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Review

Mechanisms underlying interspecific variation in photosynthetic capacity across wild plant species

Kouki Hikosaka

Graduate School of Life Sciences, Tohoku University, Sendai, Miyagi 980-8578, Japan
* E-mail: hikosaka@mail.tains.tohoku.ac.jp

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Abstract Photosynthetic capacity of leaves varies greatly among C_3 species although they have the same photosynthetic metabolisms. Here we discuss mechanisms underlying interspecific variation in photosynthetic capacity. Within-species variation in photosynthetic capacity is generally explained by nitrogen concentration because photosynthetic nitrogen-use efficiency (PNUE, photosynthetic capacity per unit leaf nitrogen) tends to be constant in each species. Among-species variation, on the other hand, involves both variations in nitrogen concentration and PNUE. Species with higher photosynthetic capacity have higher nitrogen concentration per mass and PNUE. Interspecific variation in PNUE is attributable to CO_2 diffusion in the leaves, nitrogen allocation to the photosynthetic apparatus and/or specific activity of photosynthetic enzymes. Previous studies have shown that variations in mesophyll conductance and nitrogen allocation explain the variation in PNUE. As new leaves are constructed by assimilated nitrogen and carbon, increased carbon assimilation rates are expected to dilute nitrogen in the leaves. However, this expectation contradicts the fact that photosynthetic capacity and nitrogen concentration is positively related with each other across species. This paradoxical dilution effect may be compensated by root activity, i.e. species with higher photosynthetic capacity have higher root activity to maintain higher leaf nitrogen concentrations.

Key words: Growth model, leaf traits, nitrogen allocation, photosynthetic nitrogen-use efficiency, rubisco Introduction

Improvement of photosynthetic efficiency is one of the important targets of plant biotechnology (Torney et al. 2007; Zhu et al. 2008). Zhu et al. (2008) revealed that the theoretical maximum conversion efficiency of solar energy to biomass is 4.6% at 30°C under current CO_2 concentration. However, most of plants do not achieve such a high efficiency. One of the reasons may be low photosynthetic capacity. Rice and wheat have one of the highest photosynthetic capacities of any C_3 species (30-40 μmol m^{-2} s^{-1}), while some evergreen woody species have a photosynthetic capacity lower than 10 μmol m^{-2} s^{-1} even when they are grown under optimal conditions.

A recent global survey dealing with 1% of vascular plant species on the earth revealed that photosynthetic capacity varied by 120- and 40-fold when expressed on a dry mass and a leaf area basis, respectively (Glopnet; Wright et al. 2004). Such a large variation is believed to be related with strategy or niche of species. In general, herbaceous species have higher photosynthetic capacity than woody species (Larcher 1983). Similarly, higher photosynthetic capacities are found in deciduous than in evergreen species, in sun than in shade species, in early-successional than in later-successional species, in species with shorter leaf life span, in fast- than in slow-growing species and in species inhabiting lower altitudes (Chabot and Hicks 1982; Chazdon and Field 1987; Hikosaka et al. 2002; Reich et al. 1992; Wright et al. 2004; 2005).

Mechanism underlying the variation in photosynthetic capacity is an interesting question. We know that C_4 species have high photosynthetic efficiencies than C_3 species because of their CO_2 concentrating mechanism. However, a large variation still exists among C_3 species although they have the same photosynthetic metabolisms. This article reviews recent progress in understanding of interspecific variation in photosynthetic capacity.

Nitrogen as a determinant of photosynthesis

Photosynthetic capacity, defined as the light-saturated rate of CO_2 assimilation at ambient temperature under

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Abbreviations: A_{area}, photosynthetic capacity per unit leaf area; A_{mass}, photosynthetic capacity per unit leaf mass; C_i, CO_2 concentration at intercellular spaces;*k*, conversion coefficient from CO_2 to biomass; *LL,* leaf life span; *LM*, standing leaf mass; LMA, leaf mass per area; *LMF*, fraction of biomass allocated to leaves; *LNF*, fraction of N allocated to leaves; *LNP*, leaf N production; *MRT*, mean residence time of N in leaves; N_{area}, leaf N concentration per unit leaf area; N_{mass}, leaf N concentration per unit leaf dry mass; PNUE, photosynthetic nitrogen use efficiency; RBUE, Rubisco use efficiency *RL*, root life span; *RMF*, fraction of biomass allocated to roots; RNF, Rubisco nitrogen fraction; *SAR*, N uptake rate per unit standing root mass; WNF, cell wall nitrogen fraction.

This article can be found at http://www.jspcmb.jp/

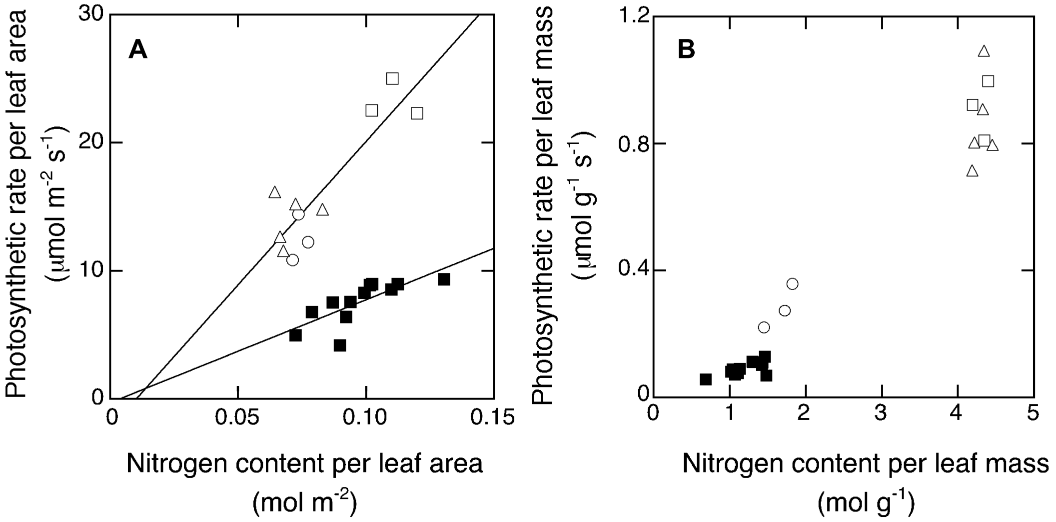

Figure 1. The photosynthesis-nitrogen relationship. Data obtained from *Chenopodium album* (annual; open symbols), and *Qercus myrsinaefolia* (evergreen tree; closed symbols). *Chenopodium album* plants were grown at high PFD and high nutrient availability (square), high PFD and low nutrient availability (circle), and at low PFD and high nutrient availability (triangle). *Quercus myrsinaefolia* plants were grown at three PFD conditions (pooled). (A) and (B) represents area- and mass-based relationship, respectively. Redrawn from Hikosaka (2004).

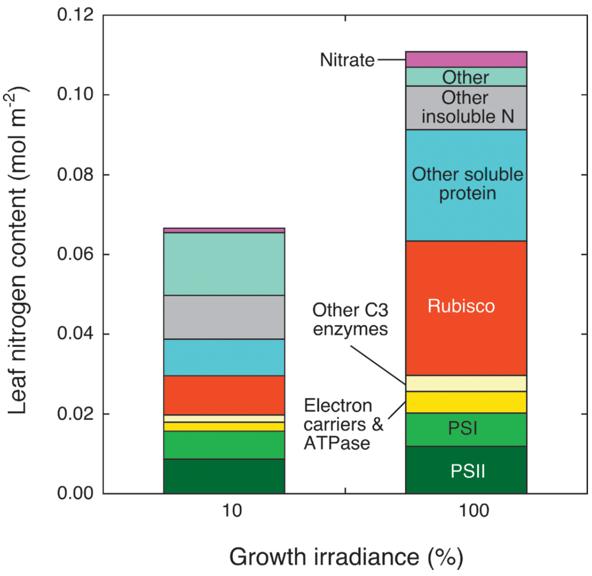

Figure 2. N partitioning in *Chenopodium album* leaves grown under two growth irradiances. Redrawn from Hikosaka and Terashima (1996).

current CO_2 concentration, is known to vary both within and between species. Within-species variation in photosynthetic capacity is well explained by the variation in leaf nitrogen content; photosynthetic capacity is correlated positively with the leaf nitrogen concentration both on leaf area or leaf mass basis (Figure 1).

When expressed on an area basis, photosynthetic capacity (A_{area}) and nitrogen content (N_{area}) are generally higher in sun than in shade leaves, under higher than under lower nutrient availability, and in younger than in older leaves (Hikosaka et al. 1994; Hikosaka 1996; Terashima and Evans 1988). Such a strong relationship is held because a large amount of nitrogen is invested in the photosynthetic apparatus (Figure 2). In particular, Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase) is known as the most abundant protein in the world because it is the largest sink of nitrogen in leaves.

As the correlation is very strong, photosynthesis-nitrogen relationship has been used in mathematical models to predict carbon gain of leaves, individual plants, and plant canopies (Hikosaka et al. 1999, 2003; Hikosaka 2003; Hirose 2005; Hirose and Werger 1987; Matsumoto et al. 2008).

When compared across species, the relationship between photosynthetic capacity and nitrogen concentration varies depending on whether the variables are expressed on area or mass basis. When expressed on a mass basis, photosynthetic capacity (A_{mass}) was strongly correlated with nitrogen concentration (N_{mass}) on a global scale (Figure 3). When expressed on an area basis, on the other hand, the correlation was significant but weak (Figure 3). In the former, both A_{mass} and N_{mass} were higher in herbaceous than in woody species, leading to a strong correlation across all the species. In the latter, A_{area} was higher in herbs but N_{area} was similar among life forms. This is because the relationship between photosynthesis and nitrogen concentration is not proportional and photosynthetic capacity per unit nitrogen, termed as photosynthetic nitrogen-use efficiency (PNUE), varies among species. Species with higher A_{mass} tend to have both higher N_{mass} and PNUE but they have low leaf mass per area (LMA), leading to similar N_{area} between low and high A_{mass} species (Hikosaka 2004).

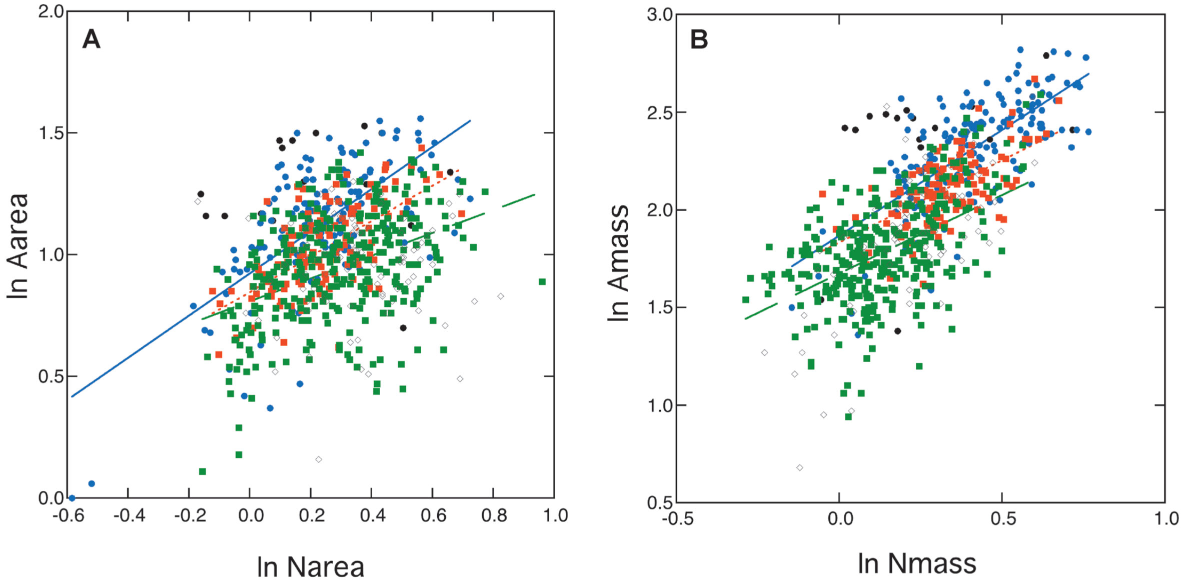

Figure 3. The relationship between photosynthetic capacity and nitrogen concentration in the Glopnet data set (Wright et al. 2004). Black circles, blue circles, red squares, and green squares represent C4 herbs, C3 herbs, deciduous woody species, and evergreen woody species, respectively. Open diamonds include other life forms (ferns, vines and so on) and woody species whose leaf habit was unknown. (A) and (B) represents area- and mass-based relationship, respectively.

Interspecific variation in photosynthetic nitrogen-use efficiency

Photosynthetic nitrogen-use efficiency (PNUE) tends to be constant within species irrespective of growth irradiance, nutrient availability and leaf age (Hikosaka 2004). Thus it has attracted much attention to improve understanding of the inherent variation in photosynthetic capacity among species (Evans 1989; Field and Mooney 1986; Hikosaka 2004; Pons et al. 1994). In the Glopnet survey, PNUE varied by 40-fold (Wright et al. 2004) and was closely linked with other leaf traits (Wright et al. 2005). For example, PNUE was negatively correlated with leaf mass per area (LMA) and leaf life span (Hikosaka 2004).

From the biochemical viewpoint, variation in PNUE is attributable to (1) CO_2 diffusion from air to carboxylation site, (2) nitrogen allocation to limiting step of photosynthesis, and (3) activity of photosynthetic enzymes (Field and Mooney 1986). In this decade many authors have analyzed mechanisms of the interspecific variation in PNUE. Most of them demonstrated that less leaf nitrogen is allocated to Rubisco in low-PNUE species (Feng et al. 2007; Hikosaka et al. 1998; Pons and Westbeek 2004; Poorter and Evans 1998; Warren and Adams 2004; Warren et al. 2006; Westbeek et al. 1999). For example, the Rubisco nitrogen fraction in leaves (RNF, Rubisco nitrogen per unit leaf nitrogen) was found to be 23% higher in an annual herb than in an evergreen tree (Hikosaka et al. 1998).

CO_2 diffusion in leaves is known to be limited at stomata and mesophyll. The contribution of stomatal condutcance to the variation in photosynthetic rates differs among previous studies. In some studies, intercellular CO_2 concentration, C_i, was similar among species irrespective of photosynthetic capacity (e.g. Poorter and Farquhar 1994; Poorter and Evans 1998; Yoshie 1986), whereas in other studies it was lower in species with low PNUE (Hikosaka et al. 1998; Hikosaka and Shigeno 2009; Warren and Adams 2004). In the Glopnet survey, C_i tended to be lower in species with lower A_{mass} or higher LMA (Wright et al. 2004). These results suggest that stomatal conductance plays a significant role in the variation in PNUE, but its effect may be different depending on species choice. It has also been indicated that mesophyll conductance for CO_2 diffusion is responsible for the variation in PNUE (Flexas et al. 2008; Hikosaka et al. 1998; Lloyd et al. 1992; Terashima et al. 2006; Warren and Adams 2006). Meta-analyses have shown that the drawdown of the CO_2 concentration from intercellular spaces to the carboxylation site was greater in sclerophytes than in non-sclerophytes (Warren 2008) and greater in leaves with higher leaf mass per area (Niinemets et al. 2009).

It has been reported that there is a significant variation in rubisco kinetics among species (Galms et al. 2005; Hikosaka et al. 1998; Makino et al. 1988). For example, Hikosaka et al. (1998) showed that an annual herb (*Chenopodium album*) had 10% higher specific activity of rubisco than an evergreen tree (*Quercus myrsinaefolia*). However, there is no comprehensive study on intersepcific variation in rubisco and its contribution to the variation in PNUE is unknown.

Recently, Hikosaka and Shigeno (2009) studied variation in PNUE among 26 species coexisting in a

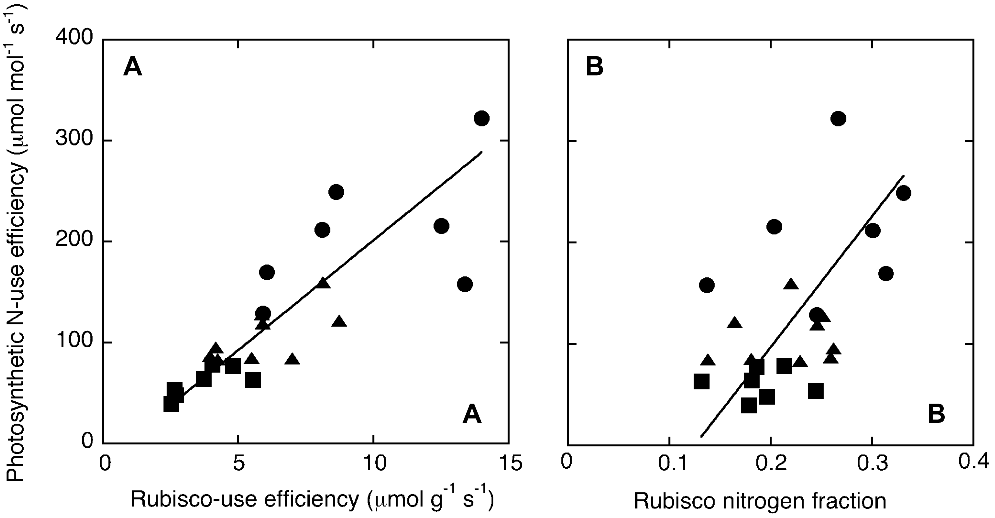

Figure 4. Photosynthetic nitrogen use efficiency as a function of rubisco-use efficiency (A) and rubisco nitrogen fraction (B) in 23 temperate species. Circles, triangles and squares denote herbs, deciduous woody species and evergreen woody species. Redrawn from Hikosaka and Shigeno (2009).

temperate region. In their data set, the PNUE varied by 8.2 fold, which was greater than that in previous studies. They analyzed PNUE as the product of rubisco-use efficiency (RBUE, photosynthetic capacity per unit rubisco) and nitrogen allocation to rubisco (RNF, rubisco nitrogen fraction). PNUE was significantly correlated both with RBUE and RNF (Figure 4). BRUE accounted for 70% of the variation in the PNUE. The variation in RBUE was partly ascribed to stomatal conductance, and other factors such as mesophyll conductance and Rubisco kinetics might also be involved. It has been suggested that cell wall thickness of mesophyll affects mesophyll conductance (Evans et al. 2009; Kogami et al. 2001). This is consistent with the result that RBUE was lower in species with higher cell wall content (Hikosaka and Shigeno 2009).

Although the contribution was smaller than RBUE, RNF was also a significant variable. In the data set of Hikosaka and Shigeno (2009), RNF explained 27% of the variation in PNUE. Then a question arises, what is nitrogeneous compound in which low PNUE species invest more nitrogen? Recently two papers proposed a trade-off in nitrogen partitioning between photosynthesis and cell walls. They reported negative relationships between RNF and cell wall nitrogen fraction (WNF) across leaves of a perennial herb (Onoda et al. 2004) and across evergreen and deciduous *Quercus* species (Takashima et al. 2004). However, studying several sclerophytes and non-sclerophytes, Harrison et al. (2009) showed that there was no trade-off in nitrogen allocation between photosynthesis and cell walls. Similar results were obtained in the data set of Hikosaka and Shigeno (2009). Increase in nitrogen allocation to cell walls will decrease PNUE if it reduces allocation to Rubisco, but this is not a general trend when we observe a broader range of species. Although nitrogen investment in cell walls is strongly related with PNUE, it does not necessarily affect nitrogen allocation to photosynthesis. There may be another nitrogen sink in leaves other than the photosynthetic apparatus and cell walls. It is known that some species accumulate secondary nitrogenous compounds. For example, some *Eucalyptus* species invest nearly 20% of leaf nitrogen in cyanogenic glucosides (Gleadow et al. 1998). Accumulation of secondary nitrogenous compounds is not necessarily general in other species. Such interspecific variations in nitrogen allocation to other functions may weaken the correlation between Rubisco and cell wall nitrogen.

Hikosaka and Shigeno (2009) suggested that the cell wall is an important component to understand the interspecific variation in leaf traits. The cell walls are an important nitrogen sink that varies in size along the variation in LMA, though N allocation to the cell wall does not directly affect PNUE. Increasing cell wall contents may affect RBUE by decreasing mesophyll conductance, which consequently causes a considerable decrease in photosynthetic capacity in species with high LMA. Greater cell wall contents may promote toughness of leaves (Onoda et al. 2008; Reich et al. 1991; Wright and Cannon 2001), tolerance to physical disturbance, and protection from herbivory and pathogen (Coley 1985), which in turn contributes to a longer leaf life span (Wright and Cannon 2001).

A paradox of the photosynthesis-nitrogen relationship

Most of previous studies on the photosynthesis-N relationship have considered that N concentration is a determinant of photosynthetic capacity. However, N concentration is also a dependent of photosynthesis. New leaves are constructed with allocated N and biomass. N concentration will decrease if biomass allocation to leaves increases relative to the N allocation. Thus if there are two species with different photosynthetic rates, we can expect that the species with a higher photosynthetic rate would have a lower leaf N concentration. However, this is discrepant to the leaf trait convergence. Why do species with a higher photosynthetic capacity have a higher leaf N concentration?

Hikosaka and Osone (2009) developed a mathematical growth model, in which leaf nitrogen concentration (N_{mass}) is expressed as a function of leaf photosynthetic rate (A_{mass}), nitrogen absorption rate in roots (*SAR*), biomass allocation to leaves (*LMF*) and roots (*RMF*), nitrogen allocation to leaves (*LNF*), life span of leaves (*LL*) and roots (*RL*), and mean residence time of nitrogen in leaves (*MRT*) as follows.

$$N_{\mathrm{mass}} = \frac{SAR\ RMF\ LNR\ RL\ MRT}{k\ A_{\mathrm{mass}} LMR^2\ LL^2} \qquad (1)$$

where k is a conversion coefficient from CO_2 to biomass. Eqn. 1 shows that N_{mass} is proportional to the inverse of A_{mass}, indicating that the relationship between A_{mass} and N_{mass} should be negative if other traits are identical among species. However, as has been discussed, the relationship between N_{mass} and A_{mass} is positive across wild plant species. This suggests that there is a significant among-species variation in other variables.

Hikosaka and Osone (2009) argued that interspecific variation in root activity (*SAR*) is most likely to account for this paradox based on following facts. (1) Species with high N_{mass} tend to appear at a habitat with high nutrient availability (Poorter and Remkes 1990), which potentially enhances *SAR*. (2) Experiments using potted plants have shown that species with higher A_{mass} and N_{mass} tend to have higher *SAR* (Garnier 1991; Osone et al. 2008; Poorter et al. 1991). (3) Contribution of other parameters is not supported by previous experimental results. If *SAR* is the solo factor that contributes to the positive relationship between N_{mass} and A_{mass}, the variation in *SAR* should be greater than that in A_{mass}. This is consistent with previous experiments using potted plants (Osone et al. 2008; Poorter et al. 1991; Reich et al. 1998). In the Glopnet dataset, A_{mass} varied 130-fold (5 to 660 nmol $g^{-1}\ s^{-1}$). If this prediction is true, *SAR* varies more than 2000-fold.

Although coordination between leaf and root traits has been suggested by several field studies (Craine et al. 2005; Tjoelker et al. 2005), the positive relationship between *SAR* and A_{mass} lacks a direct support by field experiments. Comas and Eissenstat (2004) found no trends in the phosphate uptake rate between fast- and slow-growing tree species growing in the field. Thus it still remains unclear what brings about the positive correlation between N_{mass} and A_{mass} at a global scale.

Conclusion

The photosynthesis-nitrogen relationship is of importance to understand interspecific variation in photosynthetic capacity. Species with higher A_{mass} have higher PNUE and N_{mass}. Higher PNUE is achieved by higher conductance of CO_2 diffusion within the leaves and by greater investment of more nitrogen in the photosynthetic apparatus. However, species with higher PNUE sacrifice leaf toughness, which imposes shorter leaf life span. As higher photosynthetic capacity leads to a dilution of nitrogen in new leaves, higher N_{mass} in species with higher A_{mass} is paradoxical. A mathematical model suggests that root activity, biomass allocation, nitrogen allocation and/or other traits are coordinated with leaf traits across species to compensate for the dilution effect. It is predicted that root activity is the most likely to account for the paradox; species with higher A_{mass} may have higher root activity.

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