Growth and carbon economy of a fast-growing and a slow-growing grass species as dependent on nitrate supply

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Abstract

In previous experiments systematic differences have been found in the morphology, carbon economy and chemical composition of seedlings of inherently fast- and slow-growing plant species, grown at a non-limiting nutrient supply. In the present experiment it was investigated whether these differences persist when plants are grown at suboptimal nutrient supply rates. To this end, plants of the inherently fast-growing *Holcus lanatus* L. and the inherently slow-growing *Deschampsia flexuosa* (L.) Trin. were grown in sand at two levels of nitrate supply. Growth, photosynthesis, respiration and carbon and nitrogen content were studied over a period of 4 to 7 weeks.

At low N-supply, the potentially fast-growing species still grew faster than the potentially slow-growing one. Similarly, differences in leaf area ratio (leaf area:total dry weight), specific leaf area (leaf area:leaf dry weight) and leaf weight ratio (leaf dry weight: total dry weight), as observed at high N-supply persisted at low N-availability. The only growth parameter for which a substantial Species × N-supply interaction was found was the net assimilation rate (increase in dry weight per unit leaf area and time). Rates of photosynthesis, shoot respiration and root respiration, expressed per unit leaf, shoot and root weight, respectively, were lower for the plants at low N-availability and higher for the fast-growing species. Species-specific variation in the daily carbon budget was mainly due to variation in carbon fixation. Lower values at low N were largely determined by both a lower C-gain of the leaves and a higher proportion of the daily gain spent in root respiration.

Interspecific variation in C-content and dry weight:fresh weight ratio were similar at low and high N-supply. Total plant organic N decreased with decreasing N-supply, without differences between species. It is concluded that most of the parameters related to growth, C-economy and chemical composition differ between species and/or are affected by N-supply, but that differences between the two species at high N-availability persist at low N-supply.

Abbreviations: LAR - leaf area ratio, LWR - leaf weight ratio, NAR - net assimilation rate, RGR - relative growth rate, RWR - root weight ratio, SLA - specific leaf area, SWR - stem weight ratio.

Introduction

When grown under near-optimal conditions, plant species show wide variation in their potential relative growth rate (RGR, rate of dry weight increase per unit dry weight present; Chapin, 1980; Grime and Hunt, 1975; Poorter, 1989b). In an analysis of the growth of 24 herbaceous species the difference in RGR was mainly due to variation in specific leaf area (SLA, leaf area:leaf dry weight) and - to a lesser extent - to vari-

ation in leaf weight ratio (LWR, leaf dry weight:total plant dry weight; Poorter and Remkes, 1990). The net assimilation rate (NAR, the rate of increase in plant weight per unit leaf area) and the rate of photosynthesis per unit leaf area did not vary systematically with RGR (Poorter et al., 1990). Differences in the rate of shoot and root respiration, expressed per unit shoot and root weight, respectively, as well as differences in chemical composition (Poorter and Bergkotte, 1992) did not account for much of the interspecific variation

in RGR either. The above conclusions were confirmed in a survey of 63 published comparative growth experiments on herbaceous species, where again SLA was the predominant factor explaining variation in RGR (Lambers and Poorter, 1992).

The above-mentioned experiments were carried out at a high and often saturating nutrient supply. What happens with the growth rate of these contrasting groups of species at low N-supply? One could envisage that species with a low potential growth rate, which are characteristic of nutrient-poor environments (Chapin, 1980; Grime and Hunt, 1975; Poorter and Remkes, 1990), have experienced selection pressure to develop attributes that enable them to grow faster under these circumstances and that this explains the exclusion of the fast-growing species at those sites. However, most of the evidence available shows the opposite with - at least in short-term experiments - potentially fast-growing species having a similar or even higher RGR under nutrient limitation than potentially slow-growing ones (Chapin, 1980 and references therein; Gray and Schlesinger, 1983; Hull and Mooney, 1990; Shipley and Keddy, 1988).

Growth components, like NAR and LAR, or photosynthesis and respiration, have all been reported to be lower at low N-supply, be it not always to the same extent. If the RGRs of fast- and slow-growing species become more or less similar at low nutrient supply, this may imply that growth components become similar as well. Alternatively, a similar RGR for the different species may be achieved with contrasting values for growth parameters. The main aim of this paper is to examine to which extent the components of growth that differ between fast- and slow-growing species at an optimum nutrient supply remain different at low N-supply. To this end, we investigated the growth of two contrasting species out of the 24 analyzed by Poorter and Remkes (1990), the potentially fast-growing grass *Holcus lanatus* and the slow-growing grass *Deschampsia flexuosa*.

Growth was analyzed at three different levels. First, we used the technique of growth analysis, determining NAR, LAR, SLA and allocation of biomass. Second, we investigated the effects of nutrient limitation on the carbon economy of the whole plant, determining photosynthesis, and shoot and root respiration, and constructing a full carbon budget. Third, we analyzed C and N concentrations in the plants, parameters which are directly linked to the carbon economy of the plant (e.g. Evans, 1983) and the dry weight:fresh weight ratio, tightly connected with leaf and root morphology (Garnier and Laurent, 1994; Ryser and Lambers, 1994).

Materials and methods

Rationale of the method used

There are several ways by which a nutrient limitation can be imposed on plants. By adding nutrients exponentially to an aqueous rooting medium a preselected submaximal RGR can be 'enforced' upon plants (Boot et al., 1992; Ingestad, 1982; Van der Werf et al., 1993). When grown in this way, any differences in root morphology, spatial distribution of roots, biomass allocation and nutrient uptake characteristics are of no consequence for the growth rate of the plants. Alternatively, nutrients can be added in different amounts to pots filled with a solid substrate at the beginning of the experiment. This approach may cause an excess of nutrients at the beginning of the experiment, when plants are small, and a progressive depletion as plants become larger. Clearly, there is a large interaction between plant size and nutrient availability in this design. A third possibility is to frequently replenish the existing soil solution with a fresh one. Provided that pots are large compared to the rooting volume, this approach provides a relatively constant supply proportional to the size of the plants, enabling them at the same time to take advantage of increased allocation of biomass to roots, or of root characteristics that enhance the uptake capacity of nutrients in one way or another. In our view, the last approach is a proper way to study the effect of a constant nutrient limitation on the whole plant, taking into account all possibilities of a plant to increase its uptake.

Growth of the plants

Seeds of *Holcus lanatus* L. were obtained commercially (Kieft, Blokker, The Netherlands), seeds of *Deschampsia flexuosa* (L.) Trin. were collected in a heathland area at the 'Uddeler Buurtveld', The Netherlands. Seeds of *D. flexuosa* were stratified for four weeks prior to sowing. Germination occurred in Petri dishes in a growth cabinet at 25/15 °C and a PPFD of 100 μmol m^{-2} s^{-1} (12h day). After germination, seedlings were planted in trays filled with sand, and supplied with half strength of a modified Hoagland solution. Full strength of this solution was of the following composition: 795 μM KNO$_3$, 603 μM

Ca(NO$_3$)$_2$, 270 μM MgSO$_4$, 190 μM KH$_2$PO$_4$, 41 μM Fe-EDTA, 20 μM H$_3$BO$_3$, 2 μM MnSO$_4$, 0.85 μM ZnSO$_4$, 0.25 μM Na$_2$MoO$_4$ and 0.15 μM CuSO$_4$. The trays were transferred to a growth room with the following conditions: PPFD 315 ± 30 μmol m^{-2} s^{-1} during 14 h a day, temperature 20 ± 0.5 °C day and night, relative humidity 70 ± 5%. When the roots reached a length of approx. 5 cm, seedlings were planted in PVC tubes (height 30 cm, diameter 10.6 cm, 2 seedlings per tube) filled with washed quartz sand (grain size 0.7 - 1.3 mm). The water-holding capacity of these pots was approx. 400 mL. The bottom of the tubes was sealed with a lid, perforated with holes to ensure free drainage. The soil surface was covered with a layer of plastic beads to reduce water loss from the soil. Every other day the pots were flushed with 450 mL nutrient solution. For half of the plants, this solution was full strength of the one described above, with a total NO$_3^-$ concentration of 2000 μM (high N). The other half of the plants received a solution with a nitrate concentration of 67 μM. CaSO$_4$ (536 $\mu M)$ was added to complement for the reduced Ca(NO$_3$)$_2$ supply. The pH of the solution was set to 5.8. This pH is higher than the pH of the soils in which *D. flexuosa* generally is found. However, the physiological optimum in pH with respect to growth is between 5.5 and 6 for this species (Hackett, 1965), and therefore we chose to use a pH similar to that of previous experiments (Poorter and Remkes, 1990).

Every other day the pots were shifted within the growth room, to minimize the effect of spatial variation in growth conditions. Prior to the first harvest, plants were thinned to one per tube, to minimize size variation within the population. The plants remained vegetative during the experiment.

Experimental design

Harvesting started when plants had reached a fresh weight of approx. 100 mg (day 0). The aim of the experiment was to compare both species over a range of similar total plant weights, thus avoiding size-dependent variation in the parameters of interest. Therefore, growth of *H. lanatus* was followed for a period of 21 and 42 days at high and low nitrate availability, respectively. For the slower-growing *D. flexuosa* the corresponding periods were 35 and 49 days, respectively. Plants were harvested 3 times a week, and each harvest consisted of 6-8 plants, selected as described by Poorter (1989a). At the first and last harvest twice the number of plants was harvested. Thus, the total

number of plants harvested per treatment varied from 80 for *H. lanatus* at high N till 155 for *D. flexuosa* at low N.

Measurements

At each harvest plants were washed out of the containers and separated into roots, leaf blades and leaf sheaths. Total leaf area of *H. lanatus* was determined with a leaf area meter (TFDL, Wageningen, The Netherlands). Total leaf area of the needle-like leaves *of D. flexuosa,* was calculated as: total leaf blade length × π × the thickness in the middle of the leaf × 1.1. Leaf thickness was measured with a thickness gauge (Peacock, Nagasaki). The value of 1.1 is a correction factor, determined by relating the light-exposed part of the circumference of leaf sections over the whole leaf, as determined with a light microscope, to the area computed from leaf thickness and leaf length. For both species, leaf area is given as half the total leaf area. Dry weight of the different plant parts was determined after 24 hat 70 °C.

For each treatment, whole shoot net photosynthesis and dark respiration were measured 6 to 8 times during the experiment (n = 4). We were not able to determine these parameters on the plants as they grew in the containers. Therefore, we chose to measure the plants after carefully removing the plants from the tubes, by gently washing off the sand with water of 20 °C. Thereafter, plants were placed in a cuvette with shoot and roots in separate compartments (Poorter and Welschen, 1993). The roots were suspended in a continuously aerated nutrient solution, similar to that supplied to the plants in the tubes. The PPFD, temperature and vapour pressure deficit were similar to those in the growth room. CO$_2$ and H$_2$O exchange were measured differentially with infrared gas analyzers (ADC, model 225 MK3, Hoddesdon, UK) in an open system after equilibration during two hours. Calculations of the rate of photosynthesis and shoot respiration were made according to Von Caemmerer and Farquhar (1981).

Root respiration was determined on detached roots as the decrease of oxygen concentration in an air-tight cuvette containing the same nutrient solution as applied to the plants (Lambers et al., 1993). This solution was air-saturated before the start of the measurements. The oxygen concentration was measured with a Clark-type electrode (Yellow Springs Instruments, OH, USA). Measurements were completed within 15 min after severing the shoot.
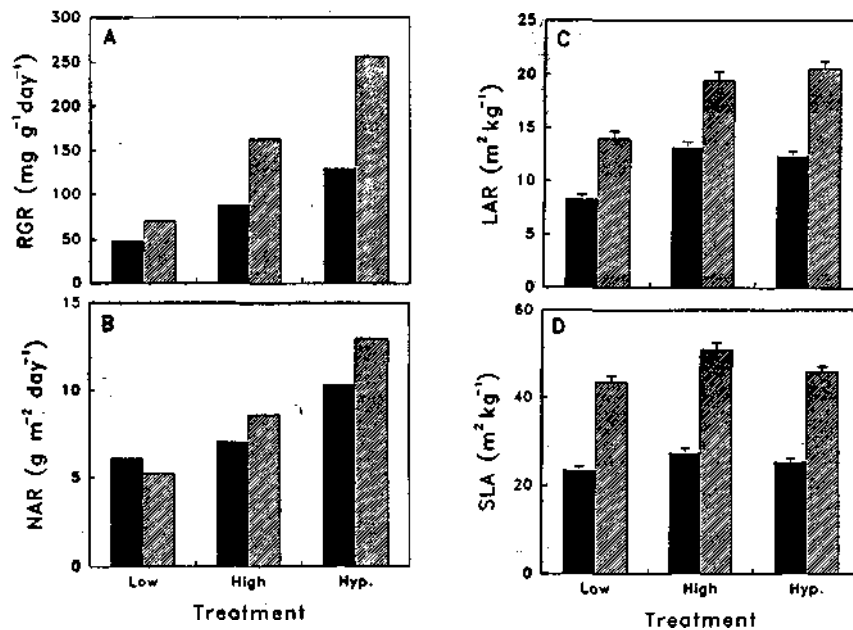
Fig. 1. **A**, RGR; **B**, NAR; **C**, LAR; and **D**, SLA of *Deschampsia flexuosa* (dark bar) and *Holcus lanatus* (hatched bar) grown at a low (Low) and high (High) N-concentration in sand, and at a high N-concentration in hydroponics (Hyp). The graph shows average values during the time that plants attained a dry weight between 30 and 200 mg, and the average SE over all harvests during that time interval (6-8 replicates per harvest). Data of plants grown in hydroponics are from Poorter and Pothmann (1992).

Chemical analyses

Prior to chemical analysis, leaves, stems and roots of each harvest were dried and combined into two independent samples. Plant material of 10 harvests per treatment was digested with a modified Kjeldahl method using 4 mL concentrated sulphuric acid and 1 gram of a mixture of Na_2SO_4, K_2SO_4 and Se in a ratio of 62:1:1 (w/w) as a catalyst. The N-content was measured colorimetrically using indophenol blue. As we did not add salicylic acid prior to digestion, we assumed all N measured to be organically bound. Carbon content was determined for plants of 3 harvests with an elemental analyzer (Carlo Erba, Milano, Italy).

Statistical analyses

Data were analyzed with the SPSS statistical package. Trends of growth parameters with time were fitted with polynomials, according to Poorter (1989a). For each parameter, the average value during the period that plants had a total dry weight between 30 to 200 mg was calculated. Differences between species and treatments were tested for plants that were harvested dur-

ing the period of interest in an analysis of covariance with ln-transformed dry weight (Size) as covariate and Species and N-availability as independent variables. A stepwise model was used in which first the overall effect of Size was taken out and thereafter data were tested for effect of Species, N-availability and the interactions. No appropriate test is available to assess the significance of differences in RGR and NAR, calculated over a specific dry weight trajectory. However, to obtain an estimate of the proportion of variance explained by the above model, we divided the time that plants were in the 30-200 mg range into 10 equal intervals, and calculated for each of these the fitted RGR and NAR values. Subsequently, these were entered into the ANCOVA and the variances attributable to each component calculated.

Results

The design followed, with nutrient solution applied regularly to pots with sand, implies that the nutrient limitation as experienced by the plant is due partly to the low N-concentration of the solution, partly due to the fact that the possibility of movement of soil solution

Table 1. Results of an ANCOVA with ln-transformed dry weight as covariate and species and N-supply as independent variables. For each model component the figures indicate the percentage of the total sum of squares explained by the full model, that could be attributed to that effect. *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$

Dependent variable	Size	Species	N-supply	Species * N-supply	Total df
RGR	3	29	57	10	-
NAR	4	0	65	31	-
LAR	6***	52***	42***	0	144
SLA	2***	93***	6***	0	144
LWR	4***	28***	63***	4***	144
SWR	0	0	93***	7***	144
RWR	3**	17***	79***	1	144
Photosynth./leaf area	0	14***	85***	0	92
Photosynth./leaf weight	5***	46***	44***	5***	92
Shoot respir./shoot weight	28***	36***	28***	8***	92
Root respir./root weight	9***	51***	37***	3*	92
Carbon concentration					
Leaf	-	89***	10*	2	8
Stem	-	57*	43*	0	8
Roots	-	99*	1	0	8
Plant	-	100**	0	0	8
Organic N concentration					
Leaf	16***	0	83***	1	56
Stem	32***	6***	61***	0	56
Roots	22***	3*	72***	2*	56
Plant	19***	0	81***	0	56
Dry weight:Fresh weight ratio					
Leaf	7***	70***	23***	0	144
Stem	7***	67***	23***	3***	144
Roots	10***	69***	20***	1	144
Plant	5***	91***	4***	0	144

through the soil is low. Such a restricted movement is relieved when plants are grown in well-stirred hydroponics. Poorter and Pothmann (1992) have grown the same two species in a hydroponic system, with a concentration equal to the high-nutrient treatment in the present experiment. All other growth conditions were exactly the same. For the purpose of comparison, the average values of that experiment over the same biomass trajectory are also included in the Figures 1-4.

Relative growth rate of *H. lanatus* was higher than that of *D. flexuosa* at both levels of nutrient supply Fig.

1A). The difference in RGR between treatments was larger for the faster-growing species than for the inherently slow-growing one. In both species, the decrease in RGR was accompanied by a decrease in NAR, LAR, SLA and LWR (Figs. l B, C, D and 2). For *H. lanatus* the reduction in NAR was larger than that in LAR 39% vs. 28%). For *D. flexuosa* the opposite happened, with NAR being less affected than LAR (13% vs. 37%). Variation in SLA (Fig. 1D) was mainly due to the difference between species, whereas variation in biomass allocation (Fig. 2) was caused mainly by the differences in treatment (Table 1). However, at both lev-
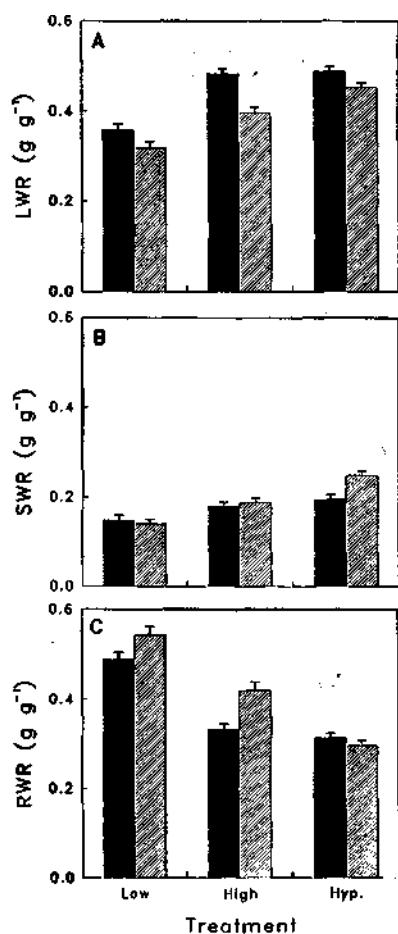
Fig. 2. **A**, LWR; **B**, SWR; and **C**, RWR of *Deschampsia flexuosa* (dark bar) and *Holcus lanatus* (hatched bar) grown at a low (Low) and high (High) N-concentration in sand, and at a high N-concentration in hydroponics (Hyp). The graph shows average values during the time that plants attained a dry weight between 30 and 200 mg, and the average SE over all harvests during that time interval (6-8 replicates per harvest).

els of N-supply *D. flexuosa* allocated relatively more biomass to leaves than *H. lanatus* did, and less to roots. There was a small but significant interaction, in that *D. flexuosa* decreased more in LWR at low N-supply than *H. lanatus* did.

The rate of photosynthesis, expressed per unit leaf area or per unit leaf weight, was lower at the low nutrient supply (Figs. 3A, B). The relative decrease was larger when expressed per unit leaf weight (40%) than when expressed per unit leaf area (30%). Relative decrease was equal for both species, but the absolute decrease in the rate of photosynthesis per unit weight was larger for *H. lanatus*. The rate of shoot respiration was lower in the low N-plants as well, the decrease

being largest in *H. lanatus* (Fig. 3C). Decreases in root respiration were quantitatively similar for both species. None of the gas exchange parameters reversed order at a low N-supply.

Similar conclusions were reached when parameters pertaining to the chemical composition of the plants were considered. There were differences between species, in that dry matter percentage and C-concentration were significantly higher for *D. flexuosa* (Figs. 4A, B). The effect of N-supply was negligible. Total plant organic N on the contrary was the same for both species, and reduced by 40-45% at low N-supply (Fig. 4C). For all three variables, Species × N-supply interaction was absent (Table 1).

Discussion

Effect of N-supply

For both plant species investigated, the high-N treatment did not ensure maximal growth in the present experiment. Compared to plants grown in hydroponics rather than in sand, with a similar concentration of nutrients in the solution administered, both species attained a lower growth rate (Poorter and Pothmann, 1992; Fig. 1), most probably due to the smaller amount of nutrients available to roots grown in sand. However, we cannot fully exclude that shortage of water, or the impedance of the soil to root growth may have played an additional role as well. Therefore, we analyzed the low N-treatment with reference to the high N-treatment, rather than the fully non-limiting hydroponics. However, for almost all parameters there is a consistent trend when treatments are ranked from low N to high N to hydroponics (Figs. 1-4).

The effect of N-supply, averaged for both species, was to decrease the growth parameters RGR, NAR and LAR (Fig. 1). Decrease in LAR was due mainly to a shift in allocation from leaves to roots, although a small decrease in SWR was found as well. As such, these observations fit in with general literature, where SLA is found to decrease only marginally (Dijkstra, 1989), most likely due to accumulation of sugars in the chloroplasts. Therefore, decreases in growth rate can be ascribed to the decrease in LWR and NAR.

The NAR, although termed the 'physiological component' in growth analysis, is in fact a complex expression, including photosynthesis and respiration, as well as biomass allocation, leaf morphology and chemical composition (Lambers and Poorter, 1992). Therefore,
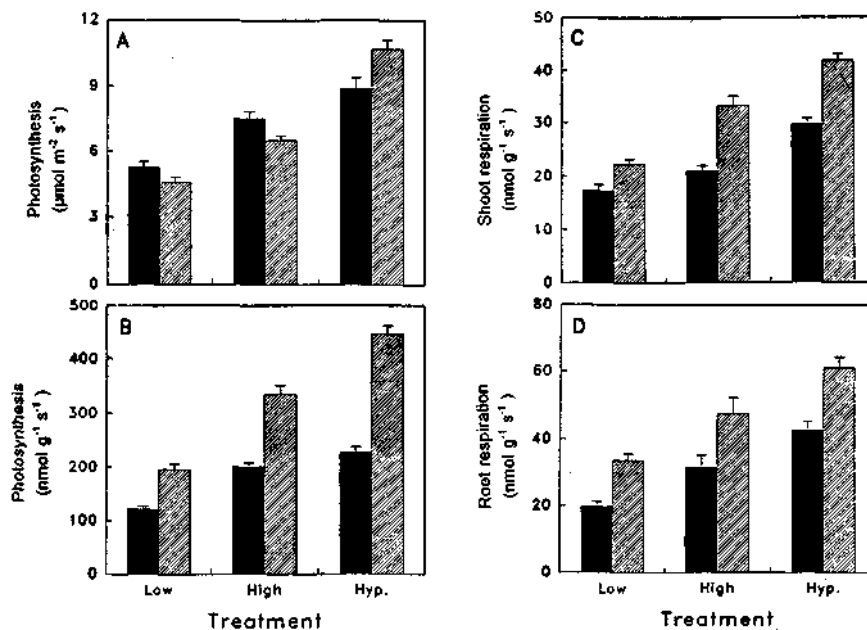
Fig. 3. Rate of **A**, Whole plant photosynthesis per unit leaf area; **B**, Whole plant photosynthesis per unit leaf weight; **C**, Shoot respiration per unit shoot weight; and **D,** root respiration per unit root weight of *Deschampsia flexuosa* (dark bar) and *Holcus lanatus* (hatched bar) grown at low (Low) and high (High) N-concentration in sand, and at a high N-concentration in hydroponics (Hyp). The graph shows average values during the time that plants attained a dry weight between 30 and 200 mg, and the average SE over all harvests during that time interval (4 replicates per harvest).

to obtain insight into the physiological responses of the whole plant, it is better to determine the carbon gain and losses. Photosynthesis was lower at low N (Fig. 3A), in accordance with the literature (e.g. Chapin et al., 1988; Evans, 1983; Sage and Pearcy, 1987; but see Garnier et al., 1989), and rates of shoot and root respiration decreased as expected (cf. Boot et al., 1992; Van der Werf et al., 1993; but see Boot and Den Dubbelden, 1990). The lower rate of photosynthesis can be explained by the lower organic N concentration of the leaves (Table 1, cf. Fig. 4B). The lower rate of respiration is partly explained by the lower rate of growth and nutrient uptake of these plants (cf. Van der Werf et al., 1993).

Changes in the rates of photosynthesis and respiration per se are not sufficient to understand the effect of a decreased N-supply on growth. To this end, it is required to determine the integrated daily carbon gain of the whole plant, thus taking into account shifts in SLA and allocation, as well as changes in the C-concentration of the plant. Surprisingly little information is available with respect to this subject. We calculated a carbon budget for plants grown at high and low N, based on the assumption that a) washing

the roots out of the pots did not affect the plants to a large extent, b) the determined rates of CO_2 exchange were proper estimates for the average values during the day and night, and c) the respiratory quotient of root respiration was 1.0. Normalizing the daily gross carbon gain per unit total plant weight relative to that of *H. lanatus* at high N, a similar picture as for RGR emerged, with total carbon gain reduced by 50% due to the low N-treatment. However, not only were there clear differences in the gross carbon gain, also the way in which the daily fixed carbon is spent varied. Although the rates of shoot and root respiration were reduced to a more or less similar extent at low N (Figs. 3C, D), the proportion of daily fixed C allocated to shoot respiration remained fairly similar, whereas a doubling was observed in the percentage of C channelled to root respiration (Fig. 5). This shift is due to the concomitant increase in biomass allocation to the root compartments at low N (Fig. 2). Thus, growth at low N was reduced, partly due to a lower carbon gain of the smaller shoot, but also as a consequence of higher losses in root respiration in the relatively larger root system. A similar conclusion was reached by Van der Werf et al. (1992), for a fast- and a slow-growing
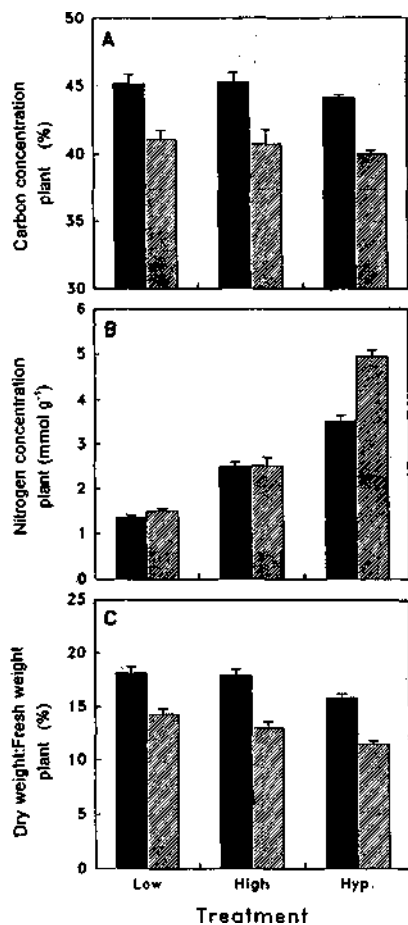
Fig. 4. **A,** C-concentration; **B,** N-concentration; and **C,** dry weight:fresh weight ratio × 100 (dry matter percentage) of *Deschampsia flexuosa* (dark bar) and *Holcus lanatus* (hatched bar) grown at a low (Low) and high (High) N-concentration in sand, and at a high N-concentration in hydroponics (Hyp). The graph shows average values during the time that plants attained a dry weight between 30 and 200 mg, and the average SE over all the harvests during that time interval (2 replicate bulk samples per harvest for C and N, 6-8 replicates per harvest for the dry weight:fresh weight ratio).

Fig. 5. Carbon budget of *Deschampsia flexuosa* (DF) and *Holcus lanatus* (HL) grown at a high and at a low N-supply. Values above the pies indicate the rate of gross carbon gain per unit total plant weight, normalized to 100% for the high N *H. lanatus* plants. In the calculations of the carbon budget it was assumed that shoot respiration continues during the day and that the respiratory quotient of root respiration was 1.0.

species grown in hydroponics with different relative addition rates of nitrate.

Apart from the net result of carbon fluxes, as described in Figure 5, growth is also determined by the C-concentration of the plant biomass as well. There was an effect of nutrient level on the C-concentration of leaves and stem (Table 1), but not on that of the whole plant. This is due to the fact that the changes in C-concentration at low-N are balanced by changes in allocation to roots, causing the net effect to be nil.
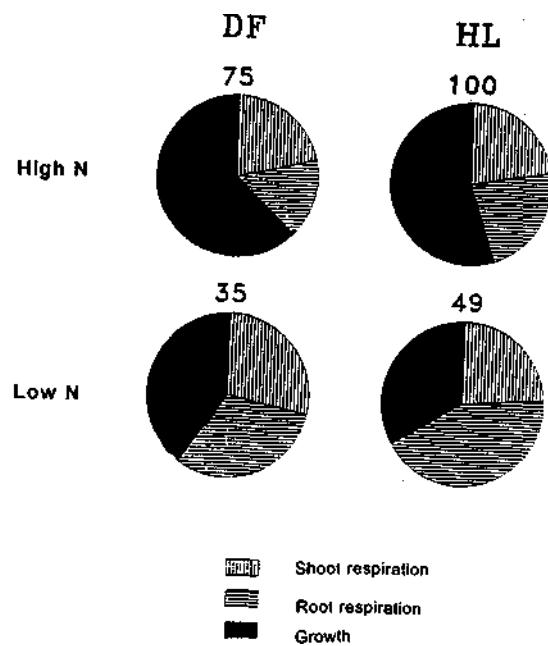
Differences between species

Do species respond differently to the decrease in N-supply, and will this imply that those parameters, that are higher for fast-growing species at high N-availability will become equal or lower at low N-supply? At low N-supply, RGR of *H. lanatus* is still higher than that of *D. flexuosa.* Thus, as in most short-term experiments, the species that grows fastest at an optimum supply of nutrients continues to do so at lower rates of nutrient supply (Gray and Schlesinger, 1983 for shrubs; Shipley and Keddy, 1988 for a range of emergent macrophytes (mono-and dicots); Hull and Mooney, 1990 for annual grasses; Boot and Mensink, 1991; Ryser and Lambers, 1994 for perennial grasses; Fichtner and Schulze, 1992 for annual dicots; but see Muller and Garnier, 1990 for an annual and perennial grass).

There is a substantial interaction term for the NAR (Table 1). However, as stated before, NAR is a complex parameter. When considering the components of NAR individually, it turns out that the proportion of variance explained by the interaction term is very small

(less than 10%, Table 1). That is, the potentially fast-growing *H. lanatus* and the slow-growing *D. flexuosa* respond in a more or less similar way to the limited N-supply. As far as there is a difference in response, e.g. in the LWR, the change is smaller for *H. lanatus* (20%) than for *D. flexuosa* (26%). This is at variance with the reviews of Chapin (1980) and Lambers and Poorter (1992), in which it was concluded that fast-growing species tend to be more plastic than slow-growing ones with respect to biomass allocation as a response to different levels of nutrient supply (cf. Van de Vijver et al. 1993). Olff (1992) did not find a substantial interaction between species and nutrient supply either, when allocation and SLA of species from habitats with different productivity were compared.

If these results, based on a large range of parameters related to growth, can be generalized, it would imply that the species-specific differences which are recurrently observed at high N-supply (Dijkstra and Lambers, 1989; Poorter et al., 1990; Walters et al., 1993) persist at low N-supply.

Ecological considerations

It has been suggested that the positive correlation between the potential growth rate of a plant species and its occurrence in nutrient-rich habitats is caused by selection for a high potential RGR in a productive environment, and selection for a low growth potential in unproductive environments (see, e.g., Chapin, 1980; Grime, 1979). The suggested explanations for a causal link between RGR and the occurrence of species in the field have been questioned (Lambers and Poorter, 1992). An additional point that has not been discussed so far is that species from unproductive environments never reach their potential growth rate in their natural habitat (cf. Fig. 1), so that selection for a low growth potential per se is impossible. An alternative explanation is that potentially fast-growing species have adapted to productive environments, but that, as a consequence of the set of characters acquired, their growth in unproductive environments is less than that of the slow-growing species that normally occur there. However, as noted above, this explanation is not supported by the data. Generally, in short-term experiments potentially fast-growing species do have similar or higher RGRs at low N-supply as the inherently slow-growing species. The question then rises what prevents potentially fast-growing species from occupying unproductive areas?

In a simulation of the long-term biomass dynamics of perennials, Aerts and Van der Peijl (1993) showed that at low N-input and similar starting weight, high-productive species initially attain higher growth rates and a higher biomass than low-productive species, but that the order is reversed after a few years. Key feature in determining the long-term success of low-productive species in nutrient-poor environments is their low nutrient loss rate (Aerts, 1990; Berendse and Elberse, 1989; cf. Chapin, 1980; Coley et al., 1985; Grime, 1979; Reich et al., 1992), mainly due to high leaf longevities (Escudero et al., 1992). How is a high leaf longevity achieved? The exact mechanism is not known, but generally, long-living leaves of slow-growing species are characterized by high C-concentrations, high dry weight:fresh weight ratios, and a high investment in sclerenchyma and other cell wall components (Chabot and Hicks, 1982; Garnier and Laurent, 1994; Poorter and Bergkotte, 1992; Van Arendonk and Poorter, 1994). From the perspective of growth analysis, these characteristics show up as a low SLA, both at low and high nutrient availability (Fichtner and Schulze, 1992; Fig. 1). In the parameters determining the carbon balance such a preference for investment in cell wall components over investment in cytoplasmic compounds becomes apparent in a low rate of photosynthesis and respiration per unit weight (Fig. 3; Poorter et al., 1989). Given that these traits differ consistently between species, not only at high N-availability but also at low-N, we conclude that selection in low-productive environments has been for a suite of traits which result in a low SLA and, consequently a low rate of photosynthesis per unit leaf weight, rather than for a low RGR per se.

Conclusions

Inherent variation in parameters related to growth (RGR, LAR, SLA), carbon economy (rates of photosynthesis and respiration per unit organ weight) and chemical composition (C-concentration), as observed at high N-supply, generally persist when plants are grown at low N-supply. We conclude that not a low RGR per se, but rather a suite of attributes leading to an inherently low SLA is advantageous in low-productive environments.

Acknowledgements

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Section editor: H Marschner