

## Nitrogen Productivity Depends on Photosynthetic Nitrogen Use Efficiency and on Nitrogen Allocation Within the Plant

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The concept of plant nitrogen productivity was introduced at the end of the 1970s to interpret the dependency of plant growth on internal nitrogen. It is defined as the increase in plant dry matter per unit time and per unit plant nitrogen content. Recently, plant nitrogen productivity has been expressed as the product of two terms: the leaf nitrogen ratio, which is the proportion of the plant's nitrogen present in the leaves, and the leaf nitrogen productivity, which is defined as the increase in plant dry matter per unit time and leaf nitrogen content. In the present paper we use two data sets obtained from  $C_3$  herbaceous species to evaluate the relative importance of variation in leaf nitrogen ratio and leaf nitrogen productivity in determining interspecific variation in plant nitrogen productivity. Further, we analyse to what extent leaf and plant nitrogen productivities depend on photosynthetic nitrogen use efficiency. Results show that in all cases, photosynthetic nitrogen use efficiency is a major determinant of both plant and leaf nitrogen productivities. A positive relationship between leaf nitrogen ratio and plant nitrogen productivity was found only when comparisons were made over broad taxonomic groups. © 1995 Annals of Botany Company

**Key words:** Interspecific variation, leaf nitrogen ratio, nitrogen productivity, photosynthetic nitrogen use efficiency.

### INTRODUCTION

The dependence of plant growth on internal nitrogen concentration has been shown when a given species responds to variation in external nitrogen concentration (e.g. Ågren and Ingestad, 1987; Freijssen and Otten, 1987; Hirose, 1988) and for different species grown under non-limiting external nitrogen supply (inherent interspecific differences: Poorter, Remkes and Lambers, 1990; Van der Werf *et al.*, 1993; Garnier and Vancaeyzeele, 1994). To interpret this dependence, Ingestad (1979) has introduced the concept of 'plant nitrogen productivity' ( $\Pi_p$ : a list of quantities and symbols is given in Table 1), defined as the increase in plant dry mass per unit time ( $dM_p/dT$ ) and per unit plant nitrogen content ( $N_p$ ):

$$\Pi_p = 1/N_p \times dM_p/dT. \quad (1)$$

The complex nature of nitrogen productivity has been thoroughly discussed by Lambers *et al.* (1990), who showed that it was dependent on photosynthetic nitrogen use efficiency, nitrogen allocation within the plant, the distribution of respiration among the different organs of the plant, and the ratio of respiration to nitrogen concentration in these organs. Here a simple, semi-empirical approach derived from that proposed by Lambers *et al.* (1990) is used to analyse the impact of two plant components of plant nitrogen productivity, namely nitrogen allocation within the plant and photosynthetic nitrogen use efficiency.

Following Hirose (1988), Garnier and Vancaeyzeele

(1994) expressed plant nitrogen productivity as the product of two terms:

$$\Pi_p = (N_L/N_p) \times (1/N_L \times dM_p/dT) = v_L \times \Pi_L \quad (2)$$

where  $N_L$  and  $v_L$  are the leaf nitrogen content and the leaf nitrogen ratio (fraction of plant nitrogen present in the leaves: Table 1), respectively, and  $\Pi_L$  is the leaf nitrogen productivity. The latter is equal to the ratio between unit leaf rate expressed on a dry mass basis ( $E_m$ ) and leaf nitrogen concentration ( $n_L$ ):

$$\Pi_L = [(1/M_L) \times (dM_p/dT)] \times (M_L/N_L) = E_m/n_L \quad (3)$$

It was argued that since photosynthesis is a major component of  $E_m$  (e.g. Konings, 1990),  $\Pi_L$  is likely to depend on photosynthetic nitrogen use efficiency ( $\Phi_N$ ), defined as the ratio between the rate of photosynthesis and leaf nitrogen concentration (Table 1: Field and Mooney, 1986).

In the present paper, we use two sets of data on herbaceous species to investigate the relative importance of the leaf nitrogen ratio and leaf nitrogen productivity in the determination of interspecific variation in plant nitrogen productivity. Further, we analyse the extent to which  $\Pi_L$  and  $\Pi_p$  depend on  $\Phi_N$ .

### MATERIAL AND METHODS

The two data sets used were obtained from wild  $C_3$  herbaceous plants cultivated hydroponically in growth chambers under non-limiting nutrient conditions. The first

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TABLE 1. List of quantities used, with their symbols, units and definitions

| Symbol          | Quantity                                 | Unit  | Definition (when required)                                     |
|-----------------|--|---|--|
| $A_m$           | Rate of shoot photosynthesis             | $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$              | —  |
| $c_L$           | Leaf carbon concentration                | $\text{mmol C g}^{-1}$  | —  |
| $c_P$           | Plant carbon concentration               | $\text{mmol C g}^{-1}$  | $(c_L \times M_L + c_{ST} \times M_{ST} + c_R \times M_R)/M_P$ |
| $c_R$           | Root carbon concentration                | $\text{mmol C g}^{-1}$  | —  |
| $c_{ST}$        | Stem carbon concentration                | $\text{mmol C g}^{-1}$  | —  |
| $d$             | Day length                               | s   | —  |
| $E_m$           | Unit leaf rate                           | $\text{g g}^{-1} \text{ d}^{-1}$                              | $1/M_L \times dM_P/dT$   |
| $M_L$           | Leaf dry mass                            | g   | —  |
| $M_P$           | Plant dry mass                           | g   | $M_L + M_{ST} + M_R$   |
| $M_R$           | Root dry mass                            | g   | —  |
| $M_{SH}$        | Shoot dry mass                           | g   | $M_L + M_{ST}$   |
| $M_{ST}$        | Stem dry mass                            | g   | —  |
| $n_L$           | Leaf nitrogen concentration              | $\text{mmol N g}^{-1}$  | —  |
| $n_P$           | Plant nitrogen concentration             | $\text{mmol N g}^{-1}$  | $(n_L \times M_L + n_{ST} \times M_{ST} + n_R \times M_R)/M_P$ |
| $n_R$           | Root nitrogen concentration              | $\text{mmol N g}^{-1}$  | —  |
| $n_{SH}$        | Shoot nitrogen concentration             | $\text{mmol N g}^{-1}$  | $(n_L \times M_L + n_{ST} \times M_{ST})/M_{SH}$               |
| $n_{ST}$        | Stem nitrogen concentration              | $\text{mmol N g}^{-1}$  | —  |
| $N_L$           | Leaf nitrogen content                    | mmol N  | $n_L \times M_L$   |
| $N_P$           | Plant nitrogen content                   | mmol N  | $n_P \times M_P$   |
| $N_R$           | Root nitrogen content                    | mmol N  | $n_R \times M_R$   |
| $N_{SH}$        | Shoot nitrogen content                   | mmol N  | $n_{SH} \times M_{SH}$   |
| $p$             | Photoperiod                              | s   | —  |
| $R_{GR}$        | Relative growth rate                     | $\text{d}^{-1}$   | $1/M_P \times dM_P/dT$   |
| $R_R$           | Rate of root respiration                 | $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$              | —  |
| $R_{SH}$        | Rate of shoot respiration                | $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$              | —  |
| $T$             | Time                                     | d   | —  |
| $\Gamma_{N,R}$  | Nitrogen specific root respiration rate  | $\mu\text{mol CO}_2 (\text{mol root N})^{-1} \text{ s}^{-1}$  | $R_R/n_R$  |
| $\Gamma_{N,SH}$ | Nitrogen specific shoot respiration rate | $\mu\text{mol CO}_2 (\text{mol shoot N})^{-1} \text{ s}^{-1}$ | $R_{SH}/n_{SH}$  |
| $\Phi_N$        | Photosynthetic nitrogen use efficiency   | $\mu\text{mol CO}_2 (\text{mol leaf N})^{-1} \text{ s}^{-1}$  | $A_m/n_L$  |
| $\mu_L$         | Leaf mass ratio                          | dimensionless   | $M_L/M_P$  |
| $\mu_R$         | Root mass ratio                          | dimensionless   | $M_R/M_P$  |
| $\mu_{SH}$      | Shoot mass ratio                         | dimensionless   | $M_{SH}/M_P$   |
| $\mu_{ST}$      | Stem mass ratio                          | dimensionless   | $M_{ST}/M_P$   |
| $\nu_L$         | Leaf nitrogen ratio                      | dimensionless   | $N_L/N_P$  |
| $\nu_R$         | Root nitrogen ratio                      | dimensionless   | $N_R/N_P$  |
| $\nu_{SH}$      | Shoot nitrogen ratio                     | dimensionless   | $N_{SH}/N_P$   |
| $\Pi_L$         | Leaf nitrogen productivity               | $\text{g (mol leaf N)}^{-1} \text{ d}^{-1}$                   | $1/N_L \times dM_P/dT$   |
| $\Pi_P$         | Plant nitrogen productivity              | $\text{g (mol plant N)}^{-1} \text{ d}^{-1}$                  | $1/N_P \times dM_P/dT$   |

set (referred to hereafter as 'Grasses') concerns a comparison of ten among the 14 grass species studied by Garnier (1992) and Garnier and Vancaeyzeele (1994); there were five annual species: *Brachypodium distachyon* L., *Bromus hordeaceus* L., *Bromus madritensis* L., *Hordeum murinum* L. and *Lolium rigidum* Gaud. and five perennial species: *Brachypodium phoenicooides* L., *Bromus erectus* Huds., *Bromus ramosus* Huds., *Hordeum secalinum* Schreb. and *Lolium perenne* L. (photosynthesis data are not available for the four remaining species of the complete data set). The second data set ('Herbs' hereafter) deals with a comparison of 24 species, both grasses (11 species) and dicotyledons (13 species: Poorter and Remkes, 1990; Poorter *et al.*, 1990). Species names for Herbs are given by Poorter and Remkes (1990).

Light conditions during growth were  $550 \mu\text{mol m}^{-2} \text{ s}^{-1}$  for  $16 \text{ h d}^{-1}$  for Grasses, and  $315 \mu\text{mol m}^{-2} \text{ s}^{-1}$  for  $14 \text{ h d}^{-1}$  for Herbs. Other details on growth conditions are given in Garnier (1992) and Poorter and Remkes (1990), respectively. In both studies, sequential harvests were carried out on juvenile plants (up to 24–30 d after transplanting the plants into the growth systems), and growth analysis components were derived. Organic nitrogen concentrations

in plant parts were determined by the Kjeldahl method in the case of Herbs, and as the difference between total nitrogen (determined with an elemental analyser) and nitrate nitrogen (determined on an autoanalyser according to Henriksen and Semer-Olsen, 1970) in the case of Grasses. In both cases, whole shoot net photosynthesis was measured by  $\text{CO}_2$  exchange on intact plants in open systems, at the same light intensity at which the plants were grown (Poorter *et al.*, 1990; O. Gobin and E. Garnier, unpubl. res.).  $\Pi_P$ ,  $\Pi_L$  and  $\Phi_N$  were calculated on an organic nitrogen basis.

## RESULTS

Figure 1A shows that for the Grasses data set, plant nitrogen productivity is positively, but not significantly, related to the leaf nitrogen ratio. By contrast, it strongly depends on leaf nitrogen productivity (Fig. 1B). For the Herbs data set, both parameters play a role when all the species are considered (Fig. 1C, D); when the analysis is restricted to the 11 grasses within Herbs, similar results as those found for the Grasses data set are obtained.

For both Grasses and Herbs, net photosynthesis per unit leaf mass is a major determinant of unit leaf rate (Fig. 2A,

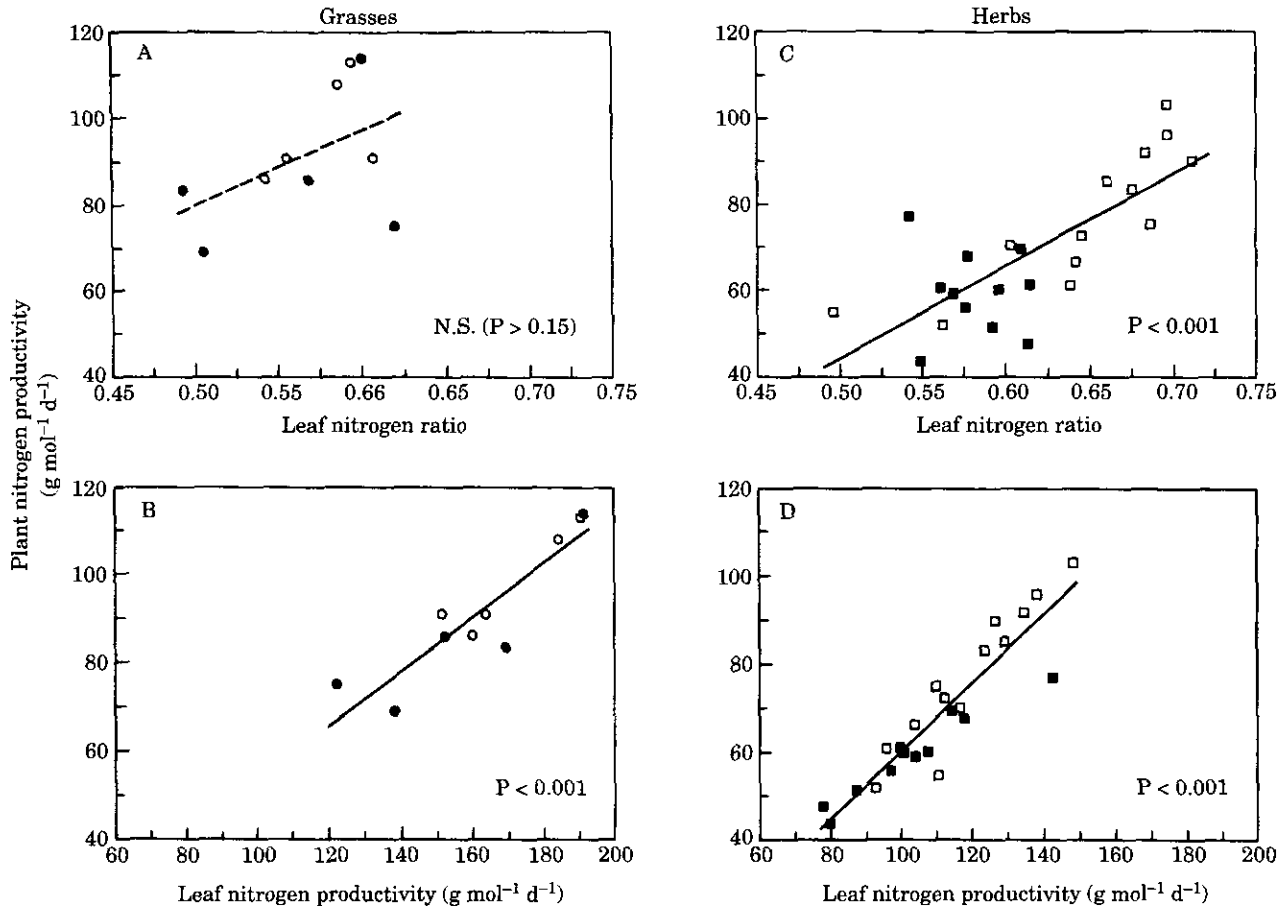


FIG. 1 Relationships between plant nitrogen productivity and: A, C, leaf nitrogen ratio ( $\nu_L$ ); B, D, leaf nitrogen productivity ( $\Pi_L$ ), for the Grasses (A, B) and Herbs (C, D) data sets. (○) Annuals, (●) perennials, (□) dicotyledons, (■) monocotyledons. A solid line denotes a significant relationship while a dashed line indicates a non-significant one (the level of significance,  $P$ , is indicated on the figure). The coefficients of determination ( $r^2$ ) for the relationships are 0.24 (A) and 0.77 (B) for Grasses, 0.58 (C) and 0.86 (D) for Herbs.

C), and the relationships between  $\Phi_N$  and  $\Pi_L$  are highly significant (Fig. 2B, D). Within Herbs, the relationship is less strong for the dicotyledons ( $r^2 = 0.35$ ,  $P < 0.05$ ,  $n = 13$ ) than for the grasses ( $r^2 = 0.60$ ,  $P < 0.01$ ,  $n = 11$ ). Finally, through its effects on  $\Pi_L$ ,  $\Phi_N$  correlates significantly with plant nitrogen productivity in both data sets (Fig. 3).

## DISCUSSION

Results presented here demonstrate that plant nitrogen productivity may (in dicotyledons in Herbs) or may not (in Grasses and in grasses within Herbs) depend on the proportion of nitrogen allocated to the leaves. The leaf nitrogen ratio depends on biomass allocation to and nitrogen concentration in the different organs, as follows:

$$\nu_L = \frac{(n_L \times \mu_L)}{(n_L \times \mu_L) + (n_{ST} \times \mu_{ST}) + (n_R \times \mu_R)} \quad (4)$$

where  $n_L$ ,  $n_{ST}$  and  $n_R$  are nitrogen concentrations in leaves, stems (or sheaths) and roots, respectively, and  $\mu_L$ ,  $\mu_{ST}$  and  $\mu_R$  are leaf, stem (sheaths for grasses) and root mass ratio (ratio of dry mass of the organ to total plant dry mass), respectively. Figure 1C shows that within Herbs,  $\nu_L$  tends to

be higher in dicotyledonous species than in grasses ( $0.65 \pm 0.02$  vs.  $0.58 \pm 0.01$  mol mol<sup>-1</sup>; significant difference at  $P < 0.01$ ). This is the consequence of a higher  $\mu_L$  in the dicotyledons ( $0.60 \pm 0.02$  vs.  $0.48 \pm 0.01$  g g<sup>-1</sup> in grasses); in fact,  $n_L$  was on average slightly higher in grasses ( $3.82 \pm 0.18$  mmol g<sup>-1</sup>) than in dicotyledons ( $3.58 \pm 0.16$  mmol g<sup>-1</sup>). A higher proportional biomass allocation to leaves in dicotyledons as compared to grasses has been found elsewhere (Garnier, 1991; Marañón and Grubb, 1993). This high  $\nu_L$  in dicotyledons contributes to some extent to their higher mean plant nitrogen productivity ( $77.0 \pm 4.6$  g mol<sup>-1</sup> d<sup>-1</sup>) as compared to monocotyledons ( $59.5 \pm 3.2$  g mol<sup>-1</sup> d<sup>-1</sup>), while variation in  $\nu_L$  within grass species does not lead to significant differences in  $\Pi_P$  (Fig. 1A, C). This result is similar to what is found when the impact of biomass allocation on  $R_{GR}$  is examined: in grasses, no relationship is found between relative growth rate and  $\mu_L$  (Poorter and Remkes, 1990; Garnier, 1992; Marañón and Grubb, 1993), while in dicotyledons, there appears to be a positive relationship between these two parameters (Poorter and Remkes, 1990; Garnier, 1991; Marañón and Grubb, 1993). Further analysis of these (and other) differences between monocotyledons and dicotyledons will be presented in a subsequent paper.

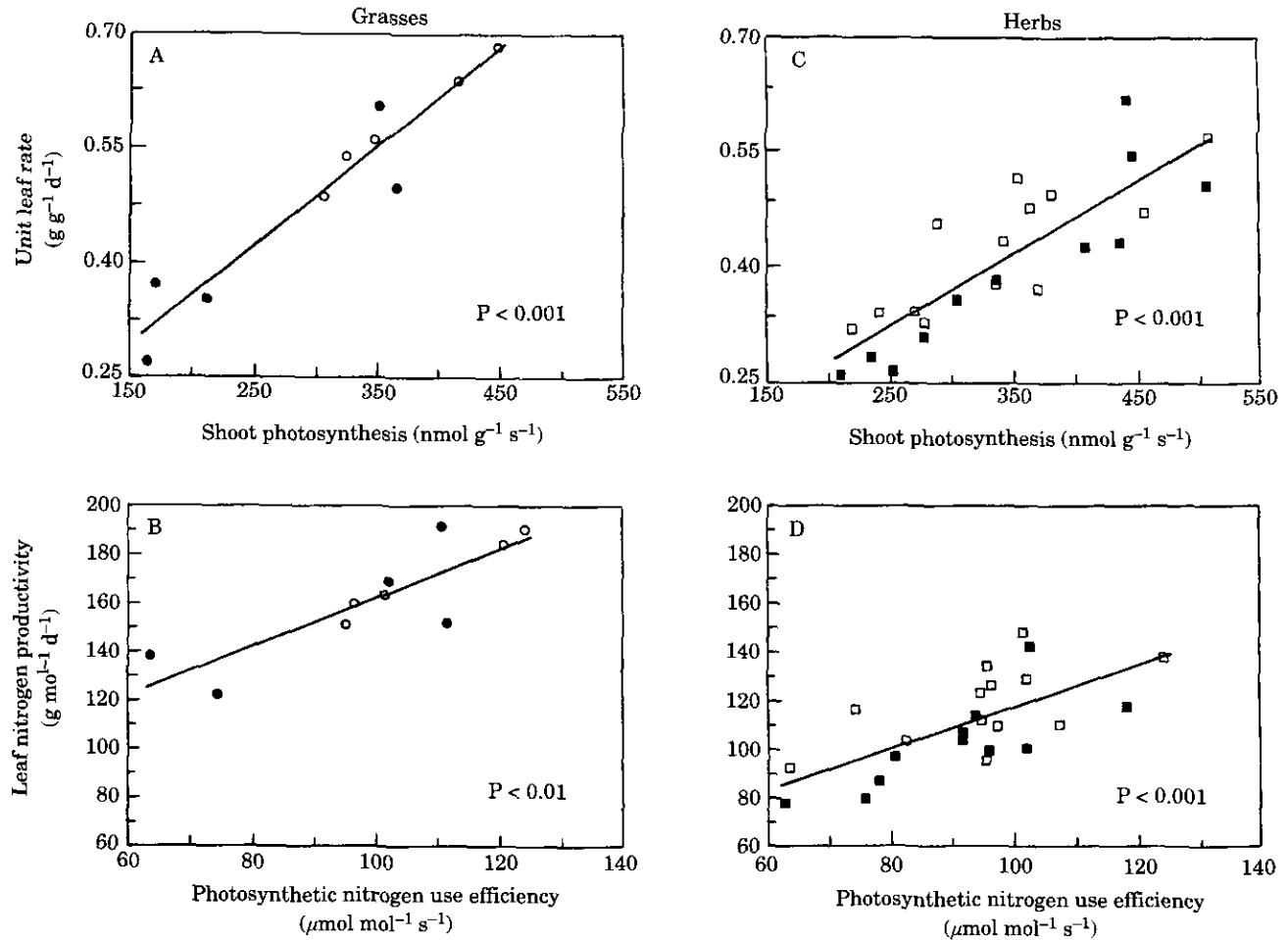


FIG. 2 Relationships between: A, C, whole shoot photosynthesis ( $A_m$ ) and unit leaf rate expressed on a dry mass basis ( $E_m$ ); B, D, photosynthetic nitrogen use efficiency ( $\Phi_N$ ) and leaf nitrogen productivity ( $\Pi_L$ ), for the Grasses (A, B) and Herbs (C, D) data sets. (○) Annuals, (●) perennials, (□) dicotyledons, (■) monocotyledons. A solid line denotes a significant relationship whose significance level is indicated on the figure. The coefficients of determination ( $r^2$ ) for the relationships are 0.92 (A) and 0.64 (B) for Grasses, 0.72 (C) and 0.46 (D) for Herbs.

For both the Herbs and Grasses data sets, unit leaf rate was tightly related to whole shoot net photosynthesis (Fig. 2A, C), as already observed from a literature survey by Konings (1990). Dividing both variables by leaf nitrogen concentration [see eqn (3)] slightly altered the relationships, but  $\Pi_L$  was still highly significantly related to  $\Phi_N$  (Fig. 2B, D). Since  $\Pi_L$  is a strong determinant of  $\Pi_p$  (Fig. 1B, D),  $\Phi_N$  and  $\Pi_p$  are positively correlated (Fig. 3). Therefore, the physiological causes leading to differences in  $\Phi_N$  among species are also likely to be important causes of interspecific differences in  $\Pi_p$ . Lambers and Poorter (1992) have listed six possible causes of interspecific differences in  $\Phi_N$  within  $C_3$  species: (1) differences in the relative proportion of leaf nitrogen partitioned to chloroplasts and to other cell components; (2) suboptimal partitioning of nitrogen within the chloroplast; (3) differences in activation of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco); (4) differences in Rubisco specific activity; (5) differential feedback inhibition of photosynthesis, and (6) differences in internal  $CO_2$  concentration. Differences in the latter did not explain variation in  $\Phi_N$  for Herbs (Poorter and Farquhar, 1994). Lambers and Poorter (1992) concluded it was not possible

to decide which among the other possibilities were actually important. A study of four monocotyledonous species by Pons, van der Werf and Lambers (1994) revealed that plants with a low  $\Phi_N$  tended to invest more of their leaf nitrogen in compounds not incorporated in the photosynthetic apparatus, and that they were using a smaller fraction of their photosynthetic potential under the relatively low light irradiance of the experiment ( $300 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), as compared to plants with a high  $\Phi_N$ . No evidence was found to support the other possibilities, but more experiments are needed to reach a definitive conclusion.

The analysis conducted in the present paper has focused only on the photosynthetic component of leaf nitrogen productivity. However,  $\Pi_L$  is a complex parameter which also depends on respiration, carbon concentration and allocation of nitrogen. The Appendix shows that  $\Pi_L$  can be written as:

$$\Pi_L = \frac{\{(\Phi_N \times p) - (I_{N,SH} \times (v_{SH}/v_L) \times (d-p)) - (I_{N,R} \times (v_R/v_L) \times d)\}}{c_p} \quad (5)$$

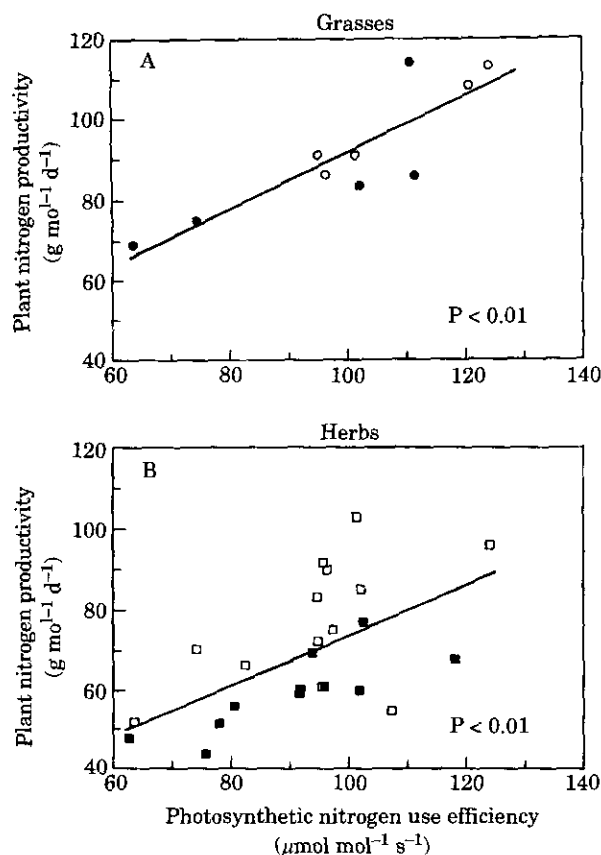


FIG. 3 Relationships between photosynthetic nitrogen use efficiency ( $\Phi_N$ ) and plant nitrogen productivity ( $\Pi_p$ ), for the Grasses (A) and the Herbs (B) data sets. (○) Annuals, (●) perennials, (□) dicotyledons, (■) monocotyledons. A solid line denotes a significant relationship whose significance level is indicated on the figure. The coefficients of determination ( $r^2$ ) for the relationships are 0.64 (A) for Grasses, and 0.36 (B) for Herbs.

where  $\Phi_N$  is the photosynthetic nitrogen use efficiency;  $\nu_L$ ,  $\nu_{SH}$  and  $\nu_R$  are the leaf, shoot and root nitrogen ratio respectively, and  $c_P$  is the mean plant carbon concentration;  $d$  and  $p$  are day length and photoperiod, respectively (see Table 1 for units).  $F_{N,SH}$  and  $F_{N,R}$  are defined as the ratios between shoot respiration and shoot organic-nitrogen concentration and root respiration and root organic-nitrogen concentration, respectively (Table 1), and will be called 'nitrogen specific respiration rates' of shoots and roots, respectively. These quantities were previously called 'respiratory nitrogen use efficiencies' (Lambers *et al.*, 1990), by analogy with the expression of 'photosynthetic nitrogen use efficiency'. However, since respiration is a loss rather than a gain to the plant, we think that the term 'efficiency' is not appropriate.

The Herbs data set was used to assess the impact of these different factors on  $\Pi_L$ , applying the following procedure: all the variables were set to their lowest value except that under study, which was varied over its full observed range (we thus assumed that each parameter was independent of the others). The variation this produces on  $\Pi_L$  was calculated with eqn (5), and normalized to the full range of variation in  $\Pi_L$ . Results of this sensitivity analysis are shown in Table

TABLE 2. Sensitivity analysis for the impact of the variables given in eqn (5) on  $\Pi_L$  (calculations corresponding to the Herbs data set)

| Variable         | Value taken for lowest $\Pi_L$ | Value taken for highest $\Pi_L$ | Calculated impact on $\Pi_L$ (%) | Actual R of regression |
|------------------|--------------------------------|---------------------------------|----------------------------------|------------------------|
| $\phi_N$         | 73                             | 114                             | +79                              | +0.67***               |
| $F_{N,SH}$       | 8.9                            | 11.2                            | -4                               | +0.30 <sup>n.s.</sup>  |
| $F_{N,R}$        | 22.1                           | 24.6                            | -4                               | +0.13 <sup>n.s.</sup>  |
| $c_P$            | 35.9                           | 32.7                            | +9                               | -0.49*                 |
| $\nu_{SH}/\nu_L$ | 1.33                           | 1.19                            | +2                               | -0.28 <sup>n.s.</sup>  |
| $\nu_R/\nu_L$    | 0.43                           | 0.31                            | +9                               | -0.36 <sup>n.s.</sup>  |

For each parameter, the highest and lowest values were taken from the regression lines of  $\Pi_L$  vs. this particular parameter, or  $\Pi_L$  values of 75 and 155  $\text{g mol}^{-1} \text{d}^{-1}$ , respectively. The simulations were then carried out by fixing all the variables to their lowest values, except the one under study which was varied over its full range; the variation this produces was calculated with eqn (5), and normalized to the calculated range of variation in  $\Pi_L$ . Finally, the correlation coefficient and the significance level or the actual linear regressions between each variable and  $\Pi_L$  are also given. n.s.; Not significant; \*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ . The meaning of abbreviations and the units for the different parameters are given in Table 1.

2.  $\Phi_N$  has by far the most important impact on  $\Pi_L$ . Plant carbon concentration and the pattern of nitrogen allocation between leaves and roots also play a role, but their impact on  $\Pi_L$  is almost 10 times lower than that of  $\Phi_N$ .

In conclusion, photosynthetic nitrogen use efficiency has a strong impact on on leaf nitrogen productivity, and thus on plant nitrogen productivity. Nitrogen allocation among different plant organs affects  $\Pi_p$  to some extent when widely different taxa are compared, but within grasses, a high leaf nitrogen ratio does not lead to a high plant nitrogen productivity.

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## APPENDIX

Adopting the formulation of unit leaf rate given by Lambers and Poorter (1992) leads to the writing of  $\Pi_L$  as:

$$\Pi_L = \frac{[(A_m \times \mu_L \times p) - (R_{SH} \times \mu_{SH} \times (d-p)) - (R_R \times \mu_R \times d)]}{(c_p \times \mu_L \times n_L)} \quad (A1)$$

where  $A_m$ ,  $R_{SH}$  and  $R_R$  represent the rates of photosynthesis, shoot and root respirations, respectively (these rates are expressed on a dry mass basis),  $\mu_L$ ,  $\mu_{SH}$  and  $\mu_R$  are the leaf, shoot and root mass ratio, respectively,  $c_p$  is the mean plant carbon concentration, and  $d$  and  $p$  are day length and photoperiod, respectively (see Table 1 for units). Equation (5) may be rearranged to:

$$\Pi_L = \frac{[(\Phi_N \times p) - ((R_{SH}/n_L) \times (\mu_{SH}/\mu_L) \times (d-p)) - ((R_R/n_L) \times (\mu_R/\mu_L) \times d)]}{c_p} \quad (A2)$$

Now:

$$\begin{aligned} (R_{SH}/n_L) \times (\mu_{SH}/\mu_L) &= (R_{SH}/n_{SH}) \times (n_{SH} \times \mu_{SH}) / (n_L \times \mu_L) \\ &= (R_{SH}/n_{SH}) \times (v_{SH}/v_L) \end{aligned} \quad (A3)$$

and:

$$\begin{aligned} (R_R/n_L) \times (\mu_R/\mu_L) &= (R_R/n_R) \times (n_R \times \mu_R) / (n_L \times \mu_L) \\ &= (R_R/n_R) \times (v_R/v_L) \end{aligned} \quad (A4)$$

where  $n_{SH}$  and  $n_R$  are the shoot and root nitrogen concentrations, and  $v_{SH}$  and  $v_R$  the shoot and root nitrogen ratios. Let us define the  $R_{SH}/n_{SH}$  and  $R_R/n_R$  ratios as the nitrogen specific respiration rate of shoots and roots, respectively ( $\Gamma_{N,SH}$  and  $\Gamma_{N,R}$  respectively). Then eqn (A2) may be rewritten as:

$$\Pi_L = \frac{[(\Phi_N \times p) - (\Gamma_{N,SH} \times (v_{SH}/v_L) \times (d-p)) - (\Gamma_{N,R} \times (v_R/v_L) \times d)]}{c_p} \quad (A5)$$

which is eqn (5) presented in the text.