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

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SUMMARY

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. The present experiment was to investigate whether these differences persist when plants become larger. Plants of the inherently fast-growing *Holcus lanatus* L. and the inherently slow-growing *Deschampsia flexuosa* (L.) Trin. were grown under standardized conditions and growth, photosynthesis, respiration and carbon and nitrogen content were followed over a period of 4 to 7 weeks. Differences in relative growth rate were mainly due to the higher leaf area ratio (leaf area : plant weight) of the fast-growing species. Rates of photosynthesis differed substantially when expressed on a leaf weight basis, but only slightly when expressed per unit leaf area. Although most parameters showed some ontogenetic drift, differences found for young seedlings persisted at least until plants reached a dry weight of *circa* 3 g. Therefore, at least for these two species, the conclusions based on interspecific variation in relative growth rate of young seedlings apply to larger plants as well.

Key words: Growth analysis, interspecific variation, ontogenetic drift, photosynthesis, respiration

INTRODUCTION

Plant species may differ considerably in growth potential. When grown under more or less optimal conditions, seedlings of plant species from fertile habitats show much higher relative growth rates (RGR) than those of species from nutrient-poor environments (Grime & Hunt, 1975; Poorter, 1989*b*). In a previous paper, these differences in RGR were found to be mainly due to variation in specific leaf area (SLA, leaf area: leaf dry weight) and to a lesser extent leaf weight ratio (LWR, leaf weight : total plant dry weight) (Poorter & 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, Remkes & Lambers, 1990). Differences in the rate of shoot and root respiration, expressed per unit shoot and root weight, respectively, or in chemical composition (Poorter & Bergkotte, 1992) did not explain the interspecific variation in RGR either.

The above-mentioned parameters were determined on relatively young seedlings. Most of the parameters related to the growth of a plant have been

reported to change with ontogeny. For example, rates of photosynthesis may decrease with increasing plant age (Tichá *et al.,* 1985; Suzuki *et al.,* 1987), whereas allocation of biomass to the shoot often increases (Lambers & Posthumus, 1980; Siddique, Belford & Tennant, 1990). Four mostly interacting factors may explain these changes over time. Firstly, alterations in physiology, allocation and/or morphology may be the result of an increase in plant size. Such an increase will bring about self-shading within an individual plant (e.g. Poorter, Pot & Lambers, 1988) or may require extra investment in support tissue (Givnish, 1986). These changes in turn will alter the rate of photosynthesis and/or the fraction of photosynthetically fixed carbon that is used in respiration and may thus affect growth. Secondly, environmental changes and the subsequent alteration in transpiration or carbon balance will influence growth. Thirdly, the transition from the vegetative phase to flowering and fruit production may change physiological activity (Singh & Lal, 1935; Fujii & Kennedy, 1985). Fourthly, alteration of physiological activity can occur due to senescence (Noodén, 1988).

In this paper, we investigated whether the above-

mentioned differences between fast- and slow-growing species, which have been observed for young seedlings, also occur in later stages of growth. To this end, we determined how growth, carbon economy and chemical composition changed with ontogeny for two grasses differing in growth rate: *Holcus lanatus* and *Deschampsia flexuosa*. For the sake of simplicity we restricted ourselves to the vegetative phase and grew the plants under constant environmental conditions, similar to those used previously (Poorter & Remkes, 1990; Poorter *et al.*, 1990).

MATERIALS AND METHODS
Growth of plants

Seeds of *Holcus lanatus* L. were obtained commercially (Kieft, Blokker); seeds of *Deschampsia flexuosa* (L.) Trin. were collected in a grass heath at the 'Uddelse Heide', the Netherlands, and stratified for four weeks prior to the experiments. Germination occurred in Petri dishes in a growth cabinet at a temperature of 25/15 °C and a PPFD over the waveband 400-700 nm of 100 μmol m^{-2} s^{-1} (12 h day). When the roots reached a length of 4 cm, seedlings were transferred to a growth room and placed in 33 1 containers filled with an aerated nutrient solution. PPFD was 315 ± 30 μmol m^{-2} s^{-1} over the waveband 400-700 nm for 14 h a day; temperature was 20 ± 0.5 °C. The number of plants in a container varied between 24 and 2, depending on the size of the plants. The composition of the nutrient solution and further experimental details are given by Poorter & Remkes (1990). The plants did not flower during the experiment.

Experimental design

The experiment was repeated four times. Harvesting for each repetition started when plants had reached a fresh weight of approximately 100 mg (day 0). The first repetition formed part of the data presented by Poorter & Remkes (1990). Six harvests of 8 plants each were carried out during a period of 17 days. The aim of the other three repetitions was to compare both species over a range of similar total plant-weights, thus correcting for different constraints of small and larger plants. Therefore, plants were grown until they reached a total plant dry weight of 4 to 5 g. Thereafter, the experiments were stopped because plants became too large to ensure unlimited nutrient supply and to avoid mutual shading. *H. lanatus* plants attained this weight 20 to 26 days after the start of the experiment, the slower-growing *D. flexuosa* after 42 to 50 days. Each repetition consisted of 7 to 10 harvests per species, more or less evenly spaced over this period. In the second repetition per harvest day eight plants were selected as described

by Poorter (1989*a*); in the last two repetitions four plants were collected each time. Data for the various parameters have been combined for all repetitions together.

Measurements

At each harvest plants were separated into roots, leaf blades and leaf sheaths. Total leaf area of *H. lanatus* was determined with a leaf area meter (TFDL, Wageningen or Li-Cor, Lincoln). Total leaf area of *D. flexuosa* was calculated as: total leaf blade length × π × thickness at 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 surface area. Dry weight of the different plant parts was determined after 24 h at 80 °C.

Whole shoot net photosynthesis and dark respiration were measured as CO_2-exchange. Intact plants were placed in a cuvette with shoot and roots in separate compartments. The PPFD, temperature and vapour pressure deficit were similar to those 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 and shoot respiration were made according to Von Caemmerer & Farquhar (1981), with the correction suggested by Bunce & Ward (1985).

Root respiration was determined on detached roots as the decrease of oxygen concentration in an airtight cuvette containing a nutrient solution, which was air-saturated before the start of the measurements. The oxygen concentration was measured with a Clark-type electrode (Yellow Springs Instruments, OH, USA). The activity of the alternative pathway was assessed in a nutrient solution (without Fe) containing 18 mM salicylhydroxyamic acid (SHAM). In a preliminary experiment, in which root respiration was titrated with SHAM concentrations ranging from 0 to 25 mM both in the presence and absence of 0.5 mM KCN, this concentration had no side-effects on respiration for either species (cf. Møller *et al.*, 1988; Van der Werf *et al.*, 1991).

Chemical analyses

Prior to the chemical analyses, plants of each harvest were dried and combined into two independent samples. Plant material was digested with a modified Kjeldahl method using 4 ml concentrated sulfuric acid and 1 g of a mixture of Na_2SO_4, K_2SO_4 and Se (62:1:1, w/w) as a catalyst. The N-content was measured colorimetrically using indophenol blue.
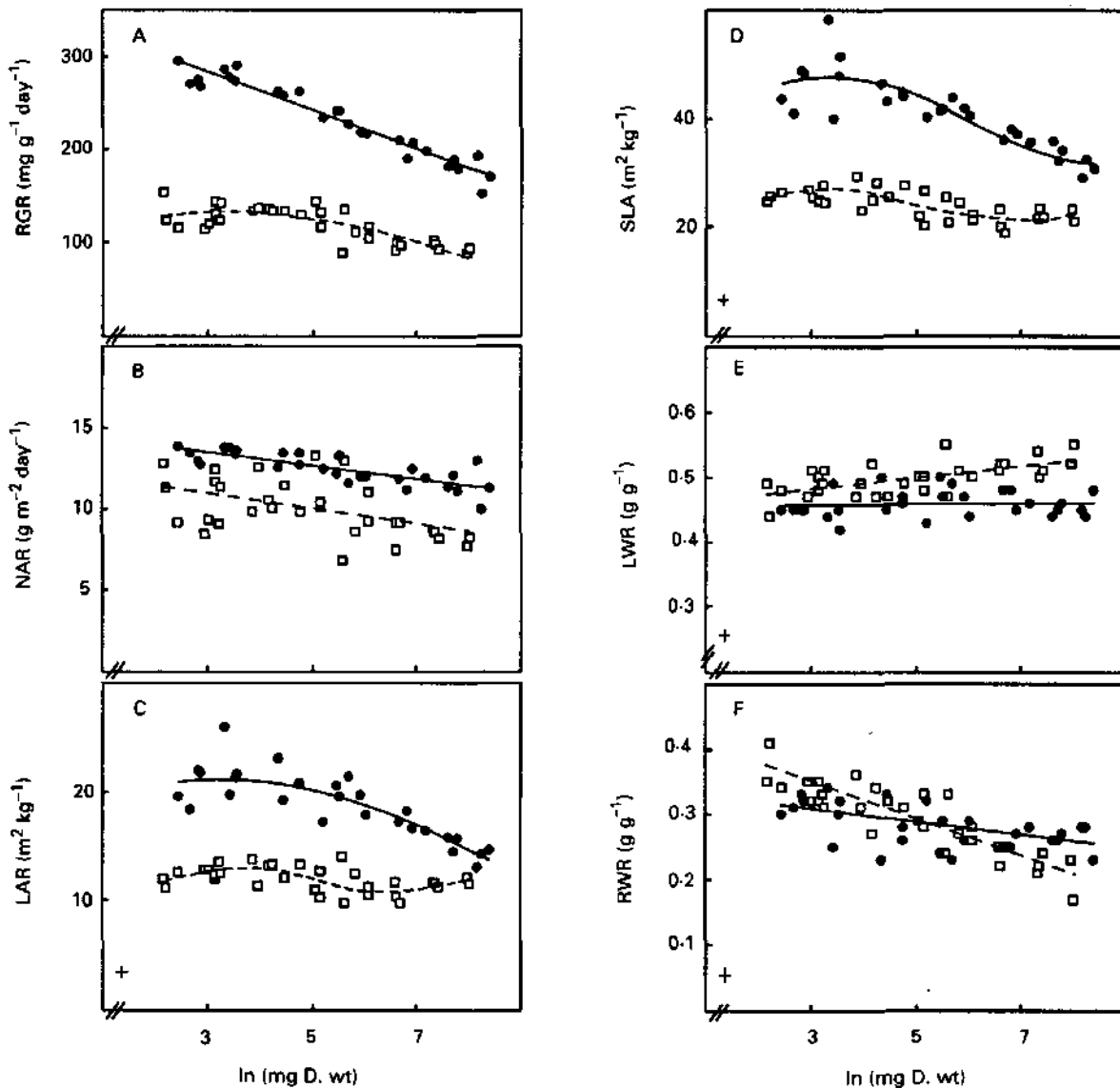
Figure 1. A, Relative growth rate; B, net assimilation rate; C, leaf area ratio; D, specific leaf area; E, leaf weight ratio; and F, root weight ratio as a function of ln-transformed plant weight for *Holcus lanatus* (filled symbols) and *Deschampsia flexuosa* (open symbols). Each point in C-E is the mean value of four or eight plants. The cross in the lower left corner of the graph indicates twice the SE for LAR, SLA, LWR and RWR (*y*-direction) and ln-transformed dry weight (*x*-direction). A polynomial was fitted through the original data points.

Carbon content was determined on freeze-dried material with an elemental analyser (Carlo Erba, Milano).

Statistical analysis

Data were analysed with the SAS statistical package (Joyner, 1985). Growth parameters were calculated for each experiment separately and the averages per harvest plotted against ln-transformed plant dry weight. RGR and NAR values were calculated according to the running average method of Wickens & Cheeseman (1988). Trends of growth parameters with plant dry weight were fitted with polynomials, according to Poorter (1989*a*). Differences between species were tested in an analysis of covariance with

ln-transformed dry weight (Size) as covariate and Species as independent variable. 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 and Species × Size interaction. A significant interaction indicates that differences between species vary for small and large plants.

RESULTS

H. lanatus and *D. flexuosa* differed considerably in relative growth rate (Fig. 1A). Averaged over the whole range of plant sizes RGR of *H. lanatus* was 238 mg g^{-1} day^{-1} versus 119 mg g^{-1} day^{-1} for *D. flexuosa*. This difference between species was significant (Table 1) and decreased with increasing

Table 1. *Results of an ANCOVA with ln-transformed dry weight as covariate and Species as independent variable. For each independent variable the figures indicate the percentage of the total sum of squares explained by the model, which could be attributed to that effect.* *, P < 0.05; **, P < 0.01; ***, P < 0.001

Dependent variable	Size	Species	Size × Species	Total d.f.
RGR	8***	88***	4***	58
NAR	19***	81***	0	58
LAR	7***	88***	5***	377
SLA	8***	89***	3***	377
LWR	15***	73***	12***	377
SWR	54***	40***	7***	377
RWR	80***	1	19***	377
Dry matter % leaf	2***	97***	0**	377
Dry matter % stem	0***	96***	4***	377
Dry matter % roots	42***	56***	1**	377
Dry matter % plant	0	96***	4***	377
PS_a	1	88***	12**	125
PS_w	1**	99***	0	125
PNUE	1	99**	0	57
ShR	55***	45***	0	111
RR	29***	68***	3	125
% Alternative pathway	83***	12**	5*	59
Organic N-content of plant	12***	88***	0	14
C-content of plant	0	97***	3	7

size of the plants (Species × Size interaction, Table 1). On average, a small part of the higher RGR of *H. lanatus* could be explained by a higher NAR (Fig. 1B), the major part by its higher LAR (Fig. 1C). However, in the last phase of the experiment (ln-transformed dry weight > 7.5; dry weight > 1.8 g), NAR and LAR became equally important in explaining the interspecific difference in growth rate. The higher LAR of *H. lanatus* was caused completely by a higher specific leaf area (SLA; Fig. 1D). The Species × Size interaction was large for LAR, in that the difference in young plants almost vanished in the last phase of the experiment. This was mainly due to a decrease in the SLA of *H. lanatus*, and, to a smaller extent, to an increase in LWR of *D. flexuosa* towards the end of the experiment (Fig. 1E). In both species allocation to the roots decreased with increasing plant weight (Fig. 1F), more pronounced for *D. flexuosa*. At the end of the experiment some of the oldest leaves had died, but compared to the total weight of the plant dead mass was negligible (<0.1%).

Small differences were found in the rate of photosynthesis per unit leaf area for young plants. During development of *H. lanatus,* the rate of photosynthesis per unit leaf area gradually increased, though not significantly, whereas the rate of photosynthesis of *D. flexuosa* decreased slightly (Fig. 2A). On average the rate of photosynthesis per unit leaf area was *circa* 21 % higher for the fast-growing species. Differences in the rate of photosynthesis were much larger when expressed per unit leaf weight (on average 107%, Fig. 2B) and no Species × Size interaction was observed. Both shoot respiration and root respiration, expressed per unit shoot and root dry weight respectively, decreased with increasing plant size (Fig. 2C, D) and were higher for *H. lanatus*. Species × Size interactions were small. Hardly any difference was found in the activity of the alternative pathway in root respiration, until plants became very large (Fig. 2E).

Parameters of the nitrogen economy differed consistently between the species, without significant differences in size trends. The organic nitrogen concentration in *H. lanatus* was higher in leaves, stem and roots (data not shown) and also in whole plants (Fig. 3A). The rate of photosynthesis per unit organic nitrogen in the leaves, the photosynthetic nitrogen use efficiency (PNUE), was higher for *H. lanatus* throughout the experiment (Fig. 3B). Due to the combination of a higher leaf nitrogen concentration and a higher PNUE, *H. lanatus* had a higher growth rate per unit organic plant nitrogen (nitrogen productivity, NP, Fig. 3C).

The carbon content per unit total plant dry weight was higher for *D. flexuosa* than for *H. lanatus* (Fig. 3D). The dry weight:fresh weight ratio of total biomass was also much higher for *D. flexuosa* (Fig. 3E), and this was associated with a higher dry matter percentage in both leaves, stem and roots throughout the entire experiment (data not shown).

DISCUSSION

Young plants of *Holcus lanatus* and *Deschampsia flexuosa* in the dry weight range used by Poorter & Remkes (1990), (30-100 mg; 3.4 < ln DW < 4.6), show a distinct difference in RGR. Such a difference between these species has been observed before (Grime & Hunt, 1975; Robinson & Rorison, 1985; Hunt & Lloyd, 1987). Part of the 101% higher growth rate is caused by a 25 % higher NAR (Fig. 1B). In that respect they deviate slightly from the general trend found by Poorter & Remkes (1990) among herbaceous C_3 species, where no consistent correlation between RGR and NAR was observed. However also in this pair of species the higher growth rate is mainly due to the high LAR and high SLA of *H. lanatus* as compared to *D. flexuosa*. The lower SLA of *D. flexuosa* is partly compensated for by a higher LWR (Fig. 1E).
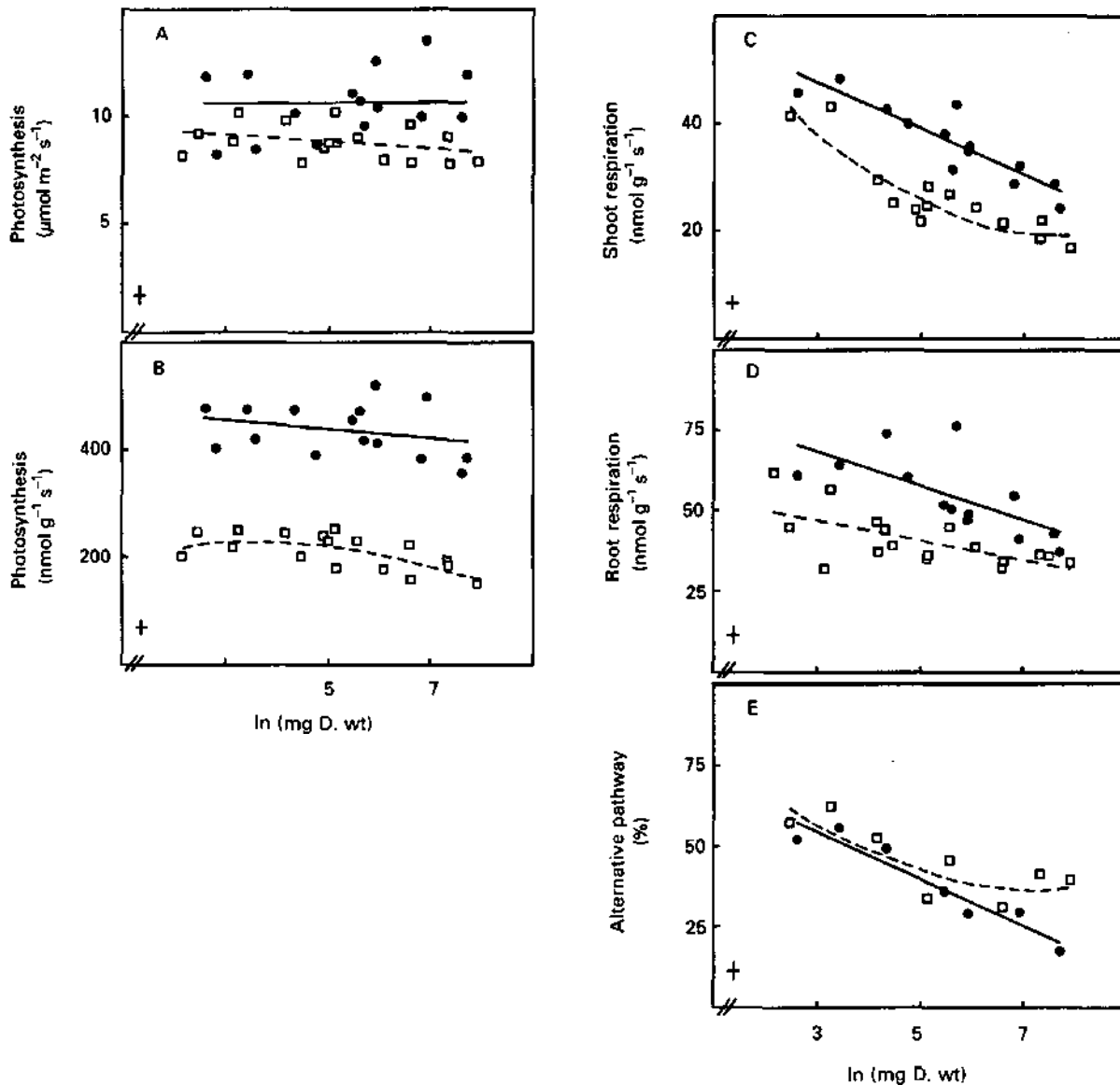
Figure 2. A, The rate of photosynthesis per unit leaf area (PS_a); B, the rate of photosynthesis per unit leaf dry weight (PS_w); C, the rate of shoot respiration per unit shoot dry weight (ShR); D, the rate of root respiration per unit root dry weight (RR); and E, the percentage of total root respiration via the alternative pathway, as a function of ln-transformed plant weight for *Holcus lanatus* (filled symbols) and *Deschampsia flexuosa* (open symbols). Each point is the mean value of four plants.

Do the differences between species, as observed for small plants, also apply to larger plants? For almost all growth parameters there are significant Species × Size interactions (Table 1). However, the proportion of variance explained by this interaction is mostly small. In general, differences in growth parameters may become smaller, but they do persist. The change is most clear for LAR. A similar result has been found in a comparison of *H. lanatus* with another slow-growing grass with a bunch-type structure, *Nardus stricta* (Hunt & Parsons, 1974), but not in a comparison of two subspecies of the dicotyledonous *Plantago major* (Dijkstra & Lambers, 1989). The large change in the LAR of *H. lanatus* is caused by a decrease in SLA, whereas both LAR and SLA of *D. flexuosa* are fairly constant. We are as yet not sure about this contrasting ontogenetic drift in

SLA. Certainly, the decrease in SLA in *H. lanatus* is not due to an extra investment in support tissue only. Leaf sections of full-grown leaves formed early and late in the development of the plant showed that there was an almost equal increase in leaf thickness and number of mesophyll cell layers as well.

There were no important Species × Size interactions in the physiological parameters related to the carbon economy. The rate of photosynthesis was higher for *H. lanatus* throughout the experiment, both when expressed per unit leaf area (Fig. 2A), leaf weight (Fig. 2B) and leaf nitrogen (Fig. 3B). The same holds for shoot respiration and root respiration, expressed per unit shoot and root dry weight, respectively (Fig. 2C, D). Apart from variation in these parameters, differences in growth can also be caused by variation in the carbon content of the plant
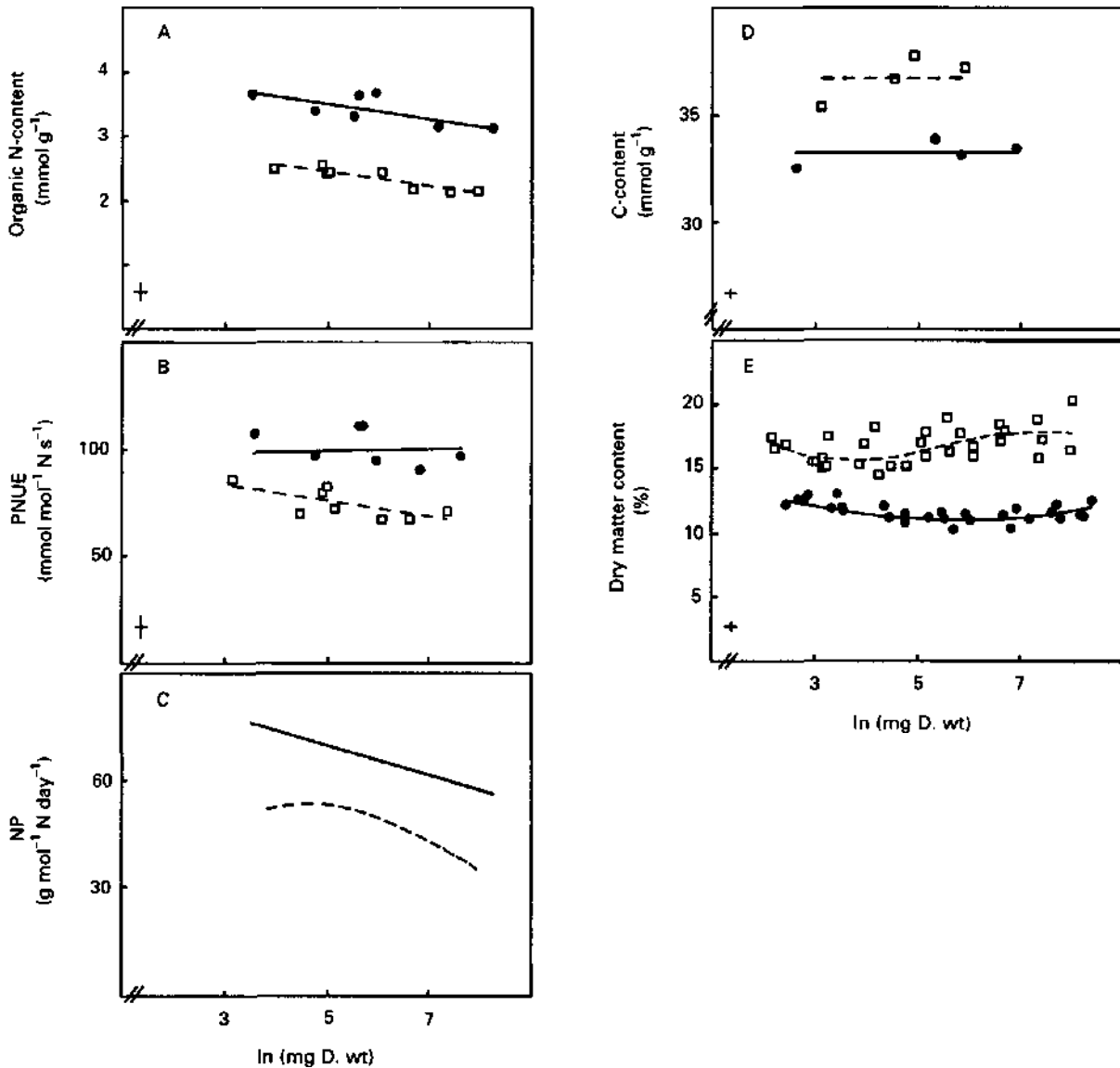
Figure 3. A, Total plant organic nitrogen concentration; B, photosynthetic nitrogen use efficiency (PNUE); C, nitrogen productivity (NP); D, total plant carbon concentration; and E, total plant dry weight: fresh weight ratio, as a function of ln-transformed plant weight for *Holcus lanatus* (filled symbols) and *Deschampsia flexuosa* (open symbols). Each point is the mean value of two independent groups of plants (A, D) or the mean of four or eight individuals (B, E).

material. Indeed, part of the lower RGR of *D. flexuosa* is caused by its higher carbon content (Fig. 3D). However, also for this parameter the Species × Size interaction is small.

It is surprising that the rate of photosynthesis per unit leaf area hardly shows any ontogenetic drift, as a decrease is often observed (e.g., Küppers, Koch & Mooney, 1988; Poorter *et al.,* 1988). To obtain an impression of the accuracy of the physiological measurements, the measured RGR can be compared with the RGR, calculated from the rate of photosynthesis, shoot and root respiration, allocation and carbon content of the plant. In formula:

$$RGR = [PS_a \times SLA \times LWR - ShR$$
$$\times (LWR + SWR) - RR \times RWR)] / C,$$

where PS_a is the rate of photosynthesis expressed per

unit leaf area, ShR and RR shoot and root respiration expressed per unit shoot and root dry weight respectively, SWR the stem weight ratio, and the carbon content. An implicit assumption in this calculation is that the mean rates of photosynthesis and respiration over an entire day are well approached by our measurements for 2 h and carbon losses due to exudation or volatilization are negligible. As we determined root respiration as oxygen consumption, we also had to assume a value for the respiratory quotient (1.2 for these NO_3^--fed plants; *cf.* Poorter *et al.,* 1990). The calculated RGRs matched the measured ones for large plants of *D. flexuosa* and intermediate and large plants of *H. lanatus,* but were lower than the measured RGRs for smaller plants (Table 2). Which determination causes this discrepancy? The underestimation of

Table 2. *Rates of photosynthesis (μmol m^{-2} s^{-1}), measured as CO_2 exchange and calculated from the RGR, shoot and root respiration, allocation and carbon content, at different plants sizes, for* Holcus lanatus *and* Deschampsia flexuosa

Species	ln DW	Photosynthesis		Calculated: Measured
		Measured	Calculated	
H. lanatus	2.5	10.7	12.6	1.18
	5.0	10.7	10.7	1.00
	7.5	10.7	10.3	0.96
D. flexuosa	2.5	9.2	12.0	1.30
	5.0	8.8	11.0	1.25
	7.5	8.4	8.5	1.01

RGR can hardly be caused by an overestimation of the rate of shoot or root respiration, as each of these rates has to be less than zero to explain the difference. If photosynthesis is to explain this difference, the measured rates should have been 20% higher in small *H. lanatus* plants and 30 and 25 % higher in small and intermediate *D. flexuosa* plants (Table 2). Although other explanations cannot be fully excluded, we consider it most likely that the light environment in the photosynthesis cuvette did not completely mirror that of the growth room, where light is radiated from a larger area and partly reflected against the walls. This will cause no serious discrepancy in the measurements when leaves are oriented more or less horizontally, as in intermediate and large plants of *H. lanatus* and also in large *D. flexuosa* plants, but may lead to an underestimation in the case of erect leaves in younger plants. Thus, rates of photosynthesis may have actually declined more strongly than shown in Fig. 2. However, this does not affect our conclusion that the interspecific difference in the rate of photosynthesis per unit leaf area is small, whereas on a leaf weight basis it is much larger.

There were hardly any Species × Size interactions for the organic nitrogen concentration, the nitrogen productivity, the C-content and the dry weight: fresh weight ratio (Fig. 3). No symptoms of senescence were observed during the period of investigation. Although the cotyledon and the first two or three leaves had died during the experiment, the leaf area of these leaves at the moment of their senescence was small compared to the total leaf area and therefore cannot have played a large role in the carbon budget of these species. Induction of the reproductive phase cannot have played a role in the ontogenetic trends either, as our plants remained vegetative during the experimental period. In fact, the physiological activity of these plants was rather constant. Therefore, the major changes which have taken place in these plants grown in a constant environment are alterations in SLA and biomass allocation.

Both the fast-growing *Holcus lanatus* and the slow-growing *Deschampsia flexuosa* showed ontogenetic drift in RGR and related parameters. However, unless plants get extremely large, the differences for seedlings persist in larger plants. From this result we infer that the conclusions based on previous experiments using young seedlings (Poorter & Remkes, 1990; Poorter *et al.,* 1990; Poorter & Bergkotte, 1992) may have wider validity.

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