Oecologia (1990) 83 : 553-559

Oecologia

Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate

Hendrik Poorter and Carlo Remkes

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

Received August 8, 1989 / Accepted in revised form February 9, 1990

Summary. Which factors cause fast-growing plant species to achieve a higher relative growth rate than slow-growing ones? To answer this question 24 wild species were grown from seed in a growth chamber under conditions of optimal nutrient supply and a growth analysis was carried out. Mean relative growth rate, corrected for possible ontogenetic drift, ranged from 113 to 365 mg g^{-1} day^{-1}. Net assimilation rate, the increase in plant dry weight per unit leaf area and unit time, varied two-fold between species but no correlation with relative growth rate was found. The correlation between leaf area ratio, the ratio between total leaf area and total plant weight, and relative growth rate was very high. This positive correlation was mainly due to the specific leaf area, the ratio between leaf area and leaf weight, and to a lesser extent caused by the leaf weight ratio, the fraction of plant biomass allocated to the leaves. Differences in relative growth rate under conditions of optimum nutrient supply were correlated with the soil fertility in the natural habitat of these species. It is postulated that natural selection in a nutrient-rich environment has favoured species with a high specific leaf area and a high leaf weight ratio, and consequently a high leaf area ratio, whereas selection in nutrient-poor habitats has led to species with an inherently low specific leaf area and a higher fraction of root mass, and thus a low leaf area ratio.

Key words: Interspecific variation - Leaf area ratio - Net assimilation rate - Relative growth rate - Specific leaf area

Plant species may differ considerably in biomass production. This can be caused by differences in seed weight, in the length of the growing period or may be related to environmental conditions. In addition, the maximum relative growth rate (RGR), the dry weight increase per unit of biomass and per unit of time under optimal conditions, may vary between species. The most extensive study on interspecific variation in RGR is that of Grime and Hunt (1975), who compared 130 herbaceous annuals and perennials and tree seedlings, all from a local flora. Although all species were grown under uniform and more or less optimal conditions, there was a large variation in growth rate, RGR ranging from 31 to 386 mg g^{-1} day^{-1}. Partly on the basis of this growth chamber experiment, Grime and Hunt (1975) and Grime (1979) distinguished 3 different groups of species: species from ruderal habitats (ruderals) or places with intensive competition (competitors), both with a high potential RGR, and species growing in various adverse environments (stress-tolerators), with a low potential RGR.

The ecological advantage of a high RGR may seem clear: Fast growth results in the rapid occupation of a large space, advantageous in competitive situations (Grime and Hunt 1975). A high RGR may also facilitate a rapid completion of the life cycle of a plant, essential for ruderals. But what is the survival value of slow growth? Several hypotheses have been offered, most of which are questionable (cf. Poorter 1989b).

An alternative to the above-mentioned explanations is that not RGR per se has been the target of natural selection, but rather characteristics linked with or underlying RGR (Grime and Hunt 1975; Chapin 1980; Lambers and Dijkstra 1987). This requires insight into the physiological functioning of a plant. Which factors cause fast-growing species, or genotypes thereof, to grow faster than slow-growing ones? How important are differences in the rate of photosynthesis and respiration, in biomass allocation, in morphology and in chemical composition to explain the observed variation in RGR? A growth analysis (Evans 1972) will provide a first clue to answer these questions. The RGR is the product of NAR (net assimilation rate) and LAR (leaf area ratio), where NAR is largely the net result of carbon gain (photosynthesis) and carbon losses (respiration, exudation, volatilization) expressed per unit leaf area. The LAR is the ratio of leaf area and total plant weight and is

Offprint requests to: H. Poorter

the product of a morphological component (SLA, specific leaf area), the ratio of leaf area and leaf weight, and the leaf weight ratio (LWR), indicating the fraction of total plant weight allocated to the leaves.

Lambers and Dijkstra (1987), reviewing the literature on inherent differences in RGR, did not find an unequivocal answer to the question which factors determine inherent differences in RGR. In experiments of Eagles (1967) and Pons (1977) growth differences between species could be ascribed totally to a difference in NAR, whereas Higgs and James (1969), Smeets and Garretsen (1986) and Dijkstra and Lambers (1986) found interspecific variation in RGR to be due to differences in LAR. In other cases both parameters were associated with the inherent difference in RGR (Jarvis and Jarvis 1964; Corré 1983).

A problem in the interpretation of these growth analyses is that mostly only 2 to 4 (sub)species have been investigated and sometimes only a small difference in RGR was found. Thus, overall trends may be obscured by variation caused by one anomalous species. Moreover, in some cases plants were grown under uncontrolled conditions or roots were not included in the harvests. To obtain more insight in the causation of interspecific differences in growth rate, a comparison including more species and covering a wider range of RGR's is needed. This paper presents data on the growth of 24 local non-woody species, all with a C_3 type of photosynthesis and grown under constant conditions. We analyze the importance of the growth parameters NAR, LAR, SLA and LWR in explaining interspecific variation in RGR and correlate these findings with the performance of fast- and slow-growing species under natural conditions.

Materials and methods

Growth of the plants. For the experiment, 24 species common in Western Europe were used, all non-woody plants with a C_3 type of photosynthesis. Table 1 lists these species, together with their main habitat. Nomenclature is according to Van der Meijden et al. (1987). Seeds of the species were collected in the field, except *Holcus lanatus* (commercially propagated), *Lolium perenne* (population GL72 in the experiments of Wilson (1982)), and *Plantago major* ssp. *major* (line Gl in the experiments of Van Dijk and Van Delden (1981)). If necessary the seeds were stratified prior to germination. Germination occurred in petri dishes in a growth cabinet (day: 12 h, 25° C; night: 12 h, 15° C). After germination the seedlings were planted in river sand moistened with half strength of the following standard nutrient solution: 795 µM KNO_3, 603 µM $Ca(NO_3)_2$, 270 µM $MgSO_4$, 190 µM KH_2PO_4, 41 µM Fe-EDTA, 20 µM H_3BO_3, 2 µM $MnSO_4$, 0.85 µM $ZnSO_4$, 0.25 µM Na_2MoO_4 and 0.15 µM $CuSO_4$. The seedlings were placed in a growth room with the following conditions: Day: 14 h, quantum flux density at mean plant height 315 ± 30 µmol m^{-2} s^{-1} (photosynthetically active radiation), temperature 20 ± 0.5°C, relative humidity ca 70%. Night: 10 h, temperature 20 ± 0.5° C. Light was provided by fluorescent lamps (Philips TL-33-RS, 215 W) and incandescent bulbs (Philips, 40 W) in a ratio of 4:1. To avoid stunted growth, the incandescent lamps also burnt during the first half hour of the night period.

When the root length of the seedlings was ca 40 mm, the seedlings were transferred to 33 1 containers with aerated nutrient solu-

Table 1. Species used in the experiment, life form and main habitat

Species	Life form	Habitat
Monocots :		
Brachypodium pinnatum (L.) Beauv.	perennial	low-productive calcareous grassland
Briza media L.	perennial	mesic low-productive grassland
Corynephorus canescens (L.) Beauv,	perennial	non-calcareous drift-sand
Cynosurus cristatus L.	perennial	haymeadow
Dactylis glomerata L.	perennial	nutrient-rich haymeadows, ruderal
Deschampsia flexuosa (L.) Trin.	perennial	grassheath, forest on sandy soil
Festuca ovina L.	perennial	on acid, dry, nutrient-poor sand
Holcus lanatus L.	perennial	nutrient-rich grassland, ruderal
Lolium perenne L.	perennial	nutrient-rich grassland
Phleum pratense L.	perennial	haymeadow on sand
Poa annua L.	annual	disturbed and trampled places
Dicots :		
Anthriscus sylvestris (L.) Hoffm.	perennial	open forest, roadside on clay
Galinsoga parviflora Cav.	annual	ruderal, segatal
Geum *urbanum* L.	perennial	slightly disturbed nutrient-rich forest
Hypericum perforatum L.	perennial	dry ruderal places
Lysimachia vulgaris L.	perennial	fens, marshes
Origanum vulgare L.	perennial	calcareous grassland
Pimpinella saxifraga L.	perennial	low-productive calcareous grassland
Plantago major ssp. *major* L.	perennial	disturbed and trampled places
Rumex crispus L.	perennial	ruderal places
Scrophularia nodosa L.	perennial	mesic, deciduous forest
Taraxacum officinale Weber	perennial	grassland
Trifolium repens L.	perennial	frequently trampled or mown grassland
Urtica dioica L.	perennial	ruderal places, nutrient-rich forest

tion. The first 3 days the nutrient solution was half strength, thereafter full strength of the above-mentioned standard medium. The pH of the solution was regularly adjusted to 5.8 with H_2SO_4.

To prevent nutrient depletion, the solution was renewed each week. To minimize mutual shading, the number of plants on each container varied between 24 and 4, depending on the size of the plants. Plants were rotated twice a week within the growth room. All species remained vegetative, except *Poa annua, Urtica dioica* and *Galinsoga parviflora,* which started flowering just before the last harvest. None of the species showed dead leaves during the experiment.

Experimental design. The experiment started when the plants had reached a fresh weight of approx. 100 mg (day 0). Harvests were carried out at day 0, 3, 7, 10, 14 and 17. Each day, 8 plants were selected as described by Poorter (1989a) and harvested, except for day 0 when a double harvest was carried out.

Measurements. Three plant parts were discerned: roots, leaf blades and a remaining fraction, which consisted mainly of stem and petioles (dicots) or leaf sheaths (monocots), but occasionally also included flower buds *(Galinsoga, Poa, Urtica)* or stolons *(Lysimachia)*. This third fraction will be termed 'stem' throughout the rest of this paper. At each harvest plants were separated into the three fractions and fresh weight of each fraction as well as the area of the leaf blades were determined. In the case of species with more or less needle-like leaves *(Corynephorus, Deschampsia, Festuca)* total area of the leaf was calculated as: leaf blade length * π * the thickness in the middle of the leaf * a correction factor. This correction factor was determined by measuring the effective light-exposed part of the circumference of leaf sections over the whole leaf using a light microscope. For the other species, leaf area was measured with a leaf area meter (TFDL, Wageningen, The Netherlands). Leaf area is given as half the total area. Dry weights were determined on oven-dried (24 h at 80° C) material. Root length was measured with a root length scanner (Comair, Melbourne, Australia). This apparatus measures the length of roots with a diameter over 0.1 mm.

Statistical analysis. Data were analyzed with the SAS statistical package (Joyner 1985). Differences in RGR were tested as a Species x Time interaction in an analysis of variance with ln-transformed dry weight as dependent variable (Poorter and Lewis 1986). Equations for the time trend of RGR and its components were obtained by a stepwise regression as described by Poorter (1989a). To avoid comparison of species with totally different plant weights, the values of all parameters were calculated over the period the plants had a dry weight ranging from 30-100 mg. These weighted values were obtained by dividing the integral of the polynomial over the period that a species had the above-mentioned range in weight, by that interval. Relations between the several parameters and RGR were tested with linear regression equations.

Results

Growth rates. Plant species differed significantly *($P < 0.001$)* in mean RGR (on a dry weight basis) during the experiment, ranging from 100 mg g^{-1} day^{-1} for *Corynephorus canescens* to 335 mg g^{-1} day^{-1} for *Galinsoga parviflora.* Consequently, total plant weight at the last day of the experiment also varied considerably between species, ranging from 115 mg for *Corynephorus* to 3600 mg for *Galinsoga.* As larger plants tend to have a lower RGR, due to self-shading (e.g. Poorter et al. 1988) or to a larger investment in supporting structures (e.g. Konings et al. 1989), comparison of species which differ in size may obscure possible trends. Therefore, all data presented here are weighted values, calculated

Table 2. Values of RGR (mg g^{-1} day^{-1}), NAR (g m^{-2} day^{-1}), LAR (m^2 kg^{-1}), SLA (m^2 kg^{-1}), LWR (g g^{-1}), SWR ('stem' weight ratio, g g^{-1}) and RWR (root weight ratio, g g^{-1}) for 24 species. All figures are mean values for the time period that the species had a total plant dry weight between 30 and 100 mg

Species	RGR	NAR	LAR	SLA	LWR	SWR	RWR
Brachypodium pinnatum	174	9.0	19.8	40.7	0.49	0.24	0.27
Briza media	157	9.1	17.5	35.1	0.51	0.19	0.30
Corynephorus canescens	113	8.3	14.2	33.1	0.43	0.27	0.31
Cynosurus cristatus	176	11.7	14.7	32.0	0.46	0.16	0.38
Dactylis glomerata	229	10.3	22.4	50.2	0.45	0.22	0.32
Deschampsia flexuosa	135	10.1	13.2	27.6	0.48	0.18	0.34
Festuca ovina	132	10.4	12.9	25.3	0.51	0.20	0.29
Holcus lanatus	268	14.1	19.4	43.7	0.43	0.22	0.34
Lolium perenne	214	11.5	19.5	38.8	0.50	0.20	0.31
Phleum pratense	227	8.9	27.2	47.8	0.54	0.17	0.30
Poa annua	272	11.8	23.9	46.7	0.50	0.21	0.29
Anthriscus sylvestris	239	11.5	21.2	40.2	0.53	0.19	0.28
Galinsoga parviflora	365	10.5	35.9	55.5	0.64	0.13	0.23
Geum urbanum	224	8.6	27.1	41.5	0.65	0.13	0.21
Hypericum perforatum	205	7.4	27.3	49.5	0.55	0.11	0.34
Lysimachia vulgaris	223	8.4	27.7	42.2	0.66	0.18	0.16
Origanum vulgare	203	8.0	25.2	40.6	0.62	0.11	0.27
Pimpinella saxifraga	171	10.2	16.5	31.2	0.54	0.13	0.33
Plantago major	240	11.8	21.1	32.8	0.64	0.12	0.24
Rumex crispus	327	10.7	32.3	49.3	0.63	0.12	0.26
Scrophularia nodosa	302	11.1	28.6	44.3	0.64	0.09	0.26
Taraxacum officinale	260	9.9	27.3	44.1	0.60	0.07	0.32
Trifolium repens	206	12.1	17.1	40.4	0.44	0.28	0.28
Urtica dioica	317	10.1	33.0	51.3	0.64	0.14	0.22

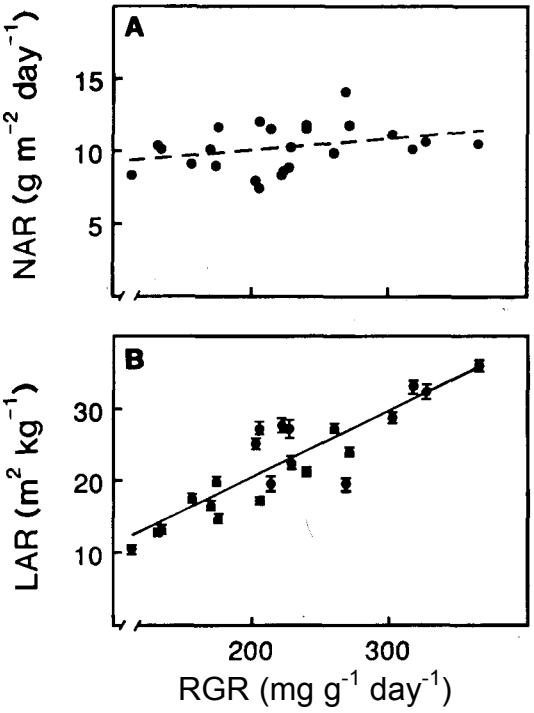

Fig. 1. A Mean NAR and **B** mean LAR for 24 species plotted against mean RGR during the time that plants had a dry weight between 30-100 mg. For calculation of the mean values see Material and methods. Error bars indicate the mean SE at the 6 harvest days (n=8). The continuous straight line indicates a significant linear regression ($P < 0.05$) of this parameter with RGR, the broken line a non-significant relation

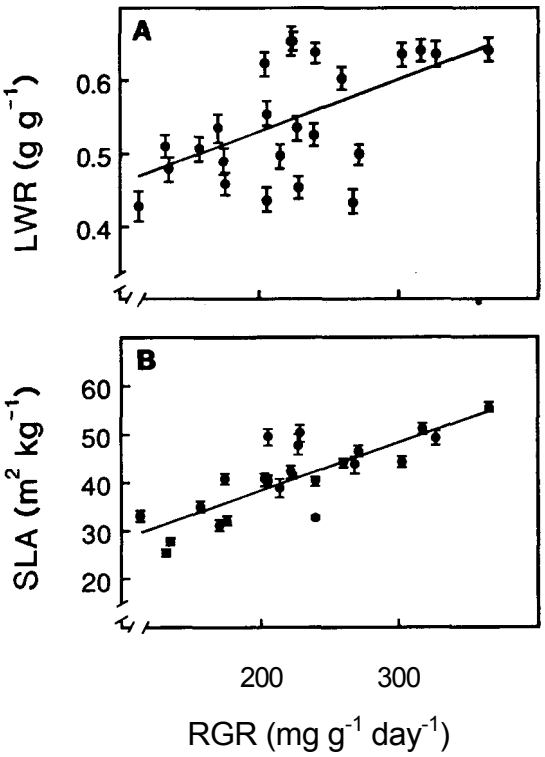

Fig. 2. A Mean LWR and **B** mean SLA plotted against mean RGR for the 24 species. Error bars indicate the mean SE at the 6 harvest days (n = 8)

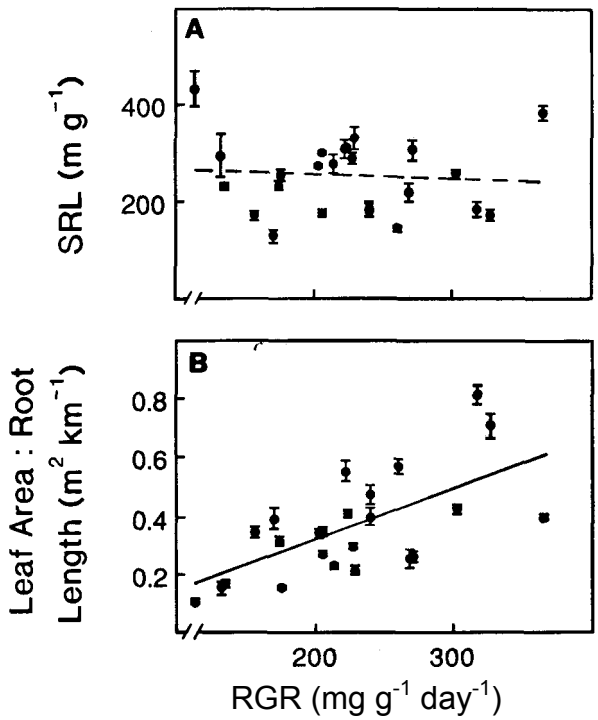

Fig. 3. A Specific root length and **B** leaf area: root length ratio plotted against mean RGR for the 24 species. Mean values ±SE (n = 8)

over the period that a species had a total dry weight between 30 and 100 mg. These weighted values of the RGR (Table 2) showed a more than three-fold difference between the slowest growing species (113 mg g^{-1} day^{-1}) and the fastest growing one (365 mg g^{-1} day^{-1}).

Growth parameters. The NAR varied two-fold between species, ranging from 7.4 for *Hypericum perforatum* to 14.1 g m^{-2} day^{-1} for *Holcus lanatus.* A slightly positive correlation between NAR and RGR was found (Fig. 1 A), but this trend was not statistically significant *(*$0.10 < P < 0.15$*).* The LAR showed a quite different pattern, as the fastest growing species had an almost three times higher LAR than the slowest growing ones (Fig. 1B, $P < 0.001$).

The LAR is a composed parameter, partly determined by allocation (LWR), partly by leaf morphology (SLA). Both LWR and SLA contributed significantly to the positive correlation of LAR and RGR. However, the correlation of LWR and RGR was rather weak (Fig. 2A, $P < 0.01$). The SLA appeared to be the factor correlated best with RGR (Fig. 2B, $P < 0.001$).

When RGR and the different growth parameters were calculated as mean values over the whole experimental period the same relationships appeared as for plants in the 30 to 100 mg range.

Specific root length (total root length divided by total root weight) showed no clear correlation with RGR (Fig. 3 A, $P > 0.65$). The leaf area: root length ratio varied three-fold and increased with increasing RGR (Fig. 3B, $P < 0.001$).

Discussion

A large variation in RGR between species was observed. As slow-growing species had a fairly constant RGR during the experiment and fast-growing species attained the dry weight range of 30-100 mg in an early stage, the RGR values in Table 2 are close (on average within 10%) to the maximum RGR as defined by Grime and Hunt (1975). In general a good correlation exists between their RGR values and the RGR's in this experiment for species used in both studies. Exceptions were *Poa annua,* which we found to grow much slower, and *Anthriscus sylvestris, Geum urbanum* and *Taraxacum officinale,* which grew over 100 mg g^{-1} day^{-1} faster in our experiment. Genotypic variation in RGR may be an explanation for the observed differences (cf. Roetman and Sterk 1986).

How is the high RGR of fast growing species achieved? Although there is variation in NAR, no clear correlation between NAR and RGR was found (Fig. 1A). Apparently, differences in the carbon economy, the balance of photosynthesis and respiration expressed per unit leaf area, are not of overriding importance in explaining variation in RGR. The correlation between LAR and RGR on the other hand was extremely tight (Fig. 1B). Thus, the more a plant invests in leaf area, the higher the total carbon gain and the faster growth will be. This was, amongst others, also found in studies on *Taraxacum* microspecies (Roetman and Sterk 1986), for two *Plantago* subspecies (Dijkstra and Lambers 1986) and for eight wild species (Poorter 1989b). Potter and Jones (1977) claimed that leaf area partitioning (LAP, the ratio between newly formed leaf area and new plant weight) is the important factor explaining genotypic differences in RGR. However, if plant growth is approximately in a steady state, as expected in the constant environment used by Potter and Jones, LAP equals LAR. In other cases no correlation at all may be found between LAP and RGR (Poorter 1989b).

It seems remarkable that RGR is only significantly correlated with LAR and not with NAR, as RGR is the product of NAR and LAR. To obtain more insight in the relative contribution of both factors, a pathway analysis was performed on these three parameters (Fig. 4). The standardized regression coefficients allow an estimation of how a change of one unit standard deviation of one variable affects another variable (also expressed in units standard deviation), independent of other variables. Taking all species together, the effect of NAR on RGR was 0.51 ($P < 0.001$) and the effect of LAR was 0.96 ($P < 0.001$). Apparently, increasing NAR itself has a positive influence on RGR. However, due to a negative correlation between NAR and LAR, an increase in NAR will also decrease LAR, and this in turn will have a negative effect, thus masking the correlation between NAR and RGR. Konings (1989) and Poorter (1989b) offer two explanations for the negative correlation between NAR and LAR. Firstly, an increase in NAR may require an increased rate of photosynthesis, which can be realized by extra investment in the photosynthetic apparatus, thus decreasing SLA. Alternatively, the balance between the amount of roots and the amount of leaf area could influence the water status of the leaves and hence the rate of photosynthesis. As the negative correlation between NAR and LAR is mainly caused by a negative correlation between NAR and LWR, we expect the second explanation to be the most probable.

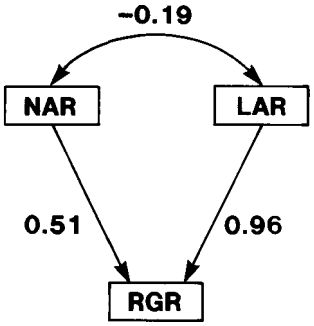

Fig. 4. Pathway analysis for the relation between mean NAR, LAR and RGR for the 24 species. For further explanation, see Results

Having shown that LAR is important in explaining differences in RGR, a further analysis of this factor is imperative. Allocation of dry matter to leaves (LWR) is higher in fast-growing species, but the correlation with RGR is not very tight. There is a distinction between monocots and dicots with regard to this aspect: fast-growing dicots invest relatively more in leaves and less in stem and roots than slow-growing dicots. For monocots no correlation is found between allocation pattern and RGR. This agrees with the results of Elias and Chadwick (1979), who grew 28 cultivars of 13 grass species, but contradicts the finding of Hunt et al. (1987) who found that fast-growing grasses allocate relatively more to roots. Both in the experiments of Elias and Chadwick and of Hunt et al. plants were grown in 0.5 1 pots with nutrient applications. A possible explanation for the observed differences may be that fast-growing, large plants easily become nutrient-limited between two fertilizer applications, if nutrient additions are not frequently enough and consequently will invest more in root growth (Brouwer 1963). In a well-stirred regularly renewed nutrient solution as used in the present experiment, nutrient supply is continuously at a high level and depletion will not occur.

Specific leaf area appeared to be the most important factor explaining variation in RGR: species with a high SLA had the highest RGR. Apparently fast growers produce leaves with a low investment in biomass. Differences in SLA can be ascribed either to morphological factors (thickness of the leaves, vein structure) or to the chemical composition of leaf biomass (cf. Dijkstra 1989). These factors will be discussed in Poorter and Bergkotte (unpublished work).

The balance between shoot and root can be derived from the LWR or the shoot to root ratio (Brouwer 1963), or better the leaf area: root length ratio (Körner and Renhardt 1987). This ratio depends both on leaf morphology, biomass allocation and the specific root length (SRL, total root length divided by total root dry

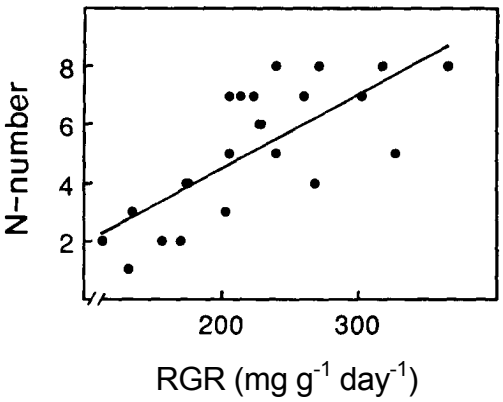

Fig. 5. N-number of Ellenberg (1979), indicating the nitrogen availability in the natural habitat of a species plotted against mean RGR for the 24 investigated species

weight). No clear correlation between RGR and SRL was found (Fig.3 A). This is in contrast with data of Boot (1989), who found that slow-growing grasses *(Corynephorus canescens, Festuca ovina)* had a much higher SRL than faster growing species *(Dactylis glomerata, Holcus lanatus)*. This discrepancy is most likely caused by a difference in the method used to determine root length. The apparatus used in the present experiment does not detect roots with a diameter less than 0.1 mm, whereas the grid-intersection method used by Boot (1989) avoids this flaw. However, a negative correlation between SRL and RGR would only strengthen the positive relationship between the leaf area: root length ratio and the RGR (Fig. 3 B). From this relationship we conclude that fast-growing species are more oriented to maximize shoot functioning, whereas slow growers tend to maximize root functioning.

What might be the ecological implications of these results? There is a positiv correlation between the potential RGR of these 24 species and the nitrogen availability in their natural habitat (Fig. 5), in accordance with the conclusion of Grime and Hunt (1975). In our opinion these differences in RGR are, at least partly, caused by the specific demands imposed to plants in different environments. Let us consider a nutrient-poor and nutrient-rich milieu, assuming for the sake of simplicity a purely herbaceous vegetation with a low standing crop at the beginning of the growing season. In the nutrient-rich environment a dense vegetation with a high leaf area index will develop. To maximize light interception in such an environment, with a strong competition for light, species have to allocate relatively much to above-ground biomass (high LWR, low root weight ratio). Moreover, new strata of leaves develop very fast and leaves are fully illuminated only during a short period of the growing season. In such cases, where fast development is more important then a physiological functioning for a long time, 'cheap' leaves with a high light-intercepting area per unit carbon invested (high SLA) should be produced.

In an infertile environment, with a lower productivity, competition for light will be less severe, whereas root competition will gain importance (Tilman 1984). In these cases a shift in allocation from above- to below-ground biomass is expected (high root weight ratio, low LWR). Moreover, it has been shown that in such an environment the conservation of previously captured nutrients is as important as acquisition of new minerals (Berendse and Aerts 1987; Aerts 1989). This can be achieved by a high leaf longevity (Monk 1966; Small 1972; Chapin 1980). However, a high leaf longevity can only be realized if a plant is protected against detrimental biotic and abiotic factors like herbivory, fungal infection, cold, drought, nutrient leakage, etc. This implies extra investment in lignin, phenolics and other types of quantitative secondary compounds, leaf hairs, cuticular waxes, cell membrane lipids, etc., all of which result in leaves with a higher construction cost per unit leaf area (Merino et al. 1984) and also a lower SLA. A further elaboration of this contention is given in Poorter (1989 b).

Conclusions

Interspecific variation in potential relative growth rate between herbaceous C_3 species is largely caused by the growth parameter SLA and to a lesser extent by the LWR. No correlation between RGR and NAR was found. The differences in growth rate reflect the variation in productivity in the natural habitat of these wild species.

Acknowledgements. We thank Hans Lambers, Adrie van der Werf, Rien Aerts, Arjen Biere and Hans de Kroon for their valuable contributions during the course of the research presented here and critical remarks on the manuscript.

References

Aerts R (1989) Nitrogen-use-efficiency in relation to nitrogen availability and plant community composition. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants, SPB Academic Publishing, The Hague, pp 285-297

Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? Funct Ecol 1 : 293-296

Boot RGA (1989) The significance of size and morphology of root systems for nutrient acquisition and competition. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants, SPB Academic Publishing, The Hague, pp 299-311

Brouwer R (1963) Some aspects of the equilibrium between overground and underground plant parts. Meded Inst Biol Scheik Onderz Landb Gewas 213 : 31-39

Chapin FS (1980) The mineral nutrition of wild plants. Annu Rev Ecol Syst 11 : 233-260

Corré WJ (1983) Growth and morphogenesis of sun and shade plants. III. The combined effects of light intensity and nutrient supply. Acta Bot Neerl 32 : 277-294

Dijkstra P (1989) Cause and effect of differences in specific leaf area. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and Consequences of Variation in Growth Rate and Productivity in Plants, SPB Academic Publishing, The Hague, pp 125-140

Dijkstra P, Lambers H (1986) Photosynthesis and respiration of

two inbred lines of *Plantago major* L. differing in relative growth rate. In: Marcelle R, Clijsters H, Van Poucke M (eds) Biological Control of Photosynthesis, Martinus Nijhoff Publishers, The Hague, pp 251-255

Eagles CF (1967) The effect of temperature on vegetative growth in climatic races of *Dactylis glomerata* in controlled environments. Ann Bot 31 : 31-39

Elias CO, Chadwick MJ (1979) Growth characteristics of grass and legume cultivars and their potential for land reclamation. J Appl Ecol 16 : 537-544

Ellenberg HE (1979) Zeigerwerte der Gefässpflanze Mitteleuropas. Scripta Geobotanica 9

Evans GC (1972) The Quantitative Analysis of Plant Growth. Blackwell Scientific Publications, Oxford

Grime JP (1979) Plant Strategies & Vegetation processes. John Wiley & Sons, Chichester

Grime JP, Hunt R (1975) Relative growth-rate: its range and adaptive significance in a local flora. J Ecol 63 : 393-422

Higgs DEB, James DB (1969) Comparative studies on the biology of upland grasses. I. Rate of dry matter production and its control in four grass species. J Ecol 57 : 553-563

Hunt R, Nicholls AO, Fathy SA (1987) Growth and root-shoot partitioning in eighteen British grasses. Oikos 50 : 53-59

Jarvis PG, Jarvis MS (1964) Growth rates of woody plants. Physiol Plant 17 : 654-666

Joyner SP (1985) SAS/STAT Guide for Personal Computers, Version 6 Edition. SAS Institute Inc, Cary, NC. pp 269-336

Körner C, Renhardt U (1987) Dry matter partitioning and root length/leaf area ratios in herbaceous perennial plants with diverse altitude distribution. Oecologia 74 : 411-418

Konings H (1989) Physiological and morphological differences between plants with a high NAR or a high LAR as related to environmental conditions. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants, SPB Academic Publishing, The Hague, pp 101-123

Konings H, Koot E, Tijman-De Wolf A (1989) Growth characteristics, nutrient allocation and photosynthesis of *Carex* species from floating fens. Oecologia 80 : 111-121

Lambers H, Dijkstra P (1987) A physiological analysis of genotypic variation in relative growth rate: Can growth rate confer ecological advantage? In: Van Andel J, Bakker JP, Snaydon RW (eds) Disturbance in Grasslands, Junk Publishers, Dordrecht, pp 237-252

Merino J, Field C, Mooney HA (1984) Construction and maintenance costs of mediterranean-climate evergreen and deciduous leaves. II. Biochemical pathway analysis. Acta Oecol/Oecol Plant 5 : 211-229

Monk CD (1966) An ecological significance of evergreens. Ecology 47 : 504-505

Pons TL (1977) An ecophysiological study in the field layer of ash coppice. II. Experiments with *Geum urbanum* and *Cirsium palustre* in different light intensities. Acta Bot Neerl 26 : 251-263

Poorter H (1989a) Growth analysis: towards a synthesis of the classical and the functional approach. Physiol Plant 75 : 237-244

Poorter H (1989b) Interspecific differences in relative growth rate: On ecological causes and physiological consequences. In: Lambers H, Cambridge ML, Konings H, Pons TL (eds) Causes and Consequences of Variation in Growth Rate and Productivity in Plants, SPB Academic Publishing, The Hague, pp 45-68

Poorter H, Lewis C (1986) Testing differences in RGR: a method avoiding curve fitting and pairing. Physiol Plant 67 : 223-226

Poorter H, Pot CS, Lambers H (1988) The effect of an elevated CO_2 concentration on growth, photosynthesis and respiration of *Plantago major,* a rosette plant. Physiol Plant 73 : 553-559

Potter JR, Jones JW (1977) Leaf area partitioning as an important factor in growth. Plant Physiol 59 : 10-14

Roetman E, Sterk A A (1986) Growth of microspecies of different sections of *Taraxacum* in climatic chambers. Acta Bot Neerl 35 : 5-22

Small E (1972) Photosynthetic rates in relation to nitrogen recycling as an adaptation to nutrient deficiency in peat bog plants. Can J Bot 50 : 2227-2233

Smeets L, Garretsen F (1986) Growth analyses of tomato genotypes grown under low night temperatures and low light intensity. Euphytica 35 : 701-715

Tilman GD (1984) Plant dominance along an experimental nutrient gradient. Ecology 65 : 1445-1453

Van der Meijden R, Weeda EJ, Adema FACB, De Joncheere GJ (1987) Flora van Nederland. Wolters-Noordhoff, Groningen

Van Dijk H, Van Delden W (1981) Genetic variability in *Plantago* species in relation to their ecology. Part 1: Genetic analysis of the allozyme variation in *P. major* subspecies. Theor Appl Genet 60 : 285-290

Wilson D (1982) Response to selection for dark respiration rate of mature leaves in *Lolium perenne* and its effects on growth of young plants and simulated swards. Ann Bot 49 : 303-312