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Carbon and Nitrogen Economy of 24 Wild Species Differing in Relative Growth Rate

Hendrik Poorter*, Carlo Remkes, and Hans Lambers

Department Plant Ecology and Evolutionary Biology, Lange Nieuwstraat 106, 3512 PN Utrecht, The Netherlands

ABSTRACT

The relation between interspecific variation in relative growth rate and carbon and nitrogen economy was investigated. Twenty-four wild species were grown in a growth chamber with a nonlimiting nutrient supply and growth, whole plant photosynthesis, shoot respiration, and root respiration were determined. No correlation was found between the relative growth rate of these species and their rate of photosynthesis expressed on a leaf area basis. There was a positive correlation, however, with the rate of photosynthesis expressed per unit leaf dry weight. Also the rates of shoot and root respiration per unit dry weight correlated positively with relative growth rate. Due to a higher ratio between leaf area and plant weight (leaf area ratio) fast growing species were able to fix relatively more carbon per unit plant weight and used proportionally less of the total amount of assimilates in respiration. Fast growing species had a higher total organic nitrogen concentration per unit plant weight, allocated more nitrogen to the leaves and had a higher photosynthetic nitrogen-use efficiency, *i.e. a* higher rate of photosynthesis per unit organic nitrogen in the leaves. Consequently, their nitrogen productivity, the growth rate per unit organic nitrogen in the plant and per day, was higher compared with that of slow growing species.

Approximately 90% of a plant's dry weight originates from products fixed in photosynthesis. It is therefore not surprising, that photosynthesis has been the subject of many studies which sought to understand the basis of variation in plant growth. Especially in crop breeding the rate of photosynthesis per unit leaf area has been considered an easy parameter to select for high yielding varieties. Duncan and Hesketh (8), investigating 22 maize races, were among the first to question a positive relationship between photosynthesis per unit leaf area and the growth rate of the plant. Indeed, in a review on crop yield, Gifford *et al.* (12) state that improvement of yield has been achieved mainly by alterations in the allocation of biomass, rather than by the improvement of the rate of photosynthesis.

Until now most studies concerning the relationship between growth and physiology have concentrated on the photosynthesis of single leaves. Zelitch (34) argues that improvement of yield may be achieved if more attention is paid to the photosynthesis of whole plants. Going from leaf to whole plant photosynthesis is indeed a major step in understanding plant productivity. However, measurements of only photosynthesis and crop yield can never lead to a full understanding of variation in plant growth. First, photosynthesis is only part of the carbon economy of the plant, as approximately 30 to 50% of the carbon fixed per day is respired during the same period (18). Second, in agricultural literature yield is often considered to be only the production of the economically interesting fraction of the total above-ground biomass. Variation in this fraction or in the shoot-to-root ratio will obscure a possible relation between physiology and biomass production. Third, differences in final plant weights are not only determined by the daily carbon budget of the plant, but also by possible variation in seed weight, germination time, or duration of growth. Fourth, in agricultural field experiments climatic fluctuations and plant-to-plant competition within a crop may be complicating factors. Moreover, in such cases there is the practical problem that a difference in yield of *e.g.* 20% between strains, which gradually builds up during the whole growing season, is difficult to detect in the momentary physiology of such strains. Thus, measurements of only whole plant photosynthesis and yield of strains of species in the field is neither an easy nor a complete approach to understand the physiological basis of variation in plant growth.

A less complicated experiment to analyze the relation between carbon economy and growth is to investigate the biomass increase of whole plants in the vegetative phase for a range of different species grown in a controlled environment with a nonlimiting supply of nutrients and without mutual interference. In a previous paper (26) we have described such an experiment, carried out with 24 wild species. Growth analysis of these plants, corrected for any interactions between growth rate and plant size, revealed a wide interspecific variation in potential RGR[1]. The first aim of this paper is to link in with this growth experiment and analyze the rates of photosynthesis and both shoot and root respiration of these 24 species in relation to their RGR.

The carbon economy of a plant is closely connected with its nitrogen economy. A higher nitrogen concentration in the plant is likely to lead to a higher rate of photosynthesis, but also results in an increased rate of respiration (4, 18). Differences in allocation of nitrogen between organs or in investment in different types of compounds may thus decisively affect a plant's efficiency with respect to the use of nitrogen. Hence, the second aim of this paper is to investigate the relation between nitrogen economy on one hand and carbon economy and growth on the other.

[1] Abbreviations: RGR, relative growth rate; NP, nitrogen productivity; PNUE, photosynthetic nitrogen use efficiency; SLA, specific leaf area.

MATERIALS AND METHODS

Growth of the Plants

For the experiments 24 species were used, all nonwoody plants with a C_3 type of photosynthesis. These species were the monocotyledons *Brachypodium pinnatum* (L.) Beauv., *Briza media* L., *Corynephorus canescens* (L.) Beauv., *Cynosurus cristatus* L., *Dactylis glomerata* L., *Deschampsia flexuosa* (L.) Trin., *Festuca ovina* L., *Holcus lanatus* L., *Lolium perenne* L., *Phleum pratense* L. and *Poa annua* L., and the dicotyledons *Anthriscus sylvestris* (L.) Hoffm., *Galinsoga parviflora* Cav., *Geum urbanum* L., *Hypericum perforatum* L., *Lysimachia vulgaris* L., *Origanum vulgare* L., *Pimpinella saxifraga* L., *Plantago major* ssp. *major* L., *Rumex crispus* L., *Scrophularia nodosa* L., *Taraxacum officinale* Weber, *Trifolium repens* L., and *Urtica dioica* L. After germination on filter paper the seedlings were transferred to a growth room with the following conditions. Day: 14 h light, photosynthetic photon flux density at mean plant height 315 ± 30 μmol m^{-2} s^{-1}, temperature 20 ± 0.5°C, RH *ca.* 70%. Night: 10 h dark, temperature 20 ± 0.5 °C. Light was provided by fluorescent tubes (Philips TL-33-RS, 215 W) and incandescent bulbs (Philips, 40 W) in a ratio of 4:1. Plants were grown in 33 L containers in a modified Hoagland nutrient solution with a NO_3^- concentration of 2 mM. The nutrient solution was replenished each week. To prevent depletion and minimize mutual shading, the number of plants on each container varied between 4 and 24, depending on the size of the plants. Plants were rotated twice a week within the growth room. Full details on growth conditions are given by Poorter and Remkes (26).

Experimental Design

The growth experiment started when the plants had reached a fresh weight of approximately 100 mg (d 0). Harvests were carried out at d 0, 3, 7, 10, 14, and 17. Each day, eight plants were selected as described by Poorter (24) and harvested, except for d 0, when a double harvest was carried out. During this experiment, photosynthesis, shoot respiration, and root respiration were measured twice within a period of 3 d. As small plants are not easily measured and large plants may suffer from self-shading, this period was somewhere between d 6 and d 15, depending on the size of the plants. Each day, four individual plants were measured. Photosynthesis of the plants was determined 4 to 6 h after the start of the light period. Thereafter plants were placed in the dark. Shoot respiration was measured 1 to 3 h later. Root respiration was measured 1 to 2 h after the plants were placed in the light again.

Measurements

Whole shoot net photosynthesis and respiration were measured by CO_2 exchange. Intact plants were placed in a cuvette with shoot and roots in separate compartments. The photosynthetic photon flux density, temperature and vapor pressure deficit were the same as in the growth room. CO_2 and H_2O exchange were measured differentially with infrared gas analyzers (ADC, model 225 MK3, Hoddesdon, UK) in an open system. Calculations of the rate of photosynthesis, transpiration, and shoot respiration were made according to Von Caemmerer and Farquhar (32), with the correction suggested by Bunce and Ward (2).

Root respiration was determined on detached roots as the decrease of O_2 concentration in an airtight cuvette containing a nutrient solution, which was air-saturated before the start of the measurements. The O_2 concentration was measured with a Clark-type electrode (Yellow Springs Instruments). For the construction of the carbon budget of these NO_3^--fed plants, a respiratory quotient for root respiration of 1.2 was assumed (mean value from refs. 1,6, 17, and 33).

Chemical Analyses

Total organic nitrogen was determined on dried plant material with a modified Kjcldahl method using concentrated sulfuric acid and Na_2SO_4, K_2SO_4, and Se in a ratio of 62:1:1 (w/w) as a catalyst. The N content was determined colorometrically using indophenol blue. Leaf Chl content was determined in 80% (v/v) acetone extracts, measuring the *A* at 645 and 663 nm. Carbon content was measured with an elemental analyzer (Carlo Erba, model 1106, Milano, Italy).

Statistical Analysis

Data were analyzed with the SAS statistical package (15). Time curves of RGR were calculated with a stepwise regression as described by Poorter (24). To avoid comparison of species with totally different plant weights, mean RGR values were calculated over the period that plants had a dry weight ranging from 30 to 100 mg. The relation between the various parameters and RGR was tested with a linear regression analysis.

RESULTS

Full data on the growth of the 24 investigated species are given in Poorter and Remkes (26). Mean RGR ranged from 113 mg g^{-1} d^{-1} for *Corynephorus canescens* to 365 mg g^{-1} d^{-1} for *Galinsoga parviflora.* The rate of whole shoot photosynthesis per unit leaf area did not correlate with the RGR of these species (Fig. 1A, $P > 0.7$). When expressed on a leaf dry weight basis, the correlation of photosynthesis with RGR was positive (Fig. 1B, $P < 0.01$). Positive correlations were also obtained for shoot respiration expressed per unit shoot dry weight (Fig. 2A, $P < 0.01$) and root respiration expressed per unit root dry weight (Fig. 2B, $P < 0.001$).

In a pilot experiment with three species, little diurnal variation was found in net photosynthesis and shoot respiration. The mean rate of photosynthesis over the day period and that of shoot respiration over the night period differed less than 5% from those measured during the 2 h period as described in "Materials and Methods" (*cf.* refs. 3 and 20). The day-night rhythm in root respiration was not determined for these species. Data of Challa (3) and Veen (30) of plants grown under comparable conditions showed little variation in root respiration over 24 h. Assuming no diurnal variation in shoot and root respiration and a constant rate of photosynthesis

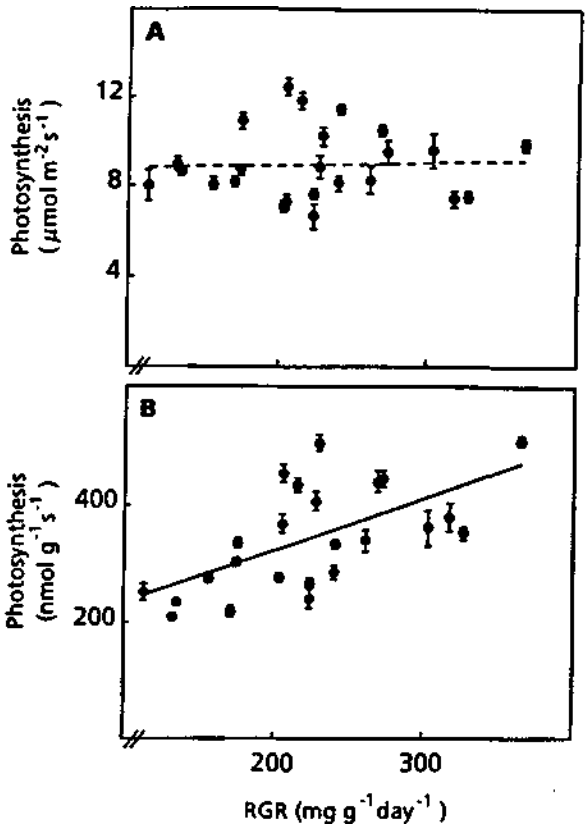

Figure 1. Rate of photosynthesis (A) per unit leaf area and (B) per unit leaf dry weight, plotted against mean RGR for 24 species (see ref. 26 for full details on the species). Mean values ± SE (n = 8). The continuous straight line indicates a significant linear regression ($P < 0.05$) of this parameter with RGR, the dashed line indicates a nonsignificant relation.

during the day for all species, the fraction of daily fixed carbon that is respired the same day can be calculated. This fraction ranged from 27 to 50% and was negatively correlated with RGR (Fig. 3C, $P < 0.001$). This appeared to be due to a lower fraction of both shoot (Fig. 3A, $P < 0.05$) and root respiration (Fig. 3B, $P < 0.01$) for the faster growing plants.

The differences between fast growing and slow growing species are summarized in Figure 4, by calculating from the regression equations what values a plant with a very low RGR (110 mg g^{-1} d^{-1}) and a very high RGR (370 mg g^{-1} d^{-1}) has for the various parameters. Per unit total plant dry weight a typical fast growing species fixes 2.7 times more CO_2 than a typical slow growing one (difference significant at $P < 0.001$). A typical fast growing plant spends a smaller percentage of this fixed CO_2 in shoot respiration (17% *versus* 24%, $P < 0.05$) and root respiration (8% *versus* 19%, $P < 0.01$). Of the remaining carbon more is allocated to the leaves (49% *versus* 27%, $P < 0.001$) and about the same percentage to stem (8% *versus* 13%, NS) and roots (17% *versus* 18%, NS).

The organic PNC increased with increasing RGR (Fig. 5A, $P < 0.01$). The same holds for the nitrogen concentration in leaves and roots separately (data not shown). However, leaf nitrogen concentration per unit leaf area was lower for rapid growing species (Fig. 5B, $P < 0.05$), as was total Chl content per unit leaf area (Fig. 5C, $P < 0.001$). A typical fast growing species accumulated 44% more organic nitrogen per unit plant weight than a typical slow growing one (Fig. 6, $P < 0.01$), and allocated more of its nitrogen to leaves (70% *versus* 55%, $P < 0.01$) and less to stems (9% *versus* 21%, $P < 0.05$). The investment in roots was comparable (21 *versus* 24%, NS).

An index of a leafs efficiency in using N to fix carbon is the PNUE (the rate of photosynthesis per unit time and per unit organic nitrogen in the leaf) (10). PNUE was higher for the fast growing species (Fig. 7A, $P < 0.001$), as was the rate of photosynthesis per unit chlorophyll (Fig. 7B, $P < 0.001$). A measure for N efficiency of total plant growth is the NP, the increase in plant weight per unit nitrogen in the plant per day) (14). The nitrogen productivity correlated positively with RGR (Fig. 7C, $P < 0.001$).

DISCUSSION

Carbon Economy

Although these wild species showed a threefold range in RGR, no correlation with the rate of photosynthesis per unit leaf area was found (Fig. 1A). How does this compare to the literature? Many authors have reported on the absence of a correlation between plant productivity and photosynthesis, expressed on a leaf area basis (21). However, as stated in the

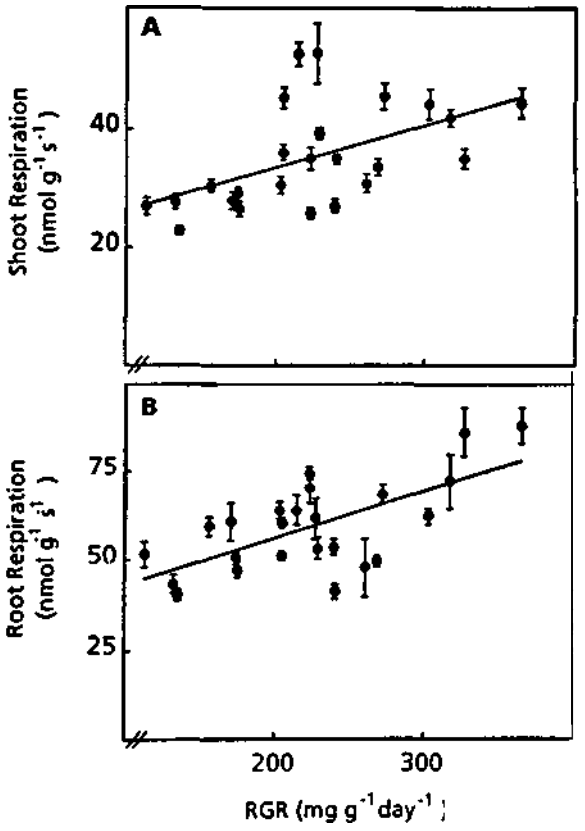

Figure 2. (A) Rate of shoot respiration per unit shoot dry weight, and (B) rate of root respiration per unit root dry weight, plotted against mean RGR for 24 species. Mean values ± SE (n = 8).

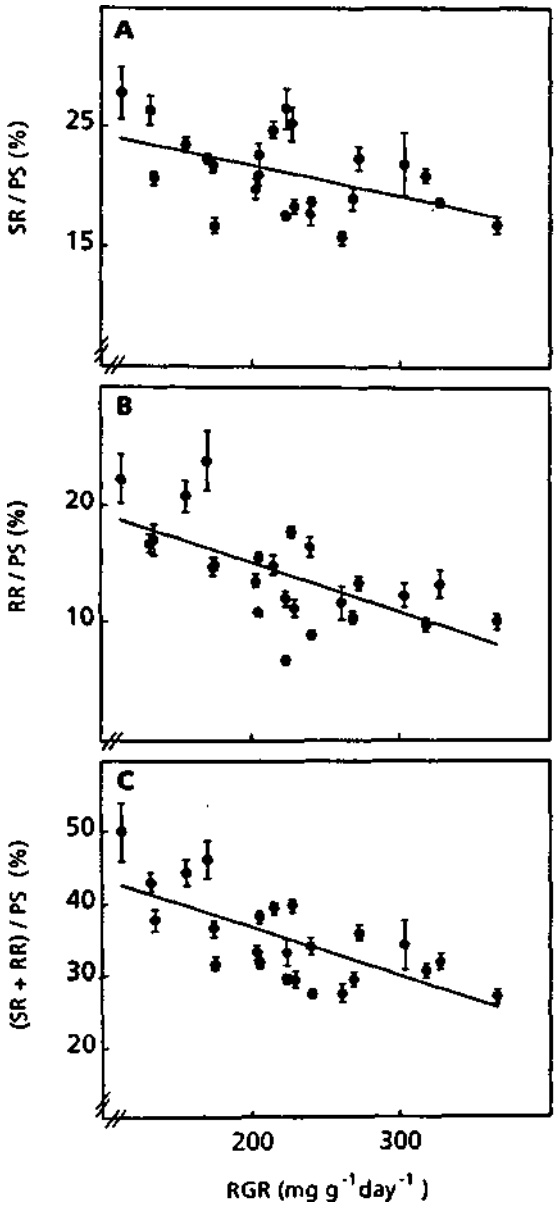

Figure 3. The percentage of the daily fixed carbon that is respired the same day, (A) in the shoot, (B) in the roots and (C) in the whole plant plotted against mean RGR for the 24 species. Mean values ± SE (n = 8).

introduction, photosynthesis is measured mostly for an individual leaf under saturating light conditions, neglecting the step to translate this parameter to the photosynthetic activity of the whole plant in situ. Moreover, plant productivity is often defined as yield of only a fraction of plant biomass. Duration of photosynthetic activity and definition of yield (grain, shoot, whole plants) then become complicating variables. In our opinion a correct comparison of photosynthesis and growth can only be made if photosynthesis is measured on whole shoots under prevailing environmental conditions and growth of whole plants is considered per unit plant weight and per unit of time. Few comparisons of this type can be found in the literature. No relation was found between the RGR of five *Eucalyptus* species and their rate of photosynthesis per unit leaf area (19). Similar results were obtained by Gottlieb (13), Delucia *et al.* (5), and Poorter (25). Dijkstra and Lambers (7), investigating the carbon economy of two inbred lines of *Plantago major,* found the fast growing genotype to have the lowest rate of photosynthesis. Pons (23) reports a positive correlation between the rate of photosynthesis per unit leaf area and RGR. However, in this case the slow growing species was a shade plant with a low maximum rate of photosynthesis when grown at higher light intensities.

Do these results imply that the photosynthetic tissue of fast growing and slow growing species is equally active? This is certainly not the case, as the rate of photosynthesis per unit leaf dry weight is higher for fast growing plants (Fig. 1B). Differences in the SLA (the leaf area:leaf dry weight ratio) between species plays an important role here. The activity of the photosynthetic tissue of fast growing species is higher, but as they have a higher SLA (26) their leaf biomass is 'diluted' over a larger area, resulting in a photosynthetic rate per unit leaf area which is equal to that of slow growing species. Results of Mooney *et al.* (19), Dijkstra and Lambers (7), and Poorter (25) support this finding.

Both shoot respiration per unit shoot weight and root respiration per unit root weight increase with increasing RGR. This may partly be explained by a higher respiration for growth (29) and, as fast growing species have a higher organic nitrogen concentration (Fig. 5A), a higher maintenance respiration (22). Moreover, due to their higher nitrogen concentration, fast growing species have to take up more nitrate than slow growers (*cf.* ref. 11) with relatively less root biomass (26). Thus, also the root respiration per unit root weight for nitrate uptake will be higher for species with a high RGR (29, 31).

What impact does respiration have on the carbon budget of these plants? Although the rates of shoot and root respiration are lower for species with a low RGR they respire

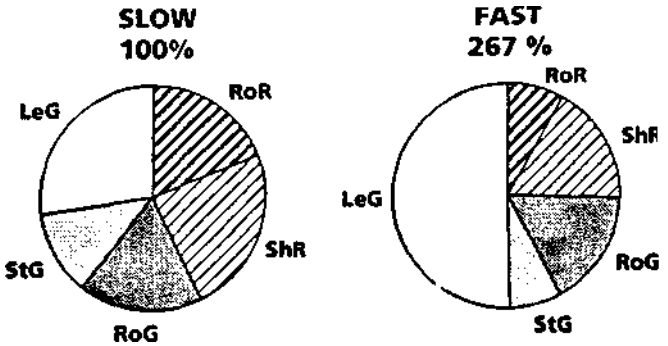

Figure 4. Carbon budget of a typically slow growing species (with a RGR of 110 mg g^{-1} day^{-1}) and a typically fast growing species (with a RGR of 370 mg g^{-1} d^{-1}), calculated from the regressions of photosynthesis, shoot respiration, root respiration, and carbon content of leaf stem and roots against RGR. The numbers above the circles indicate the rate of photosynthesis per unit total plant dry weight (for the slow grower normalized to 100%). The segments indicate the proportion of carbon used in root respiration (RoR), shoot respiration (ShR), root growth (RoG), stem growth (StG) and leaf growth (LeG).

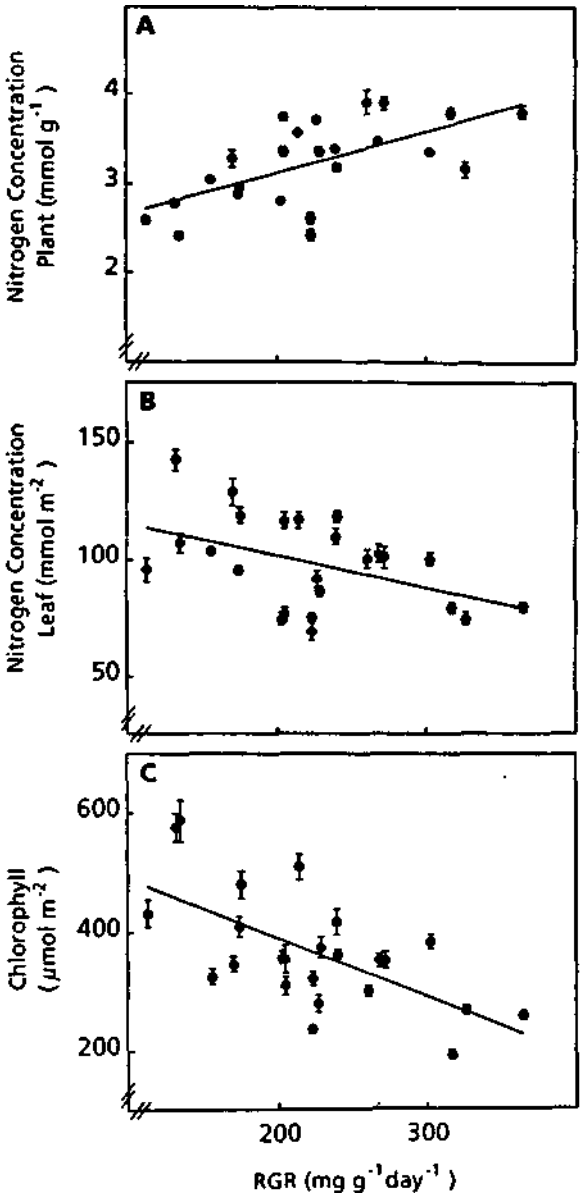

Figure 5. (A) Total organic nitrogen concentration per unit plant dry weight (PNC), (B) Organic leaf nitrogen concentration per unit leaf area and (C) Chl (*a* + *b*) content per unit leaf area, plotted against mean RGR for 24 species. Mean values ± SE (*n* = 8).

proportionally more of the daily fixed carbon (Fig. 3). This seemingly contradictory result is at least partly caused by differences in allocation patterns between species. Slow growing species have a higher shoot weight:leaf area and root weight:leaf area ratio than fast growing ones *(cf.* ref. 26). This implies that a slow-growing species has to sustain more root weight per unit photosynthesizing area than a rapid growing one. Despite the fact that these tissues have a lower respiration (Fig. 2), the respiratory burden per unit leaf area is higher (Fig. 3). Information in the literature on the relation between inherent variation in RGR and respiration of shoot and roots is scarce. Dijkstra and Lambers (7) found comparable results for whole plant respiration of two *Plantago major* subspecies differing in RGR. Shoot respiration of a slow growing shade plant (23) was lower than that of a sun plant, both on a leaf area and a shoot dry weight basis.

Integrating the three physiological processes we see that species with a high growth rate have the same photosynthesis per unit leaf area as slow growing species, but realize this rate with a lower investment of biomass per unit leaf area. This enlarges photosynthesis per unit leaf weight. Combined with a higher allocation of biomass to leaves, photosynthesis per unit total plant weight is almost three times higher for a typical fast growing than for a typical slow growing plant (Fig. 4). Due to a lower shoot weight:leaf area and root weight:leaf area ratio, a smaller proportion of these photosynthates are lost in respiration (Fig. 3). Thus, allocation of biomass (leaf weight ratio, root weight ratio) and morphology of the leaves (SLA) have an important impact on a plant's carbon economy and are major determinants of interspecific variation in growth rate.

Do these results, obtained under one set of environmental conditions also apply to other conditions? Growth analyses with two of the grasses used in this experiment, the slow growing *Deschampsia flexuosa* and the fast growing *Holcus lanatus,* have been carried out at light intensities twice as high and twice as low as in the present experiment, and at different nutrient availabilities (R. Hetem, C. v. d. Vijver, R. G. A. Boot, and H. Poorter, unpublished results). In all of these cases, the RGR of *H. lanatus* was higher than that of *D. flexuosa,* largely caused by the higher leaf area:total plant dry weight ratio (leaf area ratio) of *H. lanatus.* No substantial shift in the relative importance of the rate of photosynthesis per unit leaf area in explaining variation in RGR was found, neither at different light intensities nor at different nutrient availabilities. These data indicate that the above-mentioned conclusions are rather robust and can be generalized to a larger set of environmental conditions.

Nitrogen Economy

Despite the fact that all species had a nonlimiting supply of nutrients, total organic nitrogen concentration (PNC) of rapid

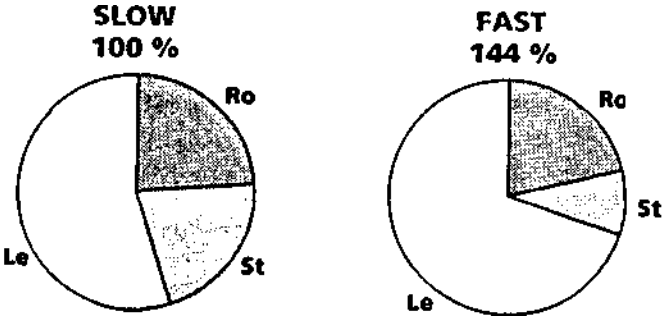

Figure 6. N allocation of a typically slow growing species (with a RGR of 110 mg g^{-1} d^{-1}) and a typically fast growing species (with a RGR of 370 mg g^{-1} d^{-1}), calculated from the regressions of N allocation against RGR. The numbers above the circles indicate the total plant nitrogen concentration (for the slow grower normalized to 100%). The segments indicate the proportion of N allocated to the leaf (Le), stem (St) and roots (Ro).

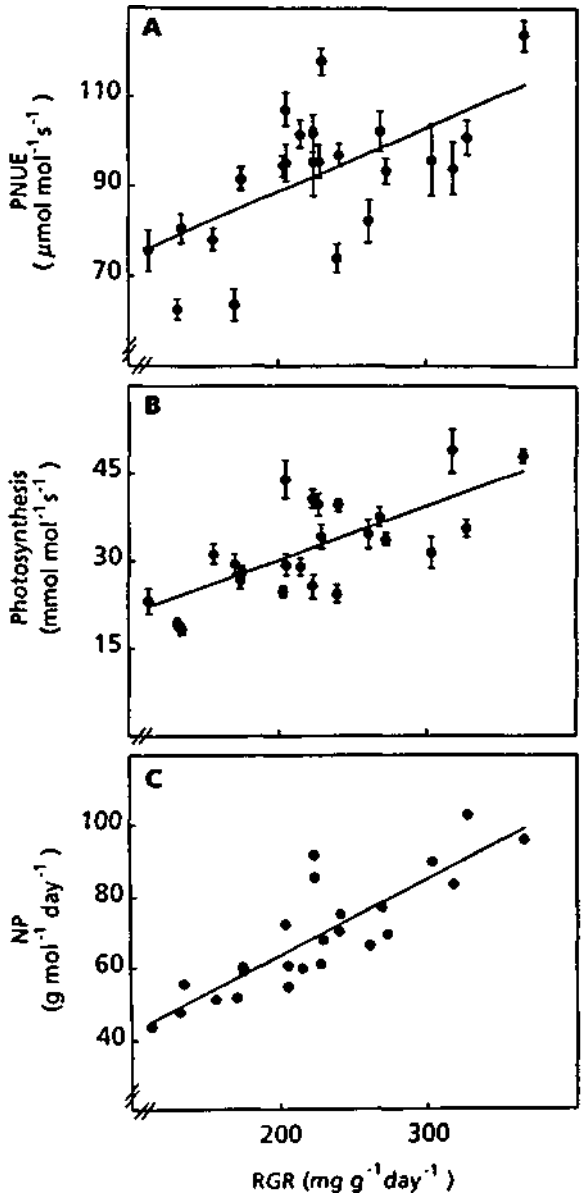

Figure 7. (A) PNUE (the rate of photosynthesis per unit of organic nitrogen in the leaf per unit of time), (B) the rate of photosynthesis per unit Chl, and (C) the NP (the dry weight increase of the plant per unit plant nitrogen per unit of time) plotted against mean RGR for the 24 species.

growing species was higher than that of slow growing ones (Fig. 5A). This is caused both by the fact that species with a high RGR allocate more biomass to the leaves (which tend to have a higher N content than stem and roots) and by a higher concentration of organic N in leaves and roots *per se.* However, due to the above-mentioned interspecific variation in SLA, the organic nitrogen content in the leaf expressed per unit leaf area is lower for fast than for slow growers. As the rate of photosynthesis on a leaf area basis does not vary with RGR (Fig. 1A), the PNUE increases with the growth rate of a species (Fig. 7A). Interspecific variation in PNUE has been found for sun *versus* shade species (28) and for C_3 *versus* C_4 species (27). The physiological basis for the positive correlation between PNUE and RGR could be internal shading. Fast growing species have a high SLA, which implies either thin leaves, or leaves with a low density of biomass. Moreover, the Chl content per unit leaf area is lower for fast growers (Fig. 5B). Therefore, it is expected that these species suffer less from internal shading within the leaf (16) than slow growing plants and consequently show a higher rate of photosynthesis per unit Chl (Fig. 7B, *cf.* ref. 9) However, other explanations are possible. Fast growing species may have a higher internal CO_2 concentration and therefore show less photorespiration, the organic N of slow growers may be invested in compounds not involved in photosynthesis, there may be a difference in the activation of ribulose-l,5-bisphosphate carboxylase/oxygenase, or a sink feedback on photosynthesis may occur which is stronger for the faster growing plants.

Fast growing species allocate more nitrogen to the leaves and use this nitrogen more efficiently in photosynthesis. Moreover, a smaller percentage of the fixed carbon is used for respiration. Consequently, nitrogen productivity, the increase in plant weight per unit time and per unit nitrogen in the plant is higher for a rapid growing species than for a slow growing one (Fig. 7B). This difference in nitrogen productivity could be a reflection of the habitat of these species, as slow growing species are found in nutrient-poor environments (26).

CONCLUSIONS

The variation in relative growth rate between the investigated species is not caused by differences in the rate of photosynthesis per unit leaf area, but rather by variation in the total amount of photosynthetically active area per unit plant weight. Due to differences in allocation, the proportion of photosynthetically fixed carbon which is respired is lower for fast than for slow growing species. Fast growing species accumulate more organic nitrogen per unit plant weight, allocate more of it to the leaves, and use this nitrogen more efficiently in photosynthesis than slow growing ones. Consequently, their nitrogen productivity is higher.

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