

A paradox of leaf-trait convergence: why is leaf nitrogen concentration higher in species with higher photosynthetic capacity?

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Abstract It is well known that leaf photosynthesis per unit dry mass (A_{mass}) is positively correlated with nitrogen concentration (N_{mass}) across naturally growing plants. In this article we show that this relationship is paradoxical because, if other traits are identical among species, plants with a higher A_{mass} should have a lower N_{mass} , because of dilution by the assimilated carbon. To find a factor to overcome the dilution effect, we analyze the $N_{\text{mass}}-A_{\text{mass}}$ relationship using simple mathematical models and literature data. We propose two equations derived from plant-growth models. Model prediction is compared with the data set of leaf trait spectrum obtained on a global scale. The model predicts that plants with a higher A_{mass} should have a higher specific nitrogen absorption rate in roots (SAR), less biomass allocation to leaves, and/or greater nitrogen allocation to leaves. From the literature survey, SAR is suggested as the most likely

factor. If SAR is the sole factor maintaining the positive relationship between N_{mass} and A_{mass} , the variation in SAR is predicted to be much greater than that in A_{mass} ; given that A_{mass} varies 130-fold, SAR may vary more than 2000-fold. We predict that there is coordination between leaf and root activities among species on a global scale.

Keywords Leaf trait variation · Photosynthesis–nitrogen relationship · Growth model · Root activity · Carbon and nitrogen economy

Abbreviations

A_{mass}	CO ₂ uptake rate per unit standing leaf mass
k	Conversion coefficient from CO ₂ to biomass
LL	Leaf life span
LM	Standing leaf mass
LMF	Fraction of biomass allocated to leaves
LMP	Leaf mass production
LN	Standing leaf N
LNF	Fraction of N allocated to leaves
LNP	Leaf N production
MRT	Mean residence time of N in leaves
N_{mass}	Leaf N concentration per unit leaf dry mass
PM	Standing plant mass
PMP	Plant biomass production
PN	Standing plant nitrogen
PNP	Plant N production
R	N resorption efficiency
RL	Root life span
RM	Standing root mass
RMF	Fraction of biomass allocated to roots
RMP	Root mass production
SAR	N uptake rate per unit standing root mass

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Introduction

Recent intensive studies have revealed convergence in the variation of leaf traits across vascular plant species on a global scale. At one end of the axis, species have higher photosynthetic capacity, a higher nitrogen (N) concentration, a greater leaf area on a dry mass basis, and a shorter leaf life span. The opposite is true at the other end (Reich et al. 1991, 1992, 1997; Wright et al. 2004, 2005). This convergence reflects a mixture of direct and indirect causal relationships (Wright et al. 2004). Higher photosynthetic capacity is beneficial for faster growth, whereas being tougher and less palatable for herbivores is needed to persist for a longer time. A leaf can hardly realize both at the same time, leading to a trade-off between photosynthesis and persistence (Reich et al. 1991; Wright and Cannon 2001; Hikosaka 2005).

The positive relationship between photosynthetic capacity and leaf N concentration seems reasonable in terms of biochemistry (Field and Mooney 1986; Evans 1989). Because about half of leaf N is invested in the photosynthetic apparatus, there is a strong correlation between photosynthetic capacity and N concentration within a species. Furthermore, species with a higher N concentration tend to have higher photosynthetic N-use efficiency (photosynthetic capacity per unit leaf N) (Hikosaka 2004; Wright et al. 2005). Because of these two factors, photosynthetic capacity increases more than proportionally with increasing leaf N concentration across species (Hikosaka 2004). In a survey on a global scale, the regression equation for photosynthetic capacity and leaf N concentration was $Y = 36.3 X^{1.72}$ (Wright et al. 2004).

Most previous studies on the photosynthesis–N relationship have considered N concentration to be a determinant of photosynthetic capacity. However, N concentration is also dependent on photosynthesis. New leaves

are constructed with allocated N and biomass (Fig. 1). N concentration will decrease if biomass allocation to leaves increases relative to N allocation. Thus, if there are two species with different photosynthetic rates, we can expect the species with a higher photosynthetic rate to have a lower leaf N concentration. However, this is discrepant to leaf-trait convergence. Why do species with a higher photosynthetic capacity have a higher leaf N concentration? In this article, using mathematical growth models, we theoretically show that the positive correlation between photosynthetic rates and nitrogen concentrations is paradoxical. Then we consider the mechanism that maintains the interspecific variation in leaf N concentration relative to photosynthetic rate, and discuss the factors responsible for leaf-trait convergence.

N concentration as a function of photosynthesis

Leaf N concentration per unit leaf dry mass (N_{mass}) is affected by various plant functions. Here N_{mass} is defined as the ratio of standing leaf N (LN) to standing leaf mass (LM) in the plant. LM at one point in time (LM_t) is determined by LM one step earlier (LM_{t-1}) and by production (ΔLMP) and loss of leaf mass (ΔLML) during the step ($LM_t = LM_{t-1} + \Delta LMP - \Delta LML$; Fig. 2). LN is also affected by the turnover of N. N_{mass} should thus be modeled as a function of these variables. To obtain simple solutions, we adopt several assumptions. First, we assume that LN and LM are balanced with each other such that each species has an inherent value of N_{mass} . N_{mass} is thus constant over short time periods (see “Assumptions in the model” for discussion).

Second, we consider two situations for plant growth. The first model (Exponential model) assumes that plants grow exponentially without any loss of tissues (no

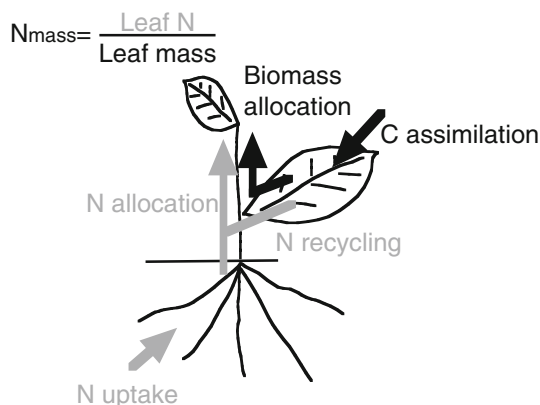


Fig. 1 Leaf nitrogen concentration as influenced by allocation of nitrogen and biomass

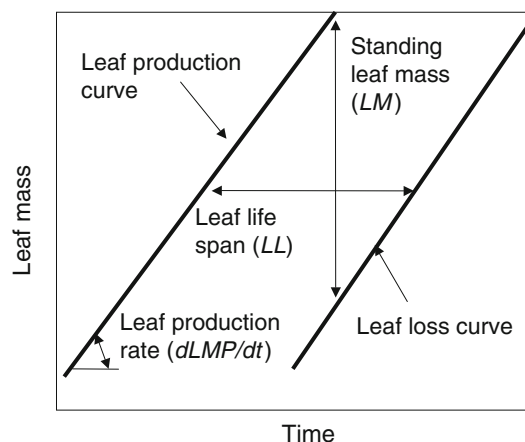


Fig. 2 Leaf mass as influenced by rates of leaf production and loss, and leaf life span

senescence) and recycling of N, in which the relative growth rate is constant. It represents initial growth of seedlings under ideal conditions, where there is no resource limitation, no mutual shading and no stress. The second model (Turnover model) assumes that LM is constant because of the same rate of leaf production and loss. This happens in climax vegetation, where the standing biomass is almost stable. These two situations are extremes in plant life and other situations may be regarded as intermediate between the two.

Exponential model

Here we use a simple plant-growth model that has been used for many growth-analysis studies (e.g., Hirose 1987; Garnier 1991). In the model, C and N are acquired by leaves and roots, respectively, and the unit rates of assimilation (photosynthetic rate per unit standing leaf mass, A_{mass} , and N absorption rate per unit standing root mass, SAR) are constant. The fractions of biomass and N in each organ are also constant and the relative growth rate does not change (plants grow exponentially). There is no senescence in organs, i.e., no loss of organs.

As mentioned above, we assumed steady-state growth where standing leaf mass and leaf N are balanced with each other. Because there is no loss of N and biomass in this model, N_{mass} is obtained from the balance between N and biomass allocation to leaves:

$$N_{mass} = LN/LM \simeq dLN/dLM \simeq (dLNP/dt)/(dLMP/dt) \tag{1}$$

where $dLNP/dt$ and $dLMP/dt$ are the rate of leaf N production (N allocated to leaves) and the rate of leaf mass production, respectively.

The rate of plant biomass production ($dPMP/dt$) is proportional to the product of photosynthetic rate per unit leaf mass (A_{mass}) and standing leaf mass (LM):

$$\frac{dPMP}{dt} = \frac{1}{LM} \frac{dPMP}{dt} LM = k A_{mass} LM \tag{2}$$

where k is the coefficient of conversion from CO_2 to biomass, which involves respiration (both construction and maintenance). Plant nitrogen uptake rate ($dPNP/dt$) is expressed as the product of specific absorption rate (SAR) and standing root mass (RM):

$$\frac{dPNP}{dt} = \frac{1}{RM} \frac{dPNP}{dt} RM = SAR RM \tag{3}$$

We define the fractions of acquired N and biomass that are allocated to leaves as LNF (= $dLNP/dPNP$) and LMF (= $dLMP/dPMP$), respectively. Note that LNF and LMF are not the ratio for standing N and mass. However, because steady-state growth without loss of biomass and N

is assumed in this model, values of LNF and LMF are equal to those of the leaf-to-plant N ratio and the leaf-to-plant mass ratio, respectively (i.e., $dLNP/dPNP \simeq LN/PN$ and $dLMP/dPMP \simeq LM/PM$, where PM and PN are the standing plant mass and N, respectively). Substituting Eqs. 2 and 3 into Eq. 1, N_{mass} is expressed as:

$$\begin{aligned} N_{mass} &\simeq (dLNP/dt)/(dLMP/dt) \\ &= (LNF dPNP/dt)/(LMF dPMP/dt) \\ &= \frac{SAR RM LNF}{k A_{mass} LM LMF} \frac{PM}{PM} \\ &= \frac{SAR RMF LNF}{k A_{mass} LMF^2} \end{aligned} \tag{4}$$

where RMF is the fraction of biomass allocated to roots, equal to the root-to-plant mass ratio in this model (i.e., $dRMP/dPMP \simeq RM/PM$). Equation 4 indicates that N_{mass} increases with increasing root activity (SAR), biomass allocation to roots (RMR), and N allocation to leaves (LNR) because an increase in these variables increases the amount of leaf nitrogen. An increase in photosynthetic rates (A_{mass}) decreases N_{mass} , because it increases biomass production. As an increase in LMF increases standing leaf mass, which not only increases biomass production but also dilutes nitrogen in leaves by increased leaf mass allocation, N_{mass} is inversely related to the square of LMF.

Turnover model

In mature vegetation, production of new leaves is balanced by loss of old leaves, leading to a constant leaf mass in the canopy (Hikosaka 2003; Oikawa et al. 2005). Assuming that the rate of leaf-mass production ($dLMP/dt$) is identical to the leaf loss rate for a certain value of leaf longevity (LL), LM is expressed as the product of leaf production rate and leaf longevity (Fig. 2; Ackerly and Bazzaz 1995; Hikosaka 2005):

$$\begin{aligned} LM &= \frac{dLMP}{dt} LL = \frac{1}{LM} \frac{dPMP}{dt} LM LMF LL \\ &= k A_{mass} LM LMF LL \end{aligned} \tag{5}$$

Thus, standing leaf mass (LM) is greater if the leaf longevity is longer. Note that in this model, the value of LMF is not equal to that of standing mass ratio of leaf to total plant. Equation 5 can be modified as follows:

$$\frac{dPMP}{dt} = \frac{LM}{LMF LL} \tag{5'}$$

Similarly, RMF can be expressed as:

$$RM = \frac{dPMP}{dt} RMF RL \tag{6}$$

where RL is the root longevity. LN is expressed as:

$$\text{LN} = \frac{\text{dPNP}}{\text{dt}} \text{LNF MRT} = \text{SAR RM LNF MRT} \quad (7)$$

where MRT is the mean residence time of N in the leaves (Berendse and Aerts 1987). MRT is higher if leaf longevity is longer and/or if plants recycle more N (Aerts and Chapin 2000). Then N_{mass} is expressed as:

$$\begin{aligned} N_{\text{mass}} &= \frac{\text{LN}}{\text{LM}} = \frac{\text{SAR RM LNF MRT}}{k A_{\text{mass}} \text{LM LMF LL}} \\ &= \frac{\text{SAR}(\text{dPMP}/\text{dt})\text{RMF RL LNF MRT}}{k A_{\text{mass}} \text{LM LMF LL}} \\ &= \frac{\text{SAR RMF LNF RL MRT}}{k A_{\text{mass}} \text{LMF}^2 \text{LL}^2} \end{aligned} \quad (8)$$

RL and MRT positively relate to N_{mass} , because an increase in these factors increases the amount of leaf nitrogen. An increase in LL increases leaf mass, which in turn increases biomass production and dilutes leaf nitrogen.

If longevity terms (MRT, RL, and LL) are assumed to be infinite, Eq. 4 is identical to Eq. 8. Therefore, the Turnover model can be regarded to include the Exponential model.

The paradox of the N–photosynthesis relationship

Here we analyze the relationship between N_{mass} and A_{mass} mainly according to the Turnover model. We define X , which is equal to $(\text{SAR RMF LNF RL MRT})/(k \text{LMF}^2 \text{LL}^2)$ in Eq. 8. Then Eq. 8 is simplified as follows:

$$\log N_{\text{mass}} = \log X - \log A_{\text{mass}} \quad (9)$$

Equation 9 suggests that, if other variables (X) are constant, N_{mass} decreases with increasing A_{mass} , i.e., N_{mass} is negatively correlated with A_{mass} (line b in Fig. 3). This is, however, inconsistent with previous studies showing a positive correlation between N_{mass} and A_{mass} . Thus, X is not constant and varies along A_{mass} . Here we use a dataset for a number of species growing in natural vegetation collected by the global plant trait network (Gloptnet; Wright et al. 2004). The slope of the log–log relationship between N_{mass} and A_{mass} across 712 species was 0.58 (line a in Fig. 3). From this, therefore, the slope of the log–log relationship between X and A_{mass} is predicted to be 1.58. This suggests that the variation in X is greater than that in A_{mass} . In the Gloptnet dataset, A_{mass} varied 130-fold (5–660 $\text{nmol g}^{-1} \text{s}^{-1}$), suggesting that X varied more than 2000-fold (line c in Fig. 3).

Which term contributes to the variation in X ?

Equation 8 suggests that to have a higher N_{mass} species with higher A_{mass} should have smaller biomass allocation

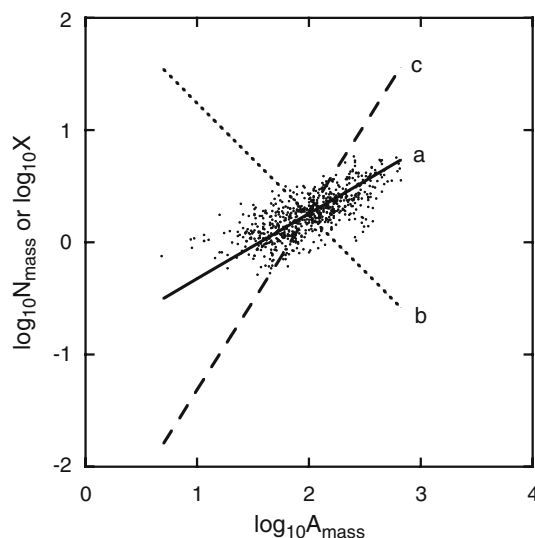


Fig. 3 The relationship between leaf nitrogen concentration (N_{mass} , %) and photosynthetic capacity (A_{mass} , $\text{nmol g}^{-1} \text{s}^{-1}$) on a dry mass basis. Values are log-transformed. Data points were obtained by Gloptnet (Wright et al. 2004). The continuous line (a) denotes a regression for the data points ($\log N_{\text{mass}} = 0.58 \log A_{\text{mass}} - 0.907$; Wright et al. 2005a). The dotted line (b) denotes a hypothetical relationship between N_{mass} and A_{mass} where X is constant ($\log N_{\text{mass}} = -\log A_{\text{mass}} + 2.24$, see text). The broken line (c) denote the relationship between X and A_{mass} ($\log X = 1.58 \log A_{\text{mass}} - 2.90$). The range of A_{mass} is based on the minimum and the maximum values in the dataset (5 and 660 $\text{nmol g}^{-1} \text{s}^{-1}$). b and c are calculated with a common mean value of N_{mass} (1.78%) and A_{mass} (98 $\text{nmol g}^{-1} \text{s}^{-1}$)

to leaves than to roots (related to LMF and RMF), greater nitrogen allocation to leaves (LNF), and/or higher nitrogen uptake rate in roots (SAR). Variables related with longevity (LL, RL, and MRT) potentially affect the relationship; N_{mass} increases with increasing RL and MRT and with decreasing LL. Hereafter, we discuss which of these factors contributes to the actual relationship.

Longevity terms

MRT is expressed as: $\text{MRT} = \text{LL}/(1 - R)$, where R is the nitrogen resorption efficiency in the leaf (Aerts and Chapin 2000). It has been suggested that R is related neither to growth form nor to leaf-trait convergence (Aerts 1996; Aerts and Chapin 2000; Wright and Westoby 2003). The MRT/LL ratio is thus regarded as a constant fraction along the variation in A_{mass} . Studying leaf and root traits in grassland and savannah species, Tjoelker et al. (2005) found that LL were positively correlated with RL. This implies that the RL/LL ratio is also a constant fraction along the variation in A_{mass} . These facts suggest that the longevity terms less contributes to the variation in X .

Biomass allocation

Biomass allocation has a large effect on the $N_{\text{mass}}-A_{\text{mass}}$ relationship, i.e., a decrease in allocation to leaves leads to concentration of nitrogen in the leaves, and an increase in allocation to roots increases nitrogen uptake rate at the plant level (Eq. 8). It should be noted that LMF and RMF in our models are not the ratio of standing mass but the fraction of assimilated biomass that is allocated to the target organ. Thus the presence of large stems does not mean low LMF. In the Glopnet survey, the $N_{\text{mass}}-A_{\text{mass}}$ relationship is less affected by the presence of large stems (trees versus herbs; Wright et al. 2005).

The contribution of biomass allocation to leaves can be estimated from the Glopnet dataset. In the turnover model, LL can be expressed as follows (see Eq. 5):

$$LL = 1/(k A_{\text{mass}} \text{ LMF}) \tag{10}$$

It has been shown that the slope of the $A_{\text{mass}}-LL$ relationship on a log-scale was -0.73 (Wright et al. 2004, 2005). Substituting Eq. 10 into the $A_{\text{mass}}-LL$ relationship in the Glopnet dataset suggests that the slope of the LMF- A_{mass} relationship was positive (0.38; Wright et al. 2005; see also Givnish 2002). However, the positive relationship between LMF and A_{mass} is inconsistent with the model prediction; if this relationship is positive and other variables are constant, N_{mass} should decrease with increasing A_{mass} (see Eq. 9). Furthermore, previous studies that analyzed plant growth under controlled conditions have also shown that interspecific variation in the leaf-to-plant mass ratio is either unrelated or positively correlated with A_{mass} or growth rates (Poorter and Remkes 1990; Garnier 1991; Aerts and Chapin 2000; Wright and Westoby 2000; Shipley 2006). This evidence suggests that biomass allocation has no positive contribution to the positive relationship between N_{mass} and A_{mass} .

Nitrogen allocation

An increase in allocation of plant nitrogen to leaves (LNF) increases N_{mass} (Eq. 8). It is known that the leaf nitrogen concentration is positively correlated with the root nitrogen concentration across species (Craine et al. 2005; Tjoelker et al. 2005). Thus, it is not likely that N_{mass} increases at the expense of root nitrogen concentration. These facts suggest that the contribution of LNF is not large.

Root activity

SAR varies among species for two reasons. One is different soil nitrogen availability, which directly affects SAR (Hirose 1987). This may contribute to the variation in X because species with a higher A_{mass} tend to inhabit fertile

soils (Poorter and Remkes 1990; Reich et al. 1991). However, such a positive relationship in N_{mass} and A_{mass} is found within a single habitat (Wright et al. 2001), suggesting that the relationship is explained not only by soil fertility.

The other reason is the inherent difference in SAR. Previous studies have shown that SAR varies greatly among species even when they are grown at the same nutrient availability and that SAR is positively related to A_{mass} in such experiments (Garnier 1991; Poorter et al. 1991; Reich et al. 1998; Comas et al. 2002). Figure 4 shows our experimental results from 11 herbaceous and tree seedlings grown under the same nitrogen condition (data from Osone et al. 2008). A_{mass} was correlated with neither leaf-to-plant mass ratio nor leaf-to-plant N ratio, but positively with SAR. The slope of the log-log relationship between SAR and A_{mass} was 1.40 (Fig. 4). Similar

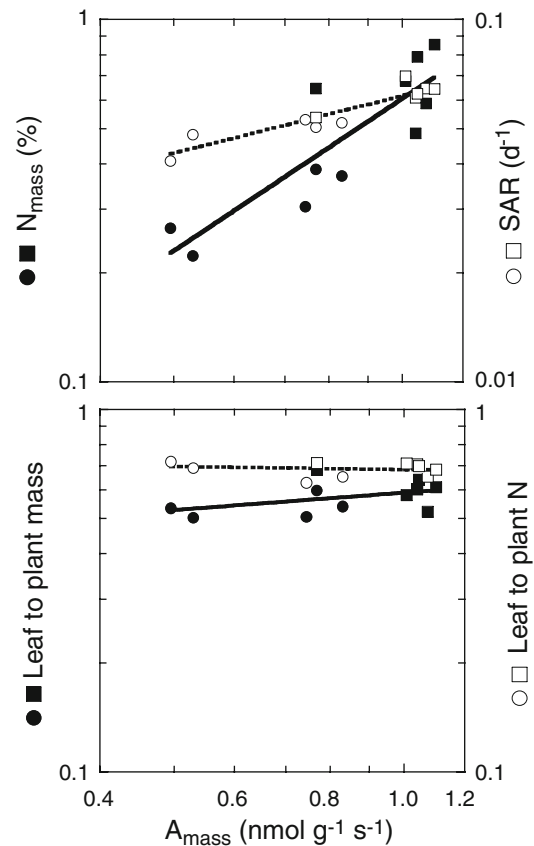


Fig. 4 The relationship between growth variables and photosynthetic capacity per dry mass (A_{mass}) in pot-grown seedlings of 11 herbaceous (*squares*) and tree (*circles*) species under high nutrient conditions (data derived from Osone et al. 2008). N_{mass} , leaf nitrogen concentration per unit dry mass; SAR, nitrogen absorption rate per unit root mass. Regression lines: $\log N_{\text{mass}} = 0.525 \log A_{\text{mass}} - 1.21$ ($r^2 = 0.85$), $\log \text{SAR} = 1.40 \log A_{\text{mass}} - 0.218$ ($r^2 = 0.68$), $\log (\text{leaf-to-plant mass}) = 0.158 \log A_{\text{mass}} - 0.230$ ($r^2 = 0.18$) and $\log (\text{leaf-to-plant N}) = -0.0267 \log A_{\text{mass}} - 0.166$ ($r^2 = 0.03$). In this experiment loss of tissues was negligible so that the leaf-to-plant mass ratio is regarded to be the same as LMF

values were obtained in studies by Poorter and coworkers (2.1) and by Reich and coworkers (1.7). These values are equivalent to the predicted slope of the $X-A_{\text{mass}}$ relationship in the Glopnet dataset, 1.58. These experimental results strongly suggest that the inherent difference in SAR contributes to the positive relationship between N_{mass} and A_{mass} .

Inherent differences in SAR may partly be ascribed to root morphology. In general, roots with higher specific root length have higher SAR (Jackson et al. 1990; Eissenstat 1992; Reich et al. 1998; Osone and Tateno 2005), but are less resistant to physical disturbance and herbivory (Eissenstat 1992; Ryser 1996; Wells and Eissenstat 2001; van der Krift and Berendse 2002). Thus, there may be a trade-off between activity and persistence in root traits, and in the leaf traits mentioned above.

Coordination between leaf and root traits has been suggested by several field studies (Craine et al. 2005; Tjoelker et al. 2005). It should be noted, however, that the positive relationship between SAR and A_{mass} lacks direct support from field experiments. Comas and Eissenstat (2004) found no trends in the phosphate uptake rate between fast-growing and slow-growing tree species growing in the field.

Assumptions in the model

We assumed a steady state in N and biomass allocation to leaves, i.e., N_{mass} is constant over short time periods (Eq. 1). This is not strictly true because N_{mass} often changes with ontogeny over longer time frames. However, if the N and biomass allocation were far from steady state, we would not find leaf-trait convergence, as observed in previous studies. For example, N_{mass} in species with a high A_{mass} would decrease faster than that in species with a low A_{mass} . Contrary to this, it is generally found that fast-growing species have higher N_{mass} than slow-growing species, suggesting that the balance between N and biomass allocation to leaves is largely fixed in each species. Our assumption is thus appropriate for addressing the question of which physiological traits are necessary for maintaining such interspecific variations. Furthermore, our results may be applicable to plants in a changing environment. Wikström and Ågren (1995) showed that results predicted by a growth model assuming steady-state growth can be applied even to cases in which growth conditions suddenly changed, because plants rapidly adjust their traits to the environmental change.

Equation 2 assumes that part of assimilated carbon is respired for construction and maintenance of tissues, where the conversion coefficient was regarded as constant (k). It is known that the construction cost of tissues varies among

functional types but the difference is generally small (e.g., Poorter and Villar 1994). It is also known that in mature leaves, the respiration rate (maintenance respiration) is almost proportional to the photosynthetic rate; for example, the slope of the log–log relationship between A_{mass} and respiration rate per unit mass was 1.18 (Wright et al. 2005). At a plant level, however, respiration rates may be affected by biomass allocation, because maintenance respiration rates vary among organs. Because respiration rates are higher in leaves than in roots and stems (e.g., Kinugasa et al. 2005), if leaf mass fraction is greater, plant respiration rates may be higher, lowering k . However, the degree of change in k may be smaller than that of changes in LMF, and its effect to N_{mass} would be canceled by the change in LMF^2 (Eqs. 4 and 8).

A_{mass} values determined in leaf-trait studies are generally measured instantaneously under saturating light, whereas Eq. 8 assumes daily carbon gain for A_{mass} . Theoretically the daily carbon gain of a leaf shows a saturating curve when plotted against the light-saturated rate of photosynthesis (Hirose and Werger 1987). The slope of the relationship between N_{mass} and daily carbon gain may thus be greater than that of the relationship between N_{mass} and the light-saturated rate. On the other hand, there is an opposite factor; A_{mass} shown in previous studies was determined for young individual leaves only while our models consider the whole plant, including older leaves. Mediavilla and Escudero (2003) showed that the slope of the relationship between mean N_{mass} and mean A_{mass} was smaller than that for the relationship between N_{mass} and A_{mass} of young leaves. Here we assume that these two effects cancel each other. In a data set by Osone et al. (2008), the slope of the log–log relationship between photosynthetic capacity and NAR (rate of biomass increment per unit leaf mass) was close to 1 (0.91; $r^2 = 0.81$), which supports our idea.

Conclusion

This study indicates that leaf-trait convergence is not only a leaf matter. If leaf carbon gain were not coordinated with other factors, we would not observe such a beautiful correlation between N_{mass} and A_{mass} across species in the field. We predict that the convergence is supported mainly by the coordinated variation in root activity. If SAR is the sole factor to overcome the nitrogen dilution effect, its interspecific variation is expected to be greater than that in A_{mass} . This prediction is consistent with previous laboratory experiments, but is not yet supported by field observations. Thus, it still remains unclear what brings about the positive correlation between N_{mass} and A_{mass} on a global scale. Further studies are needed to understand how leaf-trait convergence is maintained.

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