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The importance of tissue density for growth and life span of leaves and roots: a comparison of five ecologically contrasting grasses

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Summary

1. Under nutrient-poor conditions initially fast-growing species will in the long term be competitively inferior to slow-growing species. Here, we ask whether this phenomenon can be explained by constraints caused by tissue density. The hypothesis is that low tissue density is necessary for fast growth but has as a consequence short organ life span. This leads to a rapid loss of nutrients that cannot be sustained under nutrient-poor conditions.

2. Biomass accumulation, turnover rate of leaves and roots, and tissue density were studied for five ecologically contrasting grass species. Plants were grown in a garden experiment over two growing seasons on sand with a low nutrient supply level.

3. Species that were characteristic of nutrient-rich sites had a low leaf and root tissue density and were larger after one growing season than species of nutrient-poor sites. However, after two growing seasons the species of nutrient-poor sites were larger. These species had a high tissue density.

4. Life span of both leaves and roots was also correlated with tissue density. Species with low tissue density had a faster turnover of leaves and roots.

5. It is concluded that tissue structure is an inherent constraint that prevents simultaneous maximization of both nutrient acquisition and nutrient conservation. The short life span of fast-growing organs explains the long-term disadvantage of a high growth rate for plants in low nutrient conditions.

Key-words: Nutrient limitation, plant strategy, resource acquisition, root morphology, tissue water content

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Introduction

In short-term experiments at low nutrient supply, species that are characteristic of nutrient-rich habitats grow equally fast or even faster than species actually characteristic of nutrient-poor sites (Clarkson 1967; Mahmoud & Grime 1976; Poorter *et al.* 1995; Ryser & Lambers 1995). This fast initial growth is associated with efficient capture of above- and below-ground resources owing to a high leaf area ratio and high photosynthetic capacity per leaf mass (Poorter *et al.* 1995), high root length ratio (Ryser & Lambers 1995) and high nutrient absorption rate (Chapin 1980; Crick & Grime 1987). In natural vegetation of nutrient-poor habitats, however, these species are less abundant than slow-growing species, which dominate the vegetation in such habitats. This has often been considered to result from more efficient nutrient conservation by the slow-growing species, resulting in a low relative nutrient requirement (Berendse, Oudhof & Bol 1987). Nutrient losses can be reduced by

increased root and leaf longevity (Grime 1979; Chapin 1980; Berendse & Aerts 1987; Lambers & Poorter 1992). Negative correlation between leaf and root life span and the nutrient status of the preferred natural habitat of a species has been found among grasses (Williamson 1976; Campbell & Grime 1989; Schläpfer & Ryser 1996), woody species (Reich *et al.* 1991; Escudero *et al.* 1992) and in comparisons between deciduous grasses and evergreen shrubs (Aerts 1990; Aerts, Bakker & de Caluwe 1992). The greater importance of nutrient conservation over fast growth under low nutrient supply is also implied by the models of Sibly & Grime (1986), Aerts & van der Peijl (1993) and Berendse (1994).

Now the question arises, why fast-growing species cannot also have long-lived leaves and roots, and do not ultimately dominate nutrient-poor sites. The obvious inability of species to maximize simultaneously growth rate and nutrient conservation has been pointed out by several authors (Sibly & Grime 1986; Berendse & Aerts 1987; Lambers & Poorter 1992;

Gower, Reich & Son 1993). Ryser & Lambers (1995) suggest this is a result of constraints made by tissue structure. According to these authors, low tissue density enables a fast resource acquisition at any level of resource supply, as the plant can rapidly expand its leaf area and root system with low investment of dry matter. However, the watery tissue produced by such fast-growing species is likely to have a shorter life span than the high-density tissue of the slow-growing species. The hypothesis that tissue density plays a central role in nutrient economy of a species by determining the rate of biomass turnover is supported by the observations that low tissue density is found to be associated with high growth rate (Garnier 1992; Garnier & Laurent 1994) and with short organ life span (Koike 1988; Reich *et al.* 1991; Schläpfer & Ryser 1996).

The objective of the present study was to assess the relation between growth rate and organ turnover rate, and their net effect on plant biomass accumulation over two growing seasons. The significance of tissue density for this relation is investigated. The hypothesis is that species with low tissue density are able to grow initially faster even at low nutrient supply but have a shorter life span of their roots and leaves. This faster turnover of tissues will in the longer term lead to the disappearance of the initial advantage gained by fast growth and result in a lower biomass of these species compared with the more slowly growing species with a high tissue density.

Material and methods

The study was conducted with five grass species of contrasting habitats in respect of nutrient availability. *Arrhenatherum elatius* (L.) J. & C. Presl., *Dactylis glomerata* L. and *Holcus lanatus* L. are common species in nutrient-rich grasslands but may also occur in nutrient-poor sites. *Festuca ovina* L. and *Bromus erectus* Hudson are characteristic of nutrient-poor grasslands. Indicator values of these species for nitrogen are according to Ellenberg *et al.* (1992) 7 (*A. elatius*), 6 (*D. glomerata*), 5 (*H. lanatus*), 3 (*B. erectus*) and 1 (*F. ovina*), on a scale from 1 (indicator of sites extremely poor in available nitrogen) to 9 (indicator of extremely nitrogen-rich situations). Seeds of *A. elatius*, *D. glomerata* and *H. lanatus* were obtained from the Institute of Plant Biology ETH Zürich and originate from populations in Swiss Mittelland. Seeds of *F. ovina* were obtained commercially (Volg, Winterthur, Switzerland). Seeds of *B. erectus* were collected in a nutrient-poor limestone grassland in northern Switzerland. After germination in a greenhouse the seedlings were planted on 26 May 1993 in 0.4-l pots containing brown sand. On 20 June the plants were transferred to the experimental garden in pots of 6.5 l (diameter 15 cm, height 37 cm). The pots contained quartz sand of 0.1–0.7 mm grain size, mixed with 0.5% limestone powder. The pH of the

mixture was 7.5 (0.01 M CaCl₂). Every second week during the growing season 2.0 mg N, 1.0 mg P and 6.8 mg K were given as KNO₃ and KH₂PO₄ dissolved in 100 ml water. This combination of nutrients was chosen to provide only very low quantities of N, P and K, and to keep N the most limiting element for plant growth. The nutrients were added from 22 June until 14 September 1993, and from 9 March until 29 September 1994. During periods of dry weather the plants were watered daily with tap water.

Harvests were conducted in mid-October 1993, early March 1994, late July 1994 and late November 1994. In each harvest six plants of each species were harvested, except in March 1994 in which only five plants were harvested.

In order to prevent leaf losses owing to decomposition, dead leaves of all plants were collected in April, July and September 1994. For the same reason, flowering stems with ripe seed were collected in July and September.

At each harvest the number of tillers and the number of dead and living leaves were counted. A leaf was regarded as dead when less than one third of its length was green. The number of dead leaves collected from a plant before the harvests was added to the number of dead leaves of that plant counted at the harvest.

At harvests the plants were separated into the following component parts: leaf blades, leaf sheaths and stems, roots, flowering stems if present and dead above-ground material. The proportion of living and dead root length was determined after staining with tetrazolium. A small randomly collected root sample was stained for 48 h in a 0.3% TTC (2,3,5-triphenyltetrazolium chloride, Fluka Chemie AG, Buchs, SG, Switzerland) solution at 30 °C in darkness. TTC reacts as H-acceptor in living cells and the resulting 2,3,5-triphenylformazan is red (Larcher 1969). The diameter and the proportion of stained root was measured using a light microscope. Roots crossing a line on the object slide were considered (100–200 roots per plant). A root with any red stain inside the root was regarded as alive. Only roots less than 0.25 mm diameter were included in the viability analysis, because the epidermis of *F. ovina* roots with a diameter above about 0.5 mm was not permeable for TTC. These roots were stained red only near the edge of the cut, where TTC could penetrate the tissue.

Specific root length was measured in October 1993. The length of a small random root sample was measured using the grid-intersection method (Tennant 1975). Root tissue density is expressed as root dry weight per root volume. Root volume was calculated using root diameter distribution and assuming a cylindrical form of the roots and ignoring root hairs (Ryser & Lambers 1995).

Leaf tissue density is expressed as the ratio of leaf dry mass to leaf fresh mass. Assuming a tight relationship between volume and fresh mass of the leaves (Garnier & Laurent 1994), this ratio can be considered

to reflect specific mass of the tissue. Fresh mass of plant parts was measured immediately after separating them and after carefully drying them with soft paper tissue. Before that the plants were kept submerged in water. Dry mass was measured after drying for at least 24 h at 70 °C.

At the final harvest in November 1994 root subsamples were collected from four plants of each species and examined for mycorrhizal colonization after staining with trypan blue.

Results were analysed using one-way ANOVA (SyStat 1992) for each harvest separately. Prior to the analysis, biomass data were submitted to a logarithmic transformation and the percentages to an arcsine transformation.

Results

LIVING BIOMASS

In October 1993, after one growing season, the three species associated with nutrient-rich conditions had a higher biomass than the two species of nutrient-poor conditions (Fig. 1a), although the difference between *A. elatius* and *B. erectus* was negligible. Plants of *D. glomerata* and *H. lanatus* were the largest, those of *F. ovina* the smallest. In March 1994 the species did not

differ significantly from each other in their biomass. In July *B. erectus* had the highest biomass. In November, after two growing seasons, rank order between species from nutrient-poor and nutrient-rich habitats was inverse compared with the harvest 1 year earlier. Now the species associated with nutrient-poor conditions had a higher biomass than the species associated with nutrient-rich sites.

LEAF TURNOVER

Species from nutrient-poor sites always had a lower proportion of dead leaves of the totally produced number of leaves than species from the nutrient-rich sites (Fig. 1b). In November 1994, after two growing seasons, 40% of the leaves produced by *F. ovina* and 65% of those of *B. erectus* were dead. For *A. elatius*, *D. glomerata* and *H. lanatus* this proportion was 74–86%.

ROOT TURNOVER

After one growing season only a very small percentage of roots was dead, 1.3–3.2%, without significant differences among the species (Fig. 1c). In the later harvests differences between the species were

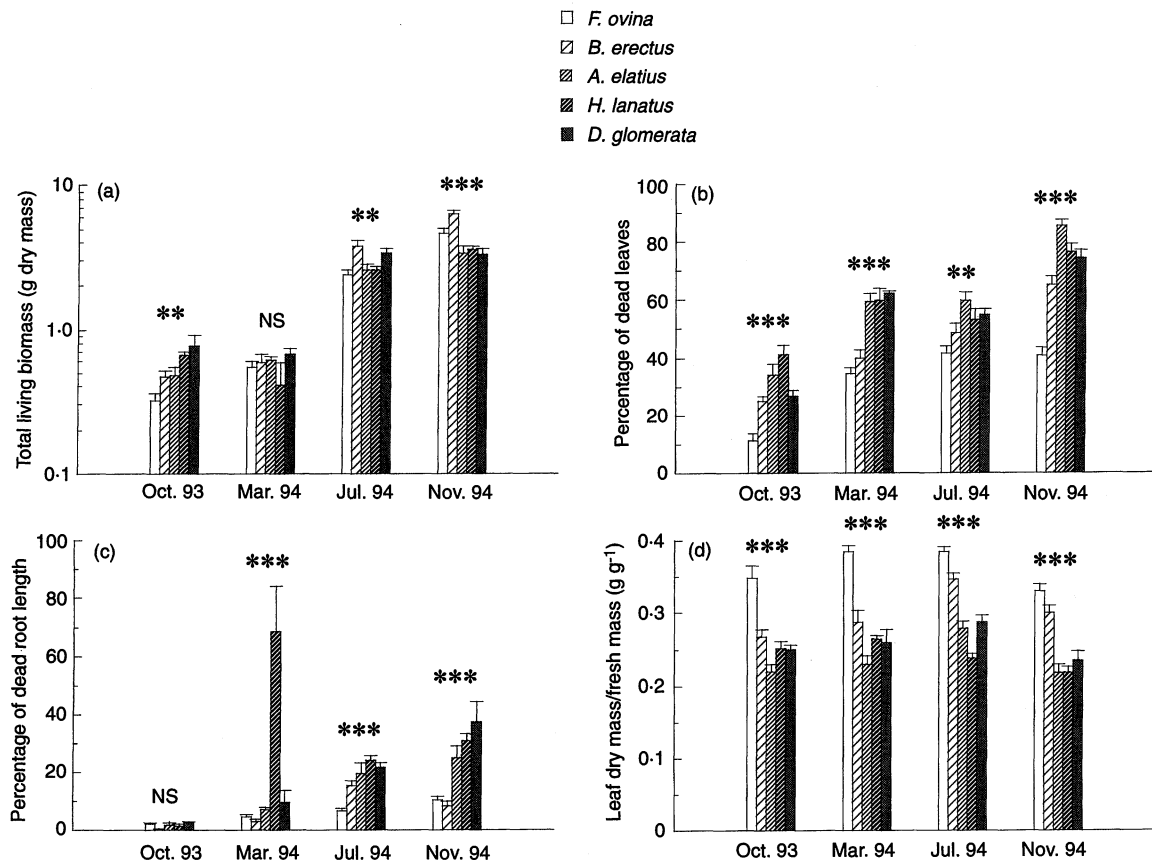


Fig. 1. (a) Total living biomass; (b) percentage of dead leaves of the total number of produced leaves; (c) percentage of dead root length of the total root length; (d) dry mass/fresh mass ratio of leaf blades, for the five grass species at the four harvests (mean \pm 1 SE). Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, NS not significant (one-way ANOVA for each harvest).

significant. In all these harvests, species of nutrient-poor sites, *B. erectus* and *F. ovina*, had a lower percentage of dead root length than the other three species. *Holcus lanatus* roots suffered a high mortality especially during the winter. In March 68% of its roots were dead, whereas for other species this percentage was below 10%. After two growing seasons the percentage of dead roots varied between 8% (*B. erectus*) and 37% (*D. glomerata*).

TISSUE DENSITY

There was a significant interspecific variation in leaf and root tissue density (Figs 1d and 2). The species characteristic of nutrient-poor sites, *B. erectus* and *F. ovina*, had at all harvests a higher tissue density both above- and below-ground than two of the species from nutrient-rich sites, *D. glomerata* and *H. lanatus*. *Arrhenatherum elatius* was an exception to this pattern having the lowest leaf tissue density but the highest root tissue density.

Species with lower tissue density produced a longer root system per plant than those with a high tissue density (Fig. 3). However, both leaf and root life span were reduced by low tissue density. This can be seen in the negative association between the proportion of dead leaves after two growing seasons and leaf tissue density (Fig. 4), and in the negative association between proportion of dead roots after two growing seasons with root tissue density (Fig. 5). Again *A. elatius* was an exception, with a relatively high proportion of dead roots compared with its high root tissue density.

OTHER ROOT CHARACTERISTICS

Root length ratio (RLR) is a product of three components: root length/root volume ratio (root fineness),

root volume/root dry mass ratio (the reciprocal value of root tissue density) and root mass ratio (RMR) (Ryser & Lambers 1995). *Holcus lanatus* and *F. ovina* had the finest roots, that is, the highest values for root length per root volume (Fig. 2). Roots of *A. elatius* and *B. erectus* had the lowest length/volume ratio. Specific root length, influenced by root fineness and tissue density, was highest for *H. lanatus*. Because of the high tissue density, SRL of *F. ovina* was lower despite the similar fineness. *Dactylis glomerata* and *F. ovina* had a significantly lower root mass ratio (RMR) than the other species. Compared with the interspecific variation in root tissue density and root fineness, the variation in biomass allocation to roots was small. Coefficients of variation of the mean values for root volume/root dry mass, root length/root volume and RMR for the species were 33, 22 and 8%, respectively.

After two growing seasons most of the plants were non-mycorrhizal. Infection by arbuscular mycorrhizas was detected only in two individuals of *D. glomerata*.

Discussion

The results emphasize tissue density as a pivotal trait for the ecological behaviour of a species. Tissue density was associated both with growth rate and organ life span. Species with a low tissue density initially grew faster than species with a higher tissue density. However, the latter species had slower leaf and root turnover, and after two growing seasons attained a larger biomass.

Tissue density was the main contributor to interspecific variation in root length ratio, low root tissue density being associated with high RLR. Low tissue density of leaf blades also enables fast-growing species to maintain a larger leaf area ratio even under

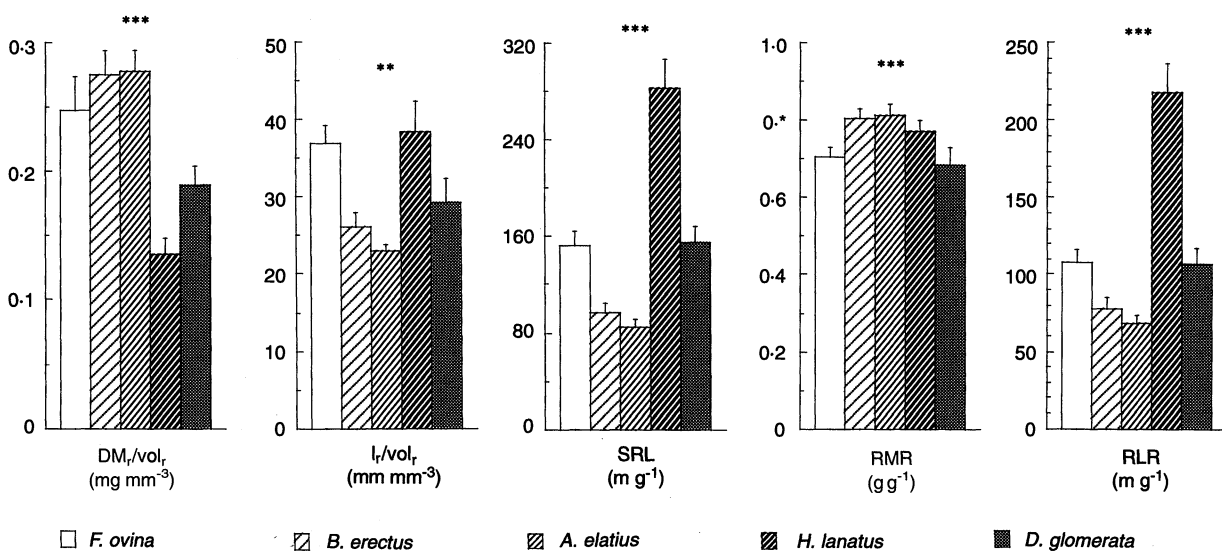


Fig. 2. Dry mass/volume of roots (DM_r/vol_r), root length/root volume (l_r/vol_r), specific root length (SRL), root mass ratio (RMR) and root length ratio (RLR) for the five grass species at the first harvest (November 1993) (mean \pm 1 SE). Significance levels: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, NS not significant (one-way ANOVA).

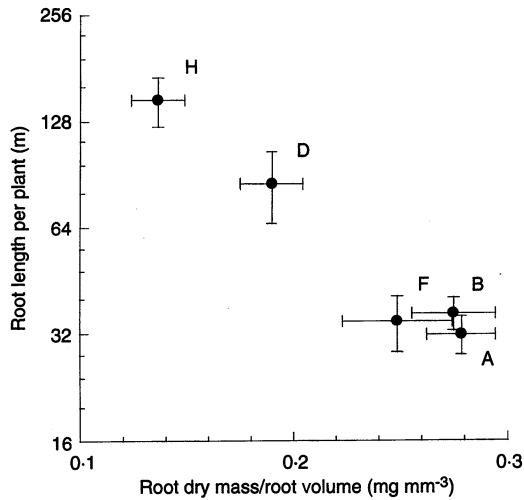


Fig. 3. Root length per plant in October 1993 plotted against root tissue density. Mean \pm 1 SE. *Arrhenatherum elatius* (a), *Bromus erectus* (b), *Dactylis glomerata* (d), *Festuca ovina* (f) and *Holcus lanatus* (h).

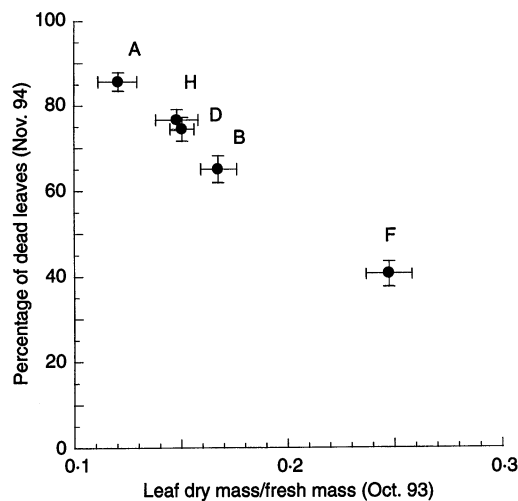


Fig. 4. Percentage of dead leaves of the total number of produced leaves in November 1994 plotted against root tissue density in October 1993. Mean \pm 1 SE. See Fig. 3 for species abbreviations.

low nutrient supply (Poorter *et al.* 1995; Ryser & Lambers 1995), although in such environments they often allocate a larger proportion of their biomass to the roots than do slow-growing species (Berendse & Elberse 1989; Olf, van Andel & Bakker 1990; Poorter *et al.* 1995).

Arrhenatherum elatius was an exception in respect of the interdependence of leaf and root characteristics. Of all the studied species, it had the lowest leaf tissue density but the highest root tissue density. These extreme values were associated with an intermediate growth compared with the other species. The growth of *A. elatius* was seemingly limited by its root structure, possibly a result of unfavourable growth conditions for this species. One reason might be the absence of a mycorrhizal infection. Field-grown *A. elatius* has a lower tissue density than *B. erectus* and

D. glomerata both in leaves and roots (Schläpfer & Ryser 1996).

Tissue density was also associated with organ turnover rate supporting the idea of a general relationship between tissue structure and organ life span (Reich 1993; Schläpfer & Ryser 1996). Reduced palatability (Southwood, Brown & Reader 1986; Coley 1988) and a better protection against adverse environment (Pammenter, Drennan & Smith 1986) may be causes for the longer life span of high density tissue. There might also be a direct functional relationship between tissue density and its longevity. The high tissue density is a result mostly of a high amount of cell wall material, sclerophyllic elements and lignin (Dijkstra & Lambers 1989; Garnier & Laurent 1994; Van Arendonk & Poorter 1994). A lower percentage of air space may also contribute to high density (Koike 1988).

Construction costs are usually expressed per g dry mass, but costs per functional unit of tissue, that is, leaf area or root length, are besides the amount of invested dry matter also determined by tissue density and organ form. As the production costs per mass unit dry matter are similar for fast- and slow-growing species (Poorter & Bergkotte 1992; Poorter 1994), a higher water content makes the tissue of fast-growing species cheaper per unit fresh mass or volume.

Williams, Field & Mooney (1989) reject the hypothesis that leaf longevity is positively related to leaf construction costs but find a positive relation between leaf longevity and the ratio of leaf construction costs ($\text{g CO}_2/\text{g leaf}$) to daily carbon gain ($\text{g CO}_2/(\text{g leaf} \times \text{day})$). An increase in this ratio is most likely to be a result of decreasing tissue density (Dijkstra & Lambers 1989; Reich *et al.* 1991; Gower *et al.* 1993), indicating that their data would also show a positive relationship between leaf longevity and construction costs expressed on a basis that includes tissue density.

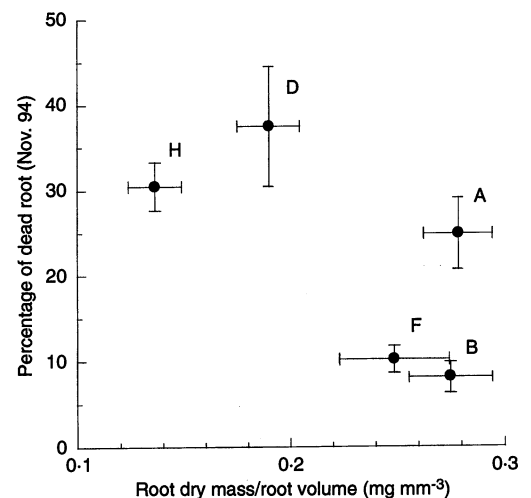


Fig. 5. Percentage of dead root length of the total root length in November 1994 plotted against root tissue density in October 1993. Mean \pm 1 SE. See Fig 3 for species abbreviations.

The lower final biomass of the species which initially grow faster, associated with their fast leaf and root turnover, supports the model of Aerts & van der Peijl (1993). According to this model, species with a high nutrient productivity initially grow faster but at low nutrient supply those species with a high mean residence time of nutrients eventually attain greater biomass. High nutrient productivity is associated with a high inherent RGR (Poorter, Remkes & Lambers 1990; Van der Werf *et al.* 1993) and fast-growing species are also more efficient in recycling nutrients. However, a long organ life span is more important for the total nutrient economy (Aerts 1990; Escudero *et al.* 1992). Mean residence time for nutrients has been shown to correlate with organ longevity in *Carex* species (Aerts & de Caluwe 1995).

In the present work proportions of dead leaves and dead root length were used to conclude interspecific differences in leaf and root life spans. Decomposition of dead leaves and roots would result in an overestimation of life spans. For the leaves this possibility was made less likely by also collecting dead leaves during the experiment, for roots this could not be done. However, if plant parts were lost owing to decomposition, the proportion lost would most likely have been larger for the fast-growing species. Organs of these species had a higher water content and they are known to contain less lignin and hemicellulose, and more organic N-compounds (Poorter & Bergkotte 1992; Van Arendonk & Poorter 1994). These characteristics correlate with a fast litter decomposition (Van Cleve 1974; Pastor, Stillwell & Tilman 1987; Enriquez, Duarte & Sand-Jensen 1993). In case of losses owing to decomposition, the interspecific differences in turnover would be even larger than was observed.

The results presented here suggest that tissue structure is an inherent constraint that prevents the simultaneous maximization of nutrient acquisition and nutrient conservation. The long-term disadvantage of a high growth rate under low nutrient conditions can thus be explained by the short life span of the low density tissue that is necessary for a rapid leaf and root expansion. Species that are superior in resource acquisition are therefore, in the long term, inferior to species with a lower growth rate but a longer organ life span, if nutrient availability is too low to compensate for these losses.

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