaf proteins and how leaf phosphorus $P_L$ is allocated to rRNA. This model is simplified provided that $N_L$ scales as some power function of $P_L$ across the leaves of different species. This approach successfully predicted the $\mu_L$ of 131 species of vascular plants based on the observation that, across these species, $N_L$ scaled, on average, as the 3/4 power of $P_L$, i.e. $N_L \propto P_L^{3/4}$. When juxtaposed with prior allometric theory and observations, our findings suggest that a transformation in N : P stoichiometry occurs when the plant body undergoes a transition from primary to secondary growth.

## Keywords

Plant allometry, plant size, protein-rRNA models, scaling laws.

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## INTRODUCTION

Dobberfuhl (1999; see Sterner & Elser 2002; Vrede *et al.* 2004) first proposed a general model that attempts to predict the relative growth rates of all manner of organisms based on how total body nitrogen $N_T$ is allocated to protein construction. Noting that some portion of total body phosphorus $P_T$ must be allocated to rRNA to maintain any specific quantity of protein, this model conceptually relates relative growth rates to N : P stoichiometry by envisioning proteins as the 'overhead' that must be produced to achieve growth and rRNA as the protein-output 'machinery' that must be maintained to recycle this overhead. As noted by Dobberfuhl and others (e.g. Ågren 2004), assuming a constant chemical composition, relative growth $\mu$ can be mathematically expressed in terms of carbon C, nitrogen N, or phosphorus P content and rate of change by the formula

$$\mu = \frac{1}{C}\left(\frac{dC}{dt}\right) = \frac{1}{N}\left(\frac{dN}{dt}\right) = \frac{1}{P}\left(\frac{dP}{dt}\right). \quad (1)$$

For any one of these essential substances, designated here by $X$, this formula takes the general form

$$\mu = \frac{1}{X}\left(\frac{dX}{dt}\right) = \ln\left(\frac{X_2}{X_1}\right)\cdot(t_2 - t_1)^{-1} \quad (2)$$

where $X_2$ is the cell (tissue or organismal) concentration of $X$ at time $t = 2$ and $X_1$ is the concentration of $X$ at time $t = 1$ (see Hunt 1990). If the expression $X$ is thought of in terms of protein synthesis, Dobberfuhl's (1999) model expresses relative growth as

$$\mu = \ln\left[\frac{f_N N_T + \left(\frac{k_s r_e F f_P P_T}{m_r}\right)}{f_N N_T}\right]\cdot t^{-1}, \quad (3)$$

where $f_N$ is the decimal fraction of $N_T$ invested in proteins, $k_s$ is the protein synthesis rate per ribosome, $r_e$ is the protein retention efficiency, $F$ is the decimal fraction of total RNA allocated to rRNA, $f_P$ is the decimal fraction of $P_T$ invested in RNA, and $m_r$ is average ribosome mass.

Using estimates or published numerical values of the variables required by this model, various authors have used eqn 3 (or its variants) to predict the relative growth rates of different unicellular plants and animals (e.g. Nielsen *et al.* 1996; Klausmeier *et al.* 2004; Vrede *et al.* 2004). This approach has been remarkably successful despite the numerous assumptions and simplifications underlying eqn 3, e.g. the assumption that N and P allocation patterns are ontogenetically invariant, the requirement that balanced growth has been achieved, and the supposition that resources are not limiting.

With these caveats in mind, we note that eqn 3 can be integrated into prior work showing that, across a broad spectrum of vascular plant species, annual growth in dry mass per individual $G_T$ scales isometrically with respect to

standing leaf dry mass $M_L$ and that the annual growth of leaf dry mass $G_L$ scales isometrically with respect to $M_L$, i.e. $G_T \propto M_L$ and $G_L \propto M_L$ (Niklas & Enquist 2001). As the relative growth rates of leaves $\mu_L$ provides a reliable gauge of the relative growth rates of the entire plant body (Niklas & Enquist 2001), it is reasonable to argue that, if the general model shown by eqn 3 is valid, $\mu_L$ should be governed by total leaf nitrogen and phosphorus, denoted here by $N_L$ and $P_L$, such that

$$\mu_L = \ln\left[\frac{f_N N_L + \left(\frac{k_s r_e F f_P P_L}{m_r}\right)}{f_N N_L}\right] \cdot t^{-1} \quad (4)$$

Equation 4 can be simplified further provided that, across diverse species, $N_L$ scales as some power function with respect to $P_L$, i.e. $N_L = \beta_0 P_L^{\alpha}$, where $\beta_0$ is the constant of proportionality and $\alpha$ is the scaling (allometric) exponent. Although the numerical values of $\alpha$ and $\beta_0$ must be determined empirically (because, in theory, they are free to vary as functions of ontogeny, phylogeny, or ecology), eqn 4 can be expressed *ad hoc* in general form as

$$\begin{aligned}\mu_L &= \ln\left[1 + \left(\frac{k_s r_e F}{m_r}\right)\left(\frac{f_P}{f_N}\right)\frac{N_L^{\frac{1}{\alpha}-1}}{\beta_0^{1/\alpha}}\right] \cdot t^{-1} \\ &= \ln\left[1 + \left(\frac{k_s r_e F}{m_r}\right)\left(\frac{f_P}{f_N}\right)\frac{P_L^{1-\alpha}}{\beta_0}\right] \cdot t^{-1}\end{aligned} \quad (5)$$

This version of the Dobberfuhl model is conceptually the same as the one proposed and explored by Vrede *et al.* (2004). However, eqn 5 differs from this and all previous versions in two important ways. First, it is mathematically and conceptually simplified because it incorporates the assertion that some form of $N_L \propto P_L^{\alpha}$ exists, and, second, it treats the N : P stoichiometry of leaves to the exclusion of all other body parts. Thus, eqn 5 attempts to wed the growing body of theoretic models relating growth to N : P stoichiometry with the equally dynamic body of literature treating broad interspecific allometric relationships.

However, a critical question is whether a model originally designed to predict the relative growth of the entire organism (like eqn 3) can be converted into one that treats leaves exclusive of the rest of the plant body (like eqn 5). From a purely theoretical perspective, we think it can because the metabolic activity of leaves drives plant growth at the level of the individual (as vouchsafed by the tight statistical one-to-one correlation between standing leaf mass and annual plant growth), particularly for plants lacking secondary growth. Here, we test eqn 5 by determining the empirical allometry of $N_L$ vs. $P_L$ for 131 angiosperm species, measuring $\mu_L$ for each species in terms of the net gain in $N_L$ during the growing season, and comparing predicted $\mu_L$ values against those observed for all 131 species.

## MATERIALS AND METHODS

We determined the relative growth rates of $N_L$ for 131 angiosperm species growing under natural (uncultivated) conditions. Each species was selected on the basis of ease of access to its growing site, the availability of healthy specimens (based on visual inspection), and the absence of secondary tissues in the stems or roots of harvested specimens (although 10 of the species selected for study are capable of secondary growth, the individuals examined were less than 1 year old, and, based on subsequent dissection at the end of the growing season, possessed no appreciable quantities of secondary xylem or phloem in roots or stems). In terms of phylogenetic and ecological composition, 78 species are dicots and 53 are monocots (*c.* 60% and *c.* 40%, respectively). A complete list of the 131 species (along with comments on local growth or soil conditions, and total leaf nitrogen and phosphorus, expressed as percentages of total leaf dry weight) is provided as an online Appendix.

Depending on the individual species, newly produced (but fully expanded, green) leaves were harvested from plants between late March and early to mid-April. Neighbouring conspecifics of equivalent age and condition were identified and marked at the time of the first leaf harvest for future collection. These conspecifics were never further than 2 m away from their harvested counterparts. The leaves of these older specimens were harvested at the end of the growing season but before any visual evidence of senescence (between mid-June and early October, depending on the species). All leaves were air-dried, weighed, and subsequently analysed by the Cornell Soil Diagnostic Laboratory (details of the analytical protocols are available upon request) to determine $N_L$ and $P_L$ (in mass units). After the second leaf harvest, each older conspecific was removed from its growing site, dissected and air-dried to determine its total body dry mass $M_T$.

Leaf relative growth in nitrogen content $\mu_L$ was calculated using the formula $\mu_L = \ln(N_{L2}/N_{L1})(t_2 - t_1)^{-1}$, where $t$ is time (in days) and the subscripts 1 and 2 refer to the first and second leaf harvests. The $\mu_L$ for each species was then modelled (see eqn 6) using the following published values $k_s = 2.5 \times 10^{-11}$ μg protein ribosome$^{-1}$ day$^{-1}$, $r_e = 60\%$, $F = 80\%$, and $m_r = 4.53 \times 10^{-12}$ μg rRNA ribosome$^{-1}$ (Campana & Schwartz 1981; Mathers *et al.* 1993; Sadava 1993; Vrede *et al.* 2004). Thus, $k_s r_e F/m_r = 2.648$. In terms of $f_N$, prior work shows that between 16 and 27% of leaf $N_L$ is incorporated in Rubisco (Evans 1989). In addition, depending on whether ambient light conditions are high or low, between 15 and 60% of leaf $N_L$ is found in chloroplast thylakoids (pigment–protein complexes, electron transport constituents, reaction centres, components of the electron transport chain, particularly cyto b/f; and ferredoxin) (Evans 1989). Based on published $N_L$ allocation to Rubisco

and thylakoids, we adopted $f_N \sim 55\%$ as a reasonable value with which to model a broad range of species. Thus, eqn 5 takes the form

$$\mu_L = \ln\left[1 + 4.815 f_P \frac{N_{L2}^{\frac{1}{\alpha}-1}}{\beta_0^{1/\alpha}}\right] \cdot t^{-1} = \ln\left[1 + 4.815 f_P \frac{P_{L2}^{1-\alpha}}{\beta_0}\right] \cdot t^{-1}, \quad (6)$$

where the subscript L2 now refers to the gain in either $N_L$ or $P_L$ between the first and second leaf harvest. Although $f_P$ is reported to range between 1 and 20% for animal species (McKee & Knowles 1987), we are unaware of reliable published estimated of $f_P$ for vascular plant leaves. Consequently, we used a range of values, noting that empirical trends for $\mu_L$ would provide *ad hoc* the numerical limits for $f_P$.

To ascertain the numerical values of $\alpha$ and $\beta_0$, we used model type II [reduced major axis (RMA)] regression analysis, because our objective was to determine the functional relationship between $N_L$ and $P_L$ and because neither can be legitimately viewed as an independent variable (see Niklas 1994). RMA regression analyses were also used to explore all other functional allometric relationships (see Table 1). The slopes (scaling exponents) of RMA regression curves are designated as $\alpha_{RMA}$.

**Table 1** Summary statistics of reduced major axis regression of $\log_{10}$-tranformed data for stoichiometric and dry mass variables. RMA scaling (allometric) exponents denoted as $\alpha_{RMA}$. For each regression, $P < 0.0001$

| $Y_2$ vs. $Y_1$ | $\alpha_{RMA} \pm$ SE | 95% CI | $r^2$ | $F$ |
|---|---|---|---|---|
| Across all species ($n = 131$) | | | | |
| $N_L$ vs. $P_L$ | 0.78 ± 0.02 | 0.72–0.85 | 0.948 | 2339 |
| $\%N_L$ vs. $\%P_L$ | 0.78 ± 0.03 | 0.71–0.84 | 0.822 | 593.7 |
| $N_L$ vs. $M_L$ | 1.02 ± 0.02 | 0.96–1.08 | 0.945 | 2200 |
| $P_L$ vs. $M_L$ | 1.36 ± 0.02 | 1.32–1.41 | 0.966 | 3717 |
| Obs. $\mu_L$ vs. $M_L$ | 0.30 ± 0.01 | 0.24–0.36 | 0.782 | 462.5 |
| Pred. $\mu_L$ vs. $M_L$ | 0.30 ± 0.01 | 0.27–0.34 | 0.961 | 3200 |
| Across dicots ($n = 78$) | | | | |
| $N_L$ vs. $P_L$ | 0.75 ± 0.02 | 0.69–0.81 | 0.936 | 1106 |
| $\%N_L$ vs. $\%P_L$ | 0.81 ± 0.05 | 0.71–0.91 | 0.763 | 244.0 |
| $N_L$ vs. $M_L$ | 1.05 ± 0.02 | 0.97–1.13 | 0.912 | 793.1 |
| $P_L$ vs. $M_L$ | 1.33 ± 0.03 | 1.27–1.39 | 0.962 | 1907 |
| Obs. $\mu_L$ vs. $M_L$ | 0.29 ± 0.02 | 0.25–0.33 | 0.706 | 182.9 |
| Pred. $\mu_L$ vs. $M_L$ | 0.28 ± 0.01 | 0.23–0.33 | 0.956 | 1669 |
| Across monocots ($n = 53$) | | | | |
| $N_L$ vs. $P_L$ | 0.74 ± 0.02 | 0.69–0.79 | 0.954 | 984.1 |
| $\%N_L$ vs. $\%P_L$ | 0.74 ± 0.03 | 0.66–0.82 | 0.889 | 400.8 |
| $N_L$ vs. $M_L$ | 1.02 ± 0.04 | 0.96–1.26 | 0.913 | 793.1 |
| $P_L$ vs. $M_L$ | 1.34 ± 0.03 | 1.27–1.41 | 0.969 | 1479 |
| Obs. $\mu_L$ vs. $M_L$ | 0.29 ± 0.02 | 0.25–0.33 | 0.848 | 263.0 |
| Pred. $\mu_L$ vs. $M_L$ | 0.31 ± 0.01 | 0.27–0.35 | 0.963 | 1239 |

## RESULTS

Across all 131 species, RMA regression analysis indicated that $N_L$ for mature (second harvest) leaves scaled as the 3/4 power $P_L$, i.e. $N_L \propto P_L^{3/4}$ (Table 1; Fig. 1a). Comparisons between the numerical values of the corresponding scaling exponents determined separately for the dicot and the monocot species represented in our data set indicated no significant difference between the allometry of these two taxonomic groups (Table 1). Similarly, comparisons of the 95% confidence intervals for the constant of proportionality for $N_L \propto P_L^{3/4}$ for all 131 species and for either the dicot or monocot species indicated no statistically significant differences at the 0.5% level, i.e. $\beta_0 = 0.18 \pm 0.07$.

Regression of $N_L$ against $P_L$ (both expressed as a percentage of leaf dry mass; $\%N_L$ and $\%P_L$) indicated that the $\%N_L$ of second harvest leaves scaled as the 0.78 power of $\%P_L$ (Table 1; Fig. 1b). Likewise, the $\%N_L \propto \%P_L^{3/4}$ scaling relationship was observed across all leaves harvested early in the growing season ($\alpha_{RMA} = 0.764 \pm 0.04$, 95%CI = 0.715–0.813, $r^2 = 0.918$, $F = 1{,}557$, $P < 0.0001$). Additionally, no statistically significant difference was observed between the mean $\%N_L$ and mean $\%P_L$ values observed across first and second harvest of leaves (i.e. $\%N_L = 2.53 \pm 0.09$ and $\%N_L = 2.69 \pm 0.11$ and $\%P_L = 0.261 \pm 0.015$ and $\%P_L = 0.257 \pm 0.013$, respectively). Clearly, however, significant differences were observed between the absolute amounts of $N_L$ and $P_L$ measured for first and second harvested leaves per plant as a result of growth in standing leaf dry mass.

Using the 95% confidence intervals as a gauge, comparisons of the scaling exponents for $\%N_L$ vs. $\%P_L$ for the dicot and the monocot species represented in our data set showed no statistically significant difference, although we note that the 95% confidence intervals for the scaling exponent of $\%N_L$ vs. $\%P_L$ for monocot leaves harvested late in the growing season include 2/3 (Table 1). To assess whether $\%N_L \propto \%P_L^{3/4}$ holds true across species other than those reported here, we examined a data base generated from 7445 observations of 1665 vascular plant species from 868 sites worldwide. These data are an expanded version of data reported by Reich & Oleksyn (2004) and differ from those studied by these authors by virtue of containing multiple entries for individual species reflecting conspecifics differing in age. For these data, $\%N_L$ scaled as the $0.72 \pm 0.05$ power of $\%P_L$ ($r^2 = 0.335$, $F = 3.753$, $P < 0.00001$) (Fig. 1c). The 95% confidence intervals for this scaling exponent included 3/4 and only marginally exclude 2/3 (i.e. 95% CI = 0.71–0.75), which has been reported for leaves across a broad spectrum of species (Wright *et al.* 2004; see Discussion).

Noting that $N_L = 0.18\ P_L^{3/4}$ across the second harvest leaves of the 131 species examined for this study, we

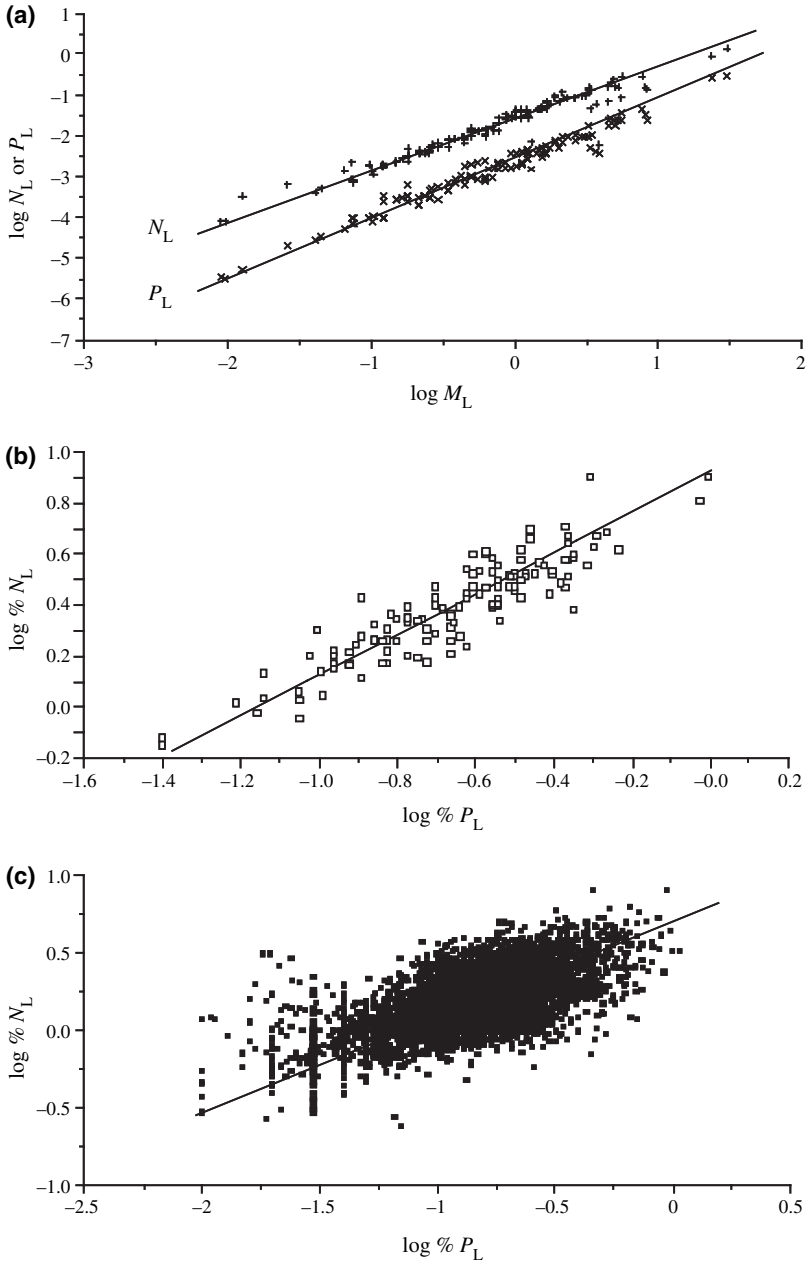


**Figure 1** Empirical relationships among $\log_{10}$-transformed data for leaf nitrogen ($N_L$), phosphorus ($P_L$), leaf dry mass ($M_L$), and $N_L$ and $P_L$ expressed as a percentage of $M_L$ (%$N_L$ and %$P_L$, respectively). Original units in g. (a) log $N_L$ and log $P_L$ vs. log $M_L$ (data from 131 species). (b) log %$N_L$ vs. log %$P_L$ (data from 131 species examined here). (c) log %$N_L$ vs. log %$P_L$ (data from 1665 species; $n = 7{,}445$). Solid lines are RMA regression curves.

modified eqn 6 to model the relative growth rates of leaves as follows

$$\mu_L = \ln\left[1 + 47.37 f_P N_{L2}^{1/3}\right] \cdot t^{-1} = \ln\left[1 + 26.75 f_P P_{L2}^{1/4}\right] \cdot t^{-1}. \quad (7)$$

Using this formula, all observed $\mu_L$ were bounded by the upper and lower limits set by $5\% < f_P \leq 15\%$ when plotted against standing dry leaf mass $M_L$ (Fig. 2). These limits were deemed biologically reasonable in light of estimates for animal species. Bivariate plots of predicted vs. observed $\mu_L$ were log–log linear and had slopes near unity (0.90 and 0.88 for $f_P = 5\%$ and $f_P = 15\%$, respectively) with coefficients of correlation $0.770 < r^2 \leq 0.774$. Additionally, the numerical values and size-dependent trends observed for predicted leaf relative growth rates were sensitive to the numerical value of the scaling exponent governing the proportional relationship between total leaf nitrogen and total leaf phosphorus. For example, regression of observed $\mu_L$ against those predicted assuming that $N_L = 0.18\ P_L^{2/3}$ rather than $N_L = 0.18\ P_L^{3/4}$ resulted in log–log linear relationships with comparable coefficients of correlations ($0.69 < r^2 \leq 0.73$

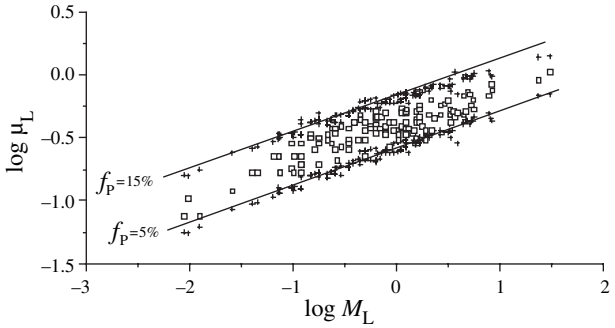


**Figure 2** $Log_{10}$-tranformed data for predicted and observed relative growth rates $\mu_L$ (denoted by + and open squares, respectively) plotted against transformed data for standing dry leaf mass ($M_L$). Predicted values of $\mu_L$ assume that $f_P$ (i.e. the decimal fraction of $P_L$ invested in RNA) is either 5 or 15%. Solid lines are reduced major axis regression curves for predicted $\mu_L$.

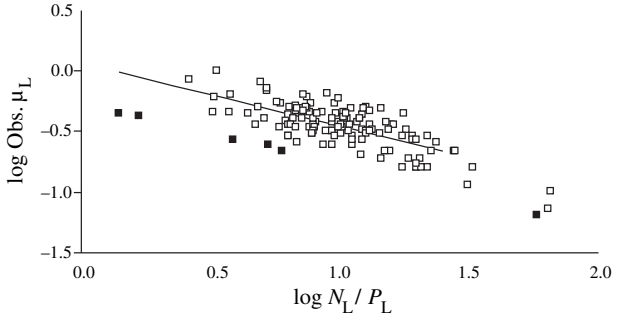


**Figure 4** $Log_{10}$-tranformed data for observed relative growth rates ($\mu_L$) plotted against the quotient of total leaf nitrogen and phosphorus ($N_L/P_L$). Solid line is reduced major axis regression curve for all data points ($n = 131$ species). Dashed lines are $\pm$ 2 SD. Regression statistics for the entire data set and after the removal of five outliers (closed squares) are provided in text.

for $f_P$ = 5% and 15%, respectively), but slopes substantially different from unity (0.44 and 0.51).

In terms of the consistency of eqn 7 with other observed stoichiometric and allometric relationships across the species we examined, it must be noted that $\ln [1 + 47.37\, f_P N_{L2}^{1/3}]$ will scale approximately as $47.37\, f_P N_{L2}^{1/3}$ provided that $47.37\, f_P N_{L2}^{1/3} \ll 1$. For our data, $N_{L2}$ equalled, on average, 0.0045 such that $47.37\, f_P N_{L2}^{1/3} = 0.391$ for $f_P$ = 5%. Therefore, because total leaf nitrogen scaled isometrically with respect to total dry leaf mass and total leaf phosphorus scaled as the 4/3 power of leaf mass such that $N_L \propto P_L^{3/4} \propto M_L$ (Table 1; Fig. 3), our model predicts that observed (and predicted) $\mu_L$ should scale approximately as the 1/3 power of $M_L$. This expectation was consistent with the 95% confidence intervals for the scaling exponents of the RMA regression curves of observed (and predicted) $\mu_L$ vs. $M_L$ (Table 1). However, the 95% intervals for this exponent also include 1/4 across all 131 species (95% CI = 0.24–0.34) as well as across either dicot or monocot species (95% CI =0.25–0.33) (Table 1).

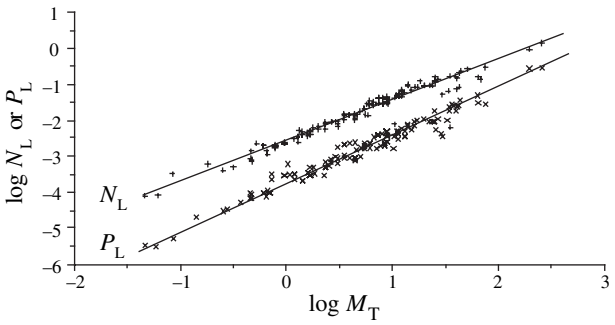


**Figure 3** Observed log $N_L$ and log $P_L$ plotted againsy log $M_L$. Solid lines are reduced major axis regression curves.

In terms of this alternative numerical value, we note that if $M_L$ scales isometrically with respect to total body dry mass ($M_L \propto M_T$), it follows from $\mu_L \propto M_L^{1/3}$ that, across species, $\mu_L \propto M_T^{1/3}$, whereas, if $\mu_L \propto M_L^{1/4}$ is true, then $\mu_L \propto M_T^{1/4}$. Regression analysis indicated that, across all 131 species, standing dry leaf biomass scaled as the 1.01 $\pm$ 0.02 power of $M_T$ (95%CI = 0.97–1.05, $r^2 = 0.7914$, $F = 1.025$, $P < 0.0001$), whereas observed $\mu_L$ scaled as the 0.31 $\pm$ 0.04 power of $M_T$ (95%CI = 0.29–0.34, $r^2 = 0.782$, $F = 462.5$, $P < 0.0001$).

Finally, the preceding scaling relationships indicated that relative leaf growth rates should decrease with increasing values of $N_L/P_L$. This prediction is consistent with our data (Fig. 4). However, it was not possible to determine whether the scaling exponent governing this relationship is −3/4 or −2/3. Specifically, observed $\mu_L$ scaled as the −0.719 $\pm$ 0.04 power of $N_L/P_L$ ($n = 131$, $r^2 = 0.518$, $F = 138.8$, $P < 0.0001$) but the 95% confidence intervals included both −3/4 and −2/3 (i.e. 95% CI = −0.834 to −0.599). Removal of the five outliers observed for observed $\mu_L$ vs. $N_L/P_L$ did not statistically significantly alter the scaling exponent (i.e. −0.744 $\pm$ 0.04; $n = 126$, $r^2 = 0.572$, $F = 166.0$, $P < 0.0001$) nor the inclusion of both numerical values for the scaling exponent (i.e. 95% CI = −0.857 to −0.628). Likewise, regression of the relative growth rates predicted by eqn 7 against $N_L/P_L$ gave slopes of −0.743 $\pm$ 0.03 and −0.641 $\pm$ 0.03 for $f_P$ = 5% and $f_P$ = 15%, respectively.

## DISCUSSION

The mathematical structure and physiological assumptions of our model resonate with those of other models (e.g. Vrede *et al.* 2004; Ågren 2004) demonstrating that N : P allocation patterns can (and do) constrain growth rates across hetero-

as well as photoautotrophs adapted to very different ecological conditions. However, to our knowledge, this paper is the first attempt to use the approach advocated by Dobberfuhl (1999) to predict the relative growth rates of vascular plants based exclusively on leaf N : P stoichiometry.

The predictions of our variant of the Dobberfuhl model and the empirical trends we report here are consistent with previous reports dealing with taxonomically and ecologically diverse (including old specimens of woody) species. For example, our observation that total leaf nitrogen scales as the 3/4 power of total leaf phosphorous when both nutrients are expressed as percentages of total leaf mass is statistically indistinguishable from the RMA regression slopes (scaling exponents) we calculate for the data reported by Thompson *et al.* (1997) and Cornelissen *et al.* (1997), respectively, for experimental and field site observations of diverse species (see Güsewell 2004 figure 7). Additionally, all of the nitrogen, phosphorus, and relative growth relationships predicted by other variants of the Dobberfuhl (1999) model for the few animal or algal systems examined are qualitatively similar, if not identical to those reported here for vascular plants (Ryser *et al.* 1997; Vrede *et al.* 2004).

Considerable variation clearly exists when predicted or observed $\mu_L$ is plotted as a function of leaf mass (see Fig. 2a). This variation is attributable to a number of factors not addressed in the model (although each can be incorporated when species-specific data become available). Among the most likely of these factors are species-specific differences or ecotypic variation in protein synthesis rates or retention efficiencies (Mathers *et al.* 1993; Sadava 1993; Güsewell 2004), differences in the fractional allocation of $N_L$ to proteins (e.g. because of differences in ambient light intensities) (Evans 1989), morphological and anatomical differences in leaf construction (e.g. leaf thickness, see Nielsen *et al.* 1996), recruitment of N and P from storage organs during early growth (e.g. tubers and bulbs, see Meyer & Tukey 1965), differences in leaf tissue ploidy, and nitrogen-use efficiency (Brown 1978), and changes in N or P allocation to leaf components during leaf ontogeny.

Arguably, however, the variation resulting from these and other factors supports rather than distracts from our model because predicted relative growth rates remain bounded within comparatively tight limits despite the ecological and taxonomic differences among the species examined. Nevertheless, the trends we report are undoubtedly influenced by ecological conditions just as they are clearly influenced by taxonomic composition. For example, the proportion of total $N_L$ in Rubisco increases with increasing leaf nitrogen and ambient light intensity (Evans 1989), whereas $C_4$ species invest comparatively smaller amounts of $N_L$ in photosynthetic carboxylation enzymes than $C_3$ species (i.e. they have greater biomass production per $N_L$ investment) (Brown 1978; Taiz & Zeiger 2002).

An equally serious concern is that our current data preclude an empirical test of the fundamental supposition that $\mu_L$ is governed by species-specific N : P allocation patterns to leaf proteins-rRNA. Size-dependent biases in either $P_L$ allocation to cellular constituents other than ribosomes (e.g. sugar phosphates, coenzymes, phospholipids; phytic acid) or N allocation to N-rich compounds other than proteins (e.g. nucleic acids and hexoamines) could in theory account for the interspecific scaling relationships we (and others) observe. When seen in this light, our variant of the Dobberfuhl (1999) model is best viewed as one among many physiologically plausible alternatives for predicting relative growth in terms of leaf N and P stoichiometry.

Yet in this regard, our model points in directions that other models do not. For example, it suggests that plant N : P stoichiometry undergoes a change during the ontogenetic transformation from the primary to the secondary plant body. Specifically, we have shown that, across diverse vascular plants lacking secondary tissues, standing dry leaf mass scales isometrically as leaf nitrogen content and as the 3/4 power of leaf phosphorus content (i.e. $M_L \propto N_L \propto P_L^{3/4}$). Prior work has shown that, across similar non-woody plants, standing leaf dry mass scales isometrically with respect to total body mass (i.e. $M_L \propto M_T$) (Niklas & Enquist 2001). Combining these observations, it follows that, for non-woody individuals, $M_T \propto N_L \propto P_L^{3/4}$. Yet, across older individuals with woody stems and roots, prior work has shown that leaf mass scales as the 3/4 power of total body mass (i.e. $M_L \propto M_T^{3/4}$) (Enquist & Niklas 2002). Thus, if $M_L \propto N_L \propto P_L^{3/4}$ holds true for older individuals with woody stems and roots, it follows that $M_T \propto N_L^{4/3} \propto P_L$. If the proportional relationship $N_L \propto P_L^{3/4}$ holds as invariant across woody as well as non-woody species, it follows that the transformation from $M_T \propto N_L \propto P_L^{3/4}$ to $M_T \propto N_L^{4/3} \propto P_L$ must be the result of changes in the N : P stoichiometry of body parts other than leaves. [In passing, it is noteworthy that, even if the alternative 2/3 scaling relationship for leaf N : P stoichiometry proves to be 'canonical' (i.e. $N_L \propto P_L^{2/3}$; see Wright *et al.* 2004), it remains the case that $M_T \propto N_L^{\alpha>1} \propto P_L$.] We think that it is reasonable to assume that this transformation reflects the accumulation of secondary tissues (as plants increase in size and age) whose N : P stoichiometry differs substantially from photosynthetic tissues.

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