

INTERSPECIFIC VARIATION IN RELATIVE GROWTH RATE: ON ECOLOGICAL CAUSES AND PHYSIOLOGICAL CONSEQUENCES

HENDRIK POORTER

*Department of Plant Ecology, University of Utrecht, Lange Nieuwstraat 106,
3512 PN Utrecht, The Netherlands*

Abstract

Large interspecific differences exist in the potential relative growth rate (RGR) of plants. Which physiological, morphological, chemical and/or allocation-related factors explain this variation in growth rate? In a first experiment growth of eight herbaceous wild species was analysed, varying twofold in RGR. No correlation was found between RGR and the rate of photosynthesis per unit leaf area. The growth parameter net assimilation rate (NAR) was even negatively correlated with RGR. Biomass allocation to the leaves (leaf weight ratio, LWR) and the ratio between leaf area and leaf weight (specific leaf area, SLA) were positively correlated with RGR. There was an even stronger correlation between RGR and the ratio of total leaf area to total plant weight (leaf area ratio, LAR). RGR also correlated positively with the photosynthetic nitrogen use efficiency and the nitrogen productivity. The paramount importance of LAR and SLA in determining potential RGR was confirmed in a review of 60 prior publications. In general an inherently higher RGR was explained for 80 - 90% by a higher LAR and only for 10 - 20% by a higher NAR. Exceptions were found for shade species, trees and C₄ species. The first two groups have a low potential RGR caused by a distinctly lower NAR. The low NAR of shade species in comparison with sun species is a consequence of their low maximum rate of photosynthesis. Trees have a lower NAR than herbaceous species, at least partly caused by a difference in chemical composition. C₄ plants mostly showed higher values for NAR than C₃ plants.

Differences in potential RGR between species are habitat related. Fast growing species are found in nutrient-rich environments with a relatively high supply of light and water. Inherently slow growing species can be found in all kinds of adverse environments. It is postulated that differences in RGR are a consequence of selection for traits underlying RGR, caused by the specific demands of a plant's environment. In a highly productive habitat with a dense canopy, a high LWR and a high SLA will improve the competitive ability of a species. Adaptation to an adverse environment, where physiological integrity of organs during a longer time is important will often decrease LWR and/or SLA. Differences in NAR are thought to be only of secondary importance.

1. Introduction

Plant species may differ considerably in relative growth rate (RGR). This may be caused by habitat-related variation in abiotic factors, like temperature, water, light and nutrients, or by biotic factors like competition, diseases or grazing pressure. But even when grown under identical, close to optimal conditions free of interference from other organisms, large interspecific variation in RGR exists. This phenomenon has been observed both for crop species (Blackman 1919, Blackman & Wilson 1951) and for wild species (Higgs & James 1969, Nicholls & Calder 1973, Shipley & Keddy 1988). The most extensive investigation in this field is that of Grime & Hunt (1975). They compared 130 wild species with respect to their potential RGR. Large differences between species were found, ranging from less than 50 mg g⁻¹ day⁻¹ for some tree seedlings up to more than 300 mg g⁻¹ day⁻¹ for several herbaceous species.

What could be the ecological significance of the observed differences in RGR?

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Grime (1979) classified the slow growers as 'stress-tolerators' and the fast growing species as either 'competitors' or 'ruderals'. In the case of competitors, the advantage of a high RGR seems clear. Due to a high RGR a plant will rapidly increase in size and may occupy a larger space, both below and above ground. Consequently, such a plant has the opportunity to acquire a larger share in limiting resources like light, nutrients or water than a slower growing individual. Ruderals may also profit from a high RGR, as they occur in disturbed habitats, and must complete their life cycle over a short and uncertain period. This completion may be facilitated by a fast vegetative growth phase.

The benefit of a low growth rate is less clear. Why do plants from very cold, dry, high-altitude or nutrient-poor habitats have such a low potential RGR? Grime & Hunt (1975) and Chapin (1980) suggest several possibilities. Firstly, slow growing species have low demands and are therefore less likely to exhaust limiting resources. Secondly, a species with a low RGR functions closer to its optimum growth rate in an adverse climate than a fast growing species. And thirdly, slow growing species might have lower rates of incorporation of photosynthates and minerals into structural material, thus building reserves for later growth. An alternative hypothesis concerning the ecological significance of a low RGR was suggested by Lambers & Dijkstra (1987). They postulated that RGR itself is not the target of selection under unfavourable conditions, but one of the components of RGR. A low value of one of the factors underlying RGR would cause these plants to have such a low potential RGR.

In this chapter I first compare different methods of breaking down RGR into components and analyse the importance of these factors in explaining interspecific variation in RGR *per se*. The various hypotheses which have been proposed in the ecological literature to account for the differences in RGR are then evaluated in the light of this analysis.

2. The components of RGR

RGR is defined as the increase in plant weight per unit plant weight (W) already present and per unit time (t):

$$\mathbf{RGR} = \frac{1}{\mathbf{W}} \cdot \frac{d\mathbf{W}}{dt} \quad (1)$$

Several methods exist to break down RGR into smaller components. The most common approach focuses on the carbon economy of the plant. Here RGR is split into a net assimilation rate (NAR) and a leaf area ratio (LAR) (Evans 1972):

$$\mathbf{RGR} = \mathbf{NAR} * \mathbf{LAR} \quad (2)$$

NAR is defined as the increase in plant weight per unit leaf area (LA) and per unit of time and is mainly the balance between the carbon gain of the plant due to photosynthesis (PS) and the carbon losses due to shoot respiration (SR) and root respiration (RR), all expressed on a leaf area basis and multiplied by a conversion factor

(CF) indicating the biomass/carbon weight ratio in the newly formed material. The balance is completed by subtracting biomass losses due to exudation (EXU) and volatilization (VOL), also expressed on a leaf area basis:

$$\mathbf{NAR} = \frac{\mathbf{1}}{\mathbf{LA}} \cdot \frac{\mathbf{dW}}{\mathbf{dt}} = \mathbf{CF} * (\mathbf{PS} - \mathbf{SR} - \mathbf{RR}) - \mathbf{EXU} - \mathbf{VOL} \quad (3)$$

LAR is the product of the leaf weight ratio (LWR), the fraction of material invested in the leaves and the specific leaf area (SLA), the leaf area per unit leaf weight:

$$\mathbf{LAR} = \mathbf{SLA} * \mathbf{LWR} = \frac{\mathbf{LA}}{\mathbf{WL}} * \frac{\mathbf{WL}}{\mathbf{W}} \quad (4)$$

where WL is leaf weight.

Potter & Jones (1977) introduced another approach to analyse RGR. They used the leaf area partitioning (LAP) and relative growth rate of the leaf area (RLGR) as descriptive parameters. The LAP is defined as the total leaf area increase per increase in total plant weight:

$$\mathbf{LAP} = \frac{\mathbf{dLA}}{\mathbf{dW}} \quad (5)$$

The RLGR is the amount of leaf area formed per unit leaf area and per unit time:

$$\mathbf{RLGR} = \frac{\mathbf{1}}{\mathbf{LA}} \cdot \frac{\mathbf{dLA}}{\mathbf{dt}} \quad (6)$$

RLGR and LAP are related via the formula

$$\mathbf{RLGR} = \mathbf{NAR} * \mathbf{LAP} \quad (7)$$

A third approach focuses on nitrogen as a key factor in plant growth. Here RGR is the product of plant nitrogen concentration (PNC) and nitrogen productivity (NP) (Ingestad 1982). NP is defined as the dry weight increase per unit plant nitrogen and per unit time. Thus,

$$\mathbf{RGR} = \mathbf{NP} * \mathbf{PNC} = \frac{\mathbf{1}}{\mathbf{N}} \cdot \frac{\mathbf{dW}}{\mathbf{dt}} * \frac{\mathbf{N}}{\mathbf{W}} \quad (8)$$

where N is the total amount of nitrogen in the plant.

Which of the three methods provides the best way to analyse RGR? The merit of the second approach is its emphasis on the formation of new leaf area. However, by concentrating on the growth of leaf area, only one aspect of the relative growth rate of the whole plant is covered. A second weak point is the use of leaf area partitioning (LAP) as descriptor, as it is the ratio of total leaf area and total plant weight (LAR) and not the ratio between the increase in leaf area and the increase in plant weight

Table 1. Relative growth rate (in $\text{mg g}^{-1} \text{day}^{-1}$) of eight species. To avoid too large interactions with size, mean RGR was calculated for the time period that plants had a dry weight not less than 15 mg and not more than 300 mg. Plants were grown in a 1/8 Hoagland nutrient solution. Photosynthetic photon flux density was $270 \mu\text{mol m}^{-2} \text{s}^{-1}$ during 14 h per day. During the day temperature was 20°C , RH 65%, during the night these values were 18°C and 95%, respectively.

Species	RGR
<i>Festuca ovina</i>	136
<i>Deschampsia flexuosa</i>	138
<i>Lolium perenne</i>	199
<i>Trifolium repens</i>	202
<i>Plantago major</i> ssp. <i>major</i>	222
<i>Silene dioica</i>	231
<i>Taraxacum officinale</i>	259
<i>Urtica dioica</i>	268

(LAP) which is a determining factor for the carbon economy. This is not to say that LAP and LAR are totally unrelated. If plant growth is in steady state, LAP (expressed in $(\text{m}^2 \text{day}^{-1})/(\text{kg day}^{-1})$) equals LAR (expressed in $\text{m}^2 \text{kg}^{-1}$). In other cases no correlation at all may be found between LAP and RGR. An extreme example is a plant with a high LAR that suddenly invests only in growth of roots. At first this plant may still achieve a high RGR, although LAP is zero at that moment. LAP may be of interest as a sensitive descriptor of time-dependent changes in LAR, though only in tight conjunction with LAR (but see Patterson *et al.* 1978). However, LAP used as a mean value over the whole experimental period and without LAR, as done by Potter & Jones (1977), is not likely to lead to much understanding of the process of growth.

The third approach is based on the concept of nitrogen productivity. As carbon and nitrogen economy are closely linked to each other by photosynthesis and respiration, so are the first and the third approach (cf. Lambers *et al.* 1989, This Volume). In fact they may be used complementarily to each other. However, a slight disadvantage of the third approach is that conceptually it is not as easily split into the different physiological and morphological parameters as the first one.

The first method links in best with frequently measured parameters like rate of photosynthesis per unit leaf area and allocation of biomass. It integrates physiological processes (photosynthesis, shoot respiration, root respiration, exudation and volatile losses), chemical composition (by the conversion factor and SLA), allocation (LWR) and morphology (SLA) into one composed formula. Of the three approaches it is the most appropriate tool in a first understanding of the mechanistic basis of growth.

3. NAR and LAR in relation to variation in RGR

What factors cause some species (or genotypes) to grow faster than others? How important are NAR and LAR in explaining these differences? To obtain more insight into the factors causing interspecific variation in RGR, growth of eight wild species was investigated. The plants, all herbs with a C_3 type of photosynthesis, were grown in a growth chamber with a non-limiting nutrient supply (cf. Table 1). Growth was analysed in the vegetative phase of the plants during a period of 17 days. RGR ranged from $136 \text{ mg g}^{-1} \text{day}^{-1}$ for *Festuca ovina* to $268 \text{ mg g}^{-1} \text{day}^{-1}$ for *Urtica dioica*

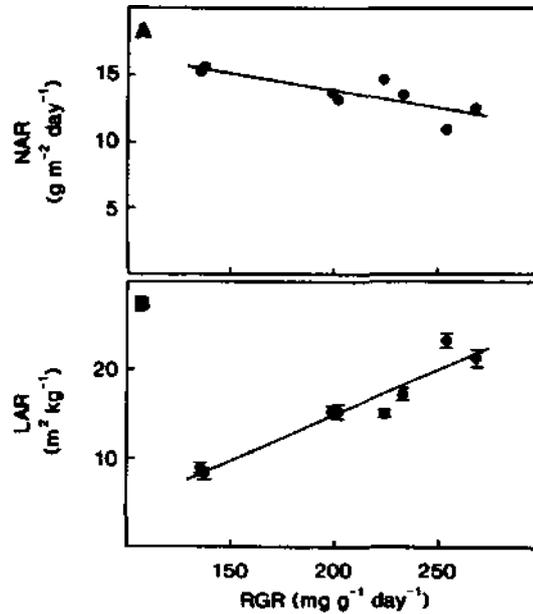


Fig. 1. A. Mean NAR of the eight species of Table 1 plotted against mean RGR. B. Idem for LAR. Error bars indicate the mean standard error at the different harvests within the growth period of 17 days (number of harvests = 6, $n = 8$). Total leaf area of species with needle-like leaves (*D. flexuosa*, *F. ovina*) was calculated as leaf blade length * the thickness in the middle of the leaf * π . For all species leaf area was determined as half the total leaf area.

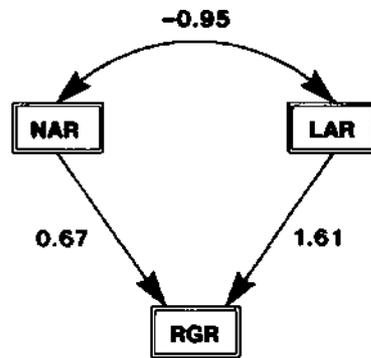


Fig. 2. Pathway analysis for the relations between RGR and its components. Values indicate the change in RGR (expressed in units standard deviation) as a result of a change of one unit standard deviation in NAR or LAR, both direct and indirect.

(Table 1). Analysis of the components of RGR revealed a slight but significant negative correlation between RGR and NAR: species with a higher RGR had a lower NAR (Fig. 1A). Correlation with LAR on the other hand was highly positive: the fastest growth was obtained by species with the highest LAR (Fig. 1B).

It is surprising that species with a high NAR have a lower RGR than species with

Table 2. Inherent differences in RGR (in $\text{mg g}^{-1} \text{day}^{-1}$), and their relation with the components NAR, LAR, SLA and LWR. Also relations with photosynthesis (PS), shoot respiration (SR) and root respiration (RR) are given, all measured on whole shoots and roots and expressed per unit leaf area. For each reference a linear regression was performed with the RGR of the investigated (sub)species as independent variable and the different components of growth as dependent variable. Thereafter the percentage increase (PI) in the fitted parameters was calculated, given a 10% increase in the overall mean RGR. The following classification was made:

--, $\text{PI} < -8$; +, $2 < \text{PI} < 8$;
 -, $-8 < \text{PI} < -2$; ++, $\text{PI} > 8$;
 o, $-2 < \text{PI} < 2$; na, difference between lowest and highest RGR value less than 10% or $10 \text{ mg g}^{-1} \text{day}^{-1}$, no analysis carried out.

In those cases where only NAR or LAR was given, the other component was calculated with the equation $\text{RGR} = \text{NAR} * \text{LAR}$. If plants were grown under a number of environmental conditions, the analysis carried out at the highest light intensity, the highest nutrient supply, the lowest windspeed, the lowest NaCl concentration, an ambient CO_2 concentration close to $350 \mu\text{l l}^{-1}$ or a mean temperature close to 23°C was chosen. Only those analyses are given where root weight was determined as well and species were grown under identical conditions.

Reference	Investigated species	range in RGR	PI						
			NAR	LAR	SLA	LWR	PS	SR	RR
A. Trees vs. Herbs									
Coombe 1960	1 tree + 1 crop species	53-93	++	-	+	--			
Whitmore & Wooi-Khoon 1983	1 tree + 1 crop species	109-129	++	-					
Jarvis & Jarvis 1964	2 tree + 1 crop species	117-239	+	+					
Poorter unpublished	1 tree + 1 grass species	152-203	++	o	+	-	+	+	
Coombe & Hadfield 1962	2 tree + 1 crop species	20-118	++	+	o	+			
Oberbauer & Donnelly 1986	6 tree + 1 crop species	19-126	+	+	+	o			
Okali 1971	3 tree + 1 crop species	40-150	+	+					
Mean PI			10	0	3	-2			
B. Between Trees									
Loach 1970	4 tree species	10-26	+	+					
Mooney <i>et al.</i> 1978	5 <i>Eucalyptus</i> species	146-178	+	+	++	o		o	
Pollard & Wareing 1968	6 tree species	14-30	+	+					
Delucia <i>et al.</i> 1989	3 tree species	11-24	o	+				o	
Kwesiga & Grace 1986	2 tree species	77-98	--	++	++	++			

Table 2. Cont.

Reference	Investigated species	range in RGR	PI							
			NAR	LAR	SLA	LWR	PS	SR	RR	
Huxley 1967	2 <i>Coffea</i> species	19-20		na						
Karlsson & Nordell 1987	2 tree species	3-4		na						
Popma & Bongers 1988	3 tree species	11-15		na						
Tolley & Strain 1984	2 tree species	46-55		na						
Mean PI			-2	11	17	4				
C. C₃ vs. C₄ species										
Bazzaz <i>et al.</i> 1989	1 C ₃ + 1 C ₄ wild species	95-127	++	-	o	o				
De Jong 1978	2 C ₃ + 1 C ₄ species	21-53	++	o	o	o				
Jones <i>et al.</i> 1970	2 C ₃ and 2 C ₄ species	110-220	++	o						
Rajan <i>et al.</i> 1973	3 C ₃ + 1 C ₄ crop species	131-210	++	o						
Saxena & Ramakrishnan 1983	2 C ₃ and 2 C ₄ weeds	8-36	++	o						
Warren Wilson 1966a	2C ₃ + 1 C ₄ species	188-332	+	o	-	+				
Roush & Radosevich 1985	2 C ₃ + 2 C ₄ weed species	232-262	+	+						
Potter & Jones 1977	9 crop + weed species (6 C ₃ , 3 C ₄)	202-482	o	++	+	o				
Sage & Pearcy 1987	1 C ₃ and 1 C ₄ weed species	340-410	o	++						
Sionit <i>et al.</i> , 1982	3 C ₃ + 1 C ₄ crop species	76-159	o	++						
Hofstra & Stienstra 1977	1 C ₃ + 1 C ₄ grass	86-91		na						
Mean PI			7	2	0	2				
D. Sun vs. Shade species										
Pons 1977	1 sun + 1 shade species	166-188	++	--	--	+		++	++	
Corré 1983c	1 sun + 1 shade species	245-339	+	+	+	o				
Corré 1983b	2 sun + 2 shade species	180-232	+	+	++	o				
Corré 1983a	2 sun + 2 shade species	165-327	o	+	+	-				
Corré 1983a	1 sun + 2 shade species	254-414	+	+	+	o				
Mean PI			8	2	-2	0				

Table 2. Cont.

Reference	Investigated species	range in RGR	PI							
			NAR	LAR	SLA	LWR	PS	SR	RR	
E. Between Herbs										
Eagles 1969	2 ecotypes <i>Dactylis glomerata</i>	165-224	++	--						
Thome 1960	3 crop species	129-180	++	--						
Blackman & Black 1951	3 <i>Trifolium</i> species	97-98	++	-						
Thorne <i>et al.</i> 1967	2 crop species	69-139	++	-						
Arnold 1974	2 wild species	99-111	+	+						
Blackman & Wilson 1951	3 crop species	77-165	+	+						
Boot & Mensink 1990	5 grass species	35-65	+	+	++	-				
Day <i>et al.</i> 1986	mutant + parent <i>Glycine max</i>	63-90	+	+						
Paul <i>et al.</i> 1984	5 cultivars <i>Lycopersicon esculentum</i>	180-220	+	+						
Roetman & Sterk 1986	13 microspecies <i>Taraxacum officinale</i>	117-211	+	+	+	o				
Woodward 1979	2 grass species	86-181	+	+						
Woodward 1983	2 <i>Poa</i> species	220-280	+	+	++	-				
Higgs & James 1969	4 grass species	55-149	+	++						
Brewster & Barnes 1981	8 cultivars <i>Allium cepa</i>	115-147	o	++	+	+				
Bruggink & Heuvelink 1987	3 crop species	310-410	o	++						
Poorter & Remkes 1990	24 wild species	113-365	o	++	+	+	o	-	-	
Kriedemann & Wong 1984	2 crop species	102-177	o	++						
Warren Wilson 1966b	2 wild + 1 crop species	187-309	o	++						
Blackman & Wilson 1951	2 crop species	42-92	-	++						
Delucia <i>et al.</i> 1989	1 shrub + 1 herb	84-154	-	++						
Dijkstra & Lambers 1986	2 genotypes <i>Plantago major</i>	212-280	-	++	++	o	-	--		
Gottlieb 1978	2 <i>Stephanomeria</i> species	120-140	-	++	++	+	o			
Poorter this article	8 wild species	136-268	-	++	++	+	o			
Shibles & MacDonald 1962	2 strains <i>Lotus corniculatus</i>	188-207	-	++						

Table 2. Cont

Reference	Investigated species	range in RGR	PI						
			NAR	LAR	SLA	LWR	PS	SR	RR
Woodward 1975	2 <i>Sedum</i> species	170-203	--	++					
De Kroon & Knops 1989	2 wild species	19-25		na					
Graves & Taylor 1986	2 <i>Geum</i> species	39-44		na					
Holt 1988	2 biotypes <i>Senecio vulgaris</i>	142-147		na					
Konings <i>et al.</i> 1989	3 <i>Carex</i> species	76-80		na					
Musgrave & Strain 1988	2 cultivars <i>Triticum aestivum</i>	85-91		na					
Myerscough & Whitehead 1967	4 wild species	120-132		na					
Pavlik 1983	2 dune grasses	55-56		na					
Pegtel 1976	2 ecotypes <i>Sonchus arvensis</i>	70-72		na					
Russell & Grace 1978	2 grass species	124-127		na					
Watson & Baptiste 1938	2 crop species	25-27		na					
Wilhelm & Nelson 1978	4 genotypes <i>Festuca</i>	20-28		na					
Wilson 1982	2 populations <i>Lolium perenne</i>	132-141		na					
Mean PI			2	8	9	1			

a low NAR. What causes this unexpected relationship? Pathway analysis showed that NAR itself, apart from any covariance with other variables, was positively correlated with RGR (Fig. 2). However, due to a strong negative correlation between NAR and LAR an increase in NAR invariably implies a decrease in LAR. And as the relationship between LAR and RGR is tight, the lower LAR will override the effect of a higher NAR. Consequently RGR will decrease as NAR increases. A possible explanation for the observed negative correlation between NAR and LAR could be the amount of compounds involved in photosynthesis. A high NAR can be achieved by a high rate of photosynthesis. This requires a large amount of enzymes and light harvesting complexes per unit leaf area, and possibly an extra layer of palisade parenchyma, all of which decrease SLA and thus LAR. For a more detailed discussion on the NAR-LAR compromise the reader is referred to Konings (1989, This Volume).

How do these findings relate to other investigations on inherent variation in RGR? Lambers & Dijkstra (1987) provide an extensive discussion of several case studies on

this subject. A comprehensive list of publications on interspecific variation in RGR and its associated parameters is given in Table 2. For each of these investigations linear regressions were performed between the components of growth of each species and their RGR. The percentage change in the fitted values of NAR, LAR, and eventually other parameters was then calculated, given an increase in RGR of 10%. An increase of, *e.g.*, 10% in LAR and 0% in NAR in association with a 10% increase in RGR would imply that, for that group of species, interspecific differences were caused solely by LAR and not at all by NAR. Thus, the relative importance of each component in explaining interspecific variation in RGR can be evaluated.

In some cases differences in RGR could be explained by differences in NAR (*e.g.* Coombe 1960, Eagles 1967, Pons 1977). Two specific groups of species appear to have a low RGR due to a low NAR. Firstly, in all the examples available, tree seedlings had a lower NAR than non-woody species (Coombe 1960, Jarvis & Jarvis 1964, Oberbauer & Donnelly 1986). Secondly, the scarce data suggest, that in moderate to high light conditions shade species have rather low NAR's in comparison with sun species (Pons 1977, Corré 1983a,c, but see Corré 1983b). Different NAR's could also be expected in C₃ and C₄ species, with C₄ species having a higher NAR due to a higher rate of photosynthesis. Indeed, most authors report higher values of NAR for C₄ than for C₃ species, but no differences were found by Warren Wilson (1966a), Rajan *et al.* (1973), Saxena & Ramakrishnan (1983) and Sage & Pearcy (1987).

Is LAR a more strongly determining factor than NAR, as far as interspecific variation in RGR is concerned? Taking together the publications in which a comparison between trees and between C₃ herbs is made, NAR appears an important factor in 55% of the investigations of Table 2, LAR in 85%. On average, a 10% higher RGR was associated with a 2% higher NAR and a 8% higher LAR. However, in most cases only two to four species (or cultivars) were investigated and sometimes the difference in RGR was rather small. A particular species adapted to a specific environment may then exert a decisive influence on the relations between RGR on one hand and NAR and LAR on the other. Therefore, investigations with many (sub)species and large differences in RGR (Potter & Jones 1977, Mooney *et al.* 1978, Brewster & Barnes 1981, Paul *et al.* 1984, Roetman & Sterk 1986, Poorter & Remkes 1990, Fig. 1) are the most appropriate to answer this question. In all of these LAR was by far the most important factor explaining differences in RGR. For these cases, a 10% increase in RGR was accompanied by a 1% increase in NAR and a 9% increase in LAR. The leaf area per unit plant weight thus appears to be a crucial attribute determining the potential RGR of a species. The physiological activity of the plant expressed per unit leaf area seems only of secondary importance.

4. The components of LAR in relation to variation in RGR

LAR is composed of two components (eq 4): one concerning the allocation of biomass to the leaves (LWR) and the other describing the amount of leaf area constructed per unit leaf weight (SLA). In the present comparison of eight wild species SLA was positively correlated with RGR (Fig. 3A). The same positive correlation was found in almost all cases in the literature (Table 2). Differences in SLA may be caused

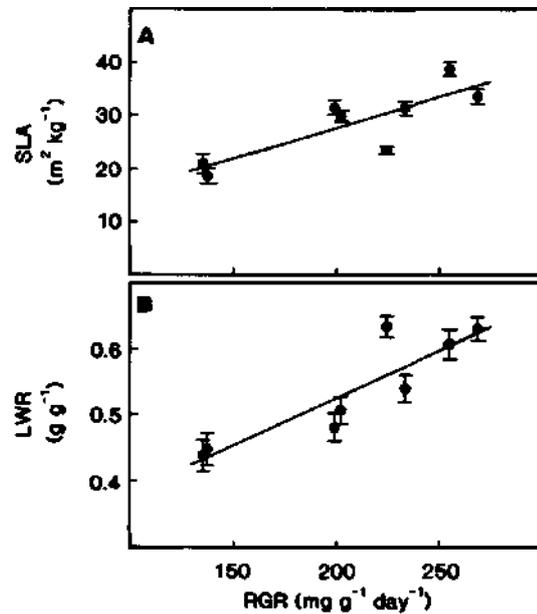


Fig. 3. A. Mean SLA of eight species plotted against mean RGR. B. idem for LWR.

by two different attributes of the leaves. Firstly, SLA may be associated with the thickness of the leaves: the higher the SLA the thinner the leaf. Secondly, the composition of the leaf material may be different. Indeed, leaves of fast growing species are thinner (Fig. 4B). They also contain a higher amount of water per unit dry weight (Fig. 4A). An explanation for the latter observation is that fast growers inflate their cells with large vacuoles and consequently accumulate a lot of water per cell in proportion to the amount of leaf material (*cf.* Dijkstra 1989, This Volume). Another possibility is that the chemical composition of the dry matter itself differs between fast and slow growing species. Slow growing species may accumulate considerable amounts of secondary compounds like lignin and phenolics, which increase the dry weight of the leaves (Mooney & Gulmon 1982).

LWR was also correlated positively with RGR (Fig. 3B), as well as in some literature sources (Brewster & Barnes 1981, Poorter & Remkes 1990). However, Potter & Jones (1977) and Roetman & Sterk (1986) did not find any correlation between LWR and RGR and neither did Elias & Chadwick (1979) in a comparison of 40 (sub)species. Boot & Mensink (1989) even found a negative correlation. Possibly, the way the plants are grown can explain these conflicting results. Most experiments have been carried out with plants grown in pots. As roots are not evenly distributed throughout the whole pot some parts of the soil may remain unexploited, whereas in other parts all available nutrients have already been taken up. The plant will react to this partial depletion by enlarging its allocation to the roots. As fast growing plants are often larger and large plants take up more nutrients, a negative relation between LWR and RGR may have been an artifact. This possible artifact was avoided for the 8 species tested here, by growing plants in culture solution, so that they were provided with

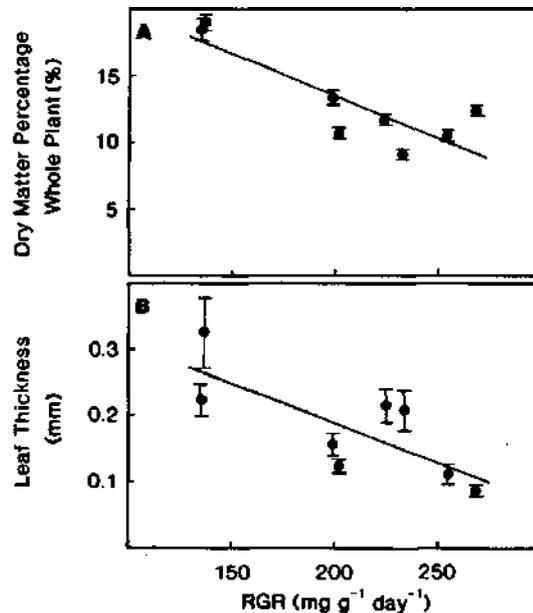


Fig. 4. A. Mean dry matter percentage (DMP, dry weight/fresh weight ratio on a whole plant basis) of eight species plotted against mean RGR. B. idem for leaf thickness.

an unlimited supply of ions in the circulating water.

Although both SLA and LWR were correlated positively with RGR, correlation with each of these factors was not as good as for the product of both, the LAR. This could imply that a plant regulates SLA and LWR interdependently. At a given LAR, a somewhat lower LWR could then be accompanied by a higher SLA and *vice versa*. Such a dependency could indicate a functional balance between total leaf area on one hand and the capacity for water uptake of the roots on the other hand (Konings 1989, This Volume).

5. The components of NAR in relation to variation in RGR

To obtain further insight into the NAR of the 8 species, aspects of the carbon and nitrogen economy were investigated. Net photosynthesis, expressed on a leaf area basis, did not show any significant correlation with RGR (Fig. 5A). Exact comparisons of NAR and the plant's carbon exchange are not possible, as no data on shoot and root respiration are available. However, both NAR and photosynthesis indicate that the physiological activity per unit leaf area is not of primary importance in explaining inherent differences in growth rates. This is in accordance with data on *Zea mays* (Duncan & Hesketh 1968), *Plantago major* genotypes (Dijkstra & Lambers 1986) and 24 herbaceous species (Poorter *et al.* 1990). However, for the group of shade species the low photosynthetic capacity (*e.g.* Pons 1977, Björkman 1981) may explain their relatively low NAR's under high light intensities.

The absence of a correlation in Fig. 5A between photosynthesis and RGR does not

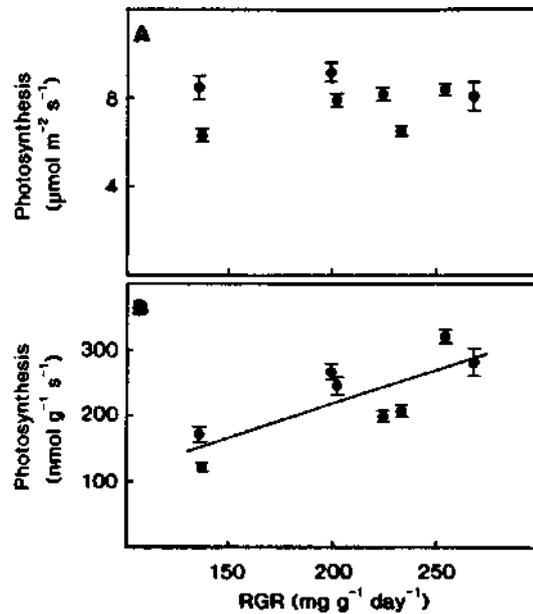


Fig. 5. A. Mean rate of photosynthesis, expressed on a leaf area basis, plotted against mean RGR for eight species. Photosynthesis was measured two times during the experimental period ($n = 4$), under the same conditions used for plant growth. B. Mean rate of photosynthesis expressed on a leaf dry weight basis.

imply that the photosynthetic tissue of slow- and fast-growers is equally active. If photosynthesis is expressed on a leaf weight basis, a positive relation with RGR is found (Fig. 5B). SLA again plays an important role here: the photosynthetic activity per unit leaf weight is higher for fast growers, but as leaf biomass is spread over a larger area, the activity per unit leaf area equals that of slow growers.

Respiration was not measured for the 8 species. Poorter *et al.* (1990) found that shoot respiration and root respiration per unit dry weight did correlate positively with RGR. However, expressed on a leaf area basis a negative correlation with RGR was found, largely due to a higher LWR and SLA of the fast growing species (*cf.* eq 3). Again, allocation and morphology appear to have a large impact on the carbon economy of the plant.

There is almost no knowledge of the relation between RGR and exudates or volatiles. This also applies to the conversion factor (CF) in equation 3. The carbon content of lignin is much higher than that of carbohydrates (Table 3). Therefore, it may be expected that slow growers which accumulate lignin will have a lower conversion factor than fast growers with little or no lignin formation. Besides self-shading and a low biomass allocation to the leaves (Kramer & Kozlowski 1979), the conversion factor also offers an explanation for the lower RGR observed for trees as compared with herbaceous species (Table 2). The conversion factor, and consequently NAR, can differ by 40% due solely to a different chemical composition (Table 3). Within the group of tree species the conversion factor may also play an important role. Oberbauer & Donnelly (1986) found that late-successional species had a lower NAR than

Table 3. A. Carbon content of different plant compounds in g g^{-1} (calculated after data of Penning de Vries *et al.* 1974). B. Chemical composition and conversion factor (CF) of the above-ground biomass of a coniferous forest (Lieth 1975). C. Chemical composition and CF of *Lepechinia calycina* leaves (Merino *et al.* 1984). A small fraction of terpenes and phenols was grouped in the category 'Lignin'. D. Idem, for a summergreen deciduous forest (Lieth 1975). E. Idem for a young, vegetative maize plant (Penning de Vries *et al.* 1974) F. Idem for the aboveground portion of grain sorghum (Lafitte & Loomis 1988). G. Chemical composition and CF for roots of *Senecio jacobea* (Lambers & Steingröver 1978). Lignin content was estimated. H, I and J. Chemical composition and CF of leaves, stem and roots respectively of cucumber (Challa 1976). Lignin content was estimated.

Fraction	carbon content	Chemical composition (%)									
		A	B	C	D	E	F	G	H	I	J
Lipids	0.776	7.8	13.4	1.9	2.5	3.0	2.5	4.1	2.6	2.7	
Lignin	0.689	30.5	21.0	20.8	8.0	2.7	8.0	2.6	4.2	4.0	
Organic N-compounds	0.530	1.3	23.5	2.6	23.0	9.5	17.0	33.8	19.3	18.2	
(Hemi)cellulose	0.461	58.9	21.6	73.5	48.0	57.8	32.0	23.5	37.8	35.9	
Fructan, starch, sugars	0.412	1.1	8.0	0.8	8.5	21.0	22.5	0.0	0.0	0.0	
Organic acids	0.375	-	3.4	-	5.0	1.3	5.0	19.1	8.1	6.2	
Minerals	0.000	0.3	9.2	0.3	5.0	4.8	13.0	17.8	28.1	33.0	
Conversion Factor		1.80	1.93	1.94	2.12	2.22	2.36	2.45	2.81	3.00	

early successional trees. Indeed, in tropical forests large differences exist in the chemical composition of pioneer species and tree species of climax vegetations, both in leaves (Coley 1983) and woody parts (*cf.* Jane *et al.* 1970). In all these cases not only the conversion factor, but also the respiration needed for biosynthesis will be affected. Lambers and Rychter (1989, This Volume) provide a more detailed discussion on this subject.

6. Nitrogen economy of fast growing vs. slow growing species

No significant correlation was found between the reduced nitrogen concentration of the plant, expressed on a dry weight basis, and RGR (Fig. 6A). This also applied to the nitrogen concentration of the several plant parts. As fast growing species have a higher SLA, reduced leaf nitrogen concentration per unit leaf area was lower for fast growers than for slow growing species (Fig. 6B). Rates of photosynthesis per unit leaf area did not show any relation with RGR (Fig. 5A). Consequently, the photosynthetic nitrogen use efficiency (PNUE), the rate of photosynthesis per unit reduced nitrogen in the leaf, is higher for fast growers than for slow growers (Fig. 7A). The reasons for this more efficient use of nitrogen may be twofold. Firstly, slow growers may invest proportionally less nitrogen in compounds involved in photosynthesis. Another possibility is that leaves of slow growers, which are thicker, use N less efficiently due to shading within a leaf (Evans 1989, This Volume). A higher allocation of N to the leaves and a higher PNUE cause fast growers to have a higher nitrogen productivity (NP, eq 8) than slow growers (Fig. 7B). Thus, fast growers use the incorporated N more efficiently in realizing biomass increase than slow growers.

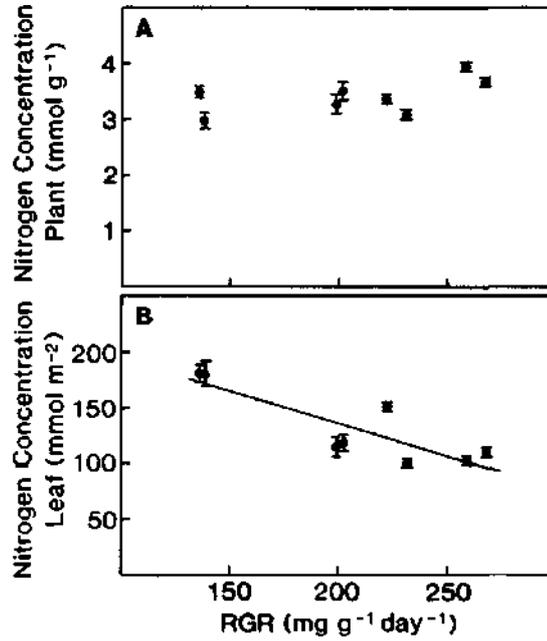


Fig. 6. A. Organic nitrogen concentration of the whole plant (PNC, on a dry weight basis) of the eight species plotted against mean RGR. B. *idem* for the organic nitrogen concentration of the leaf, expressed on a leaf area basis (LNC).

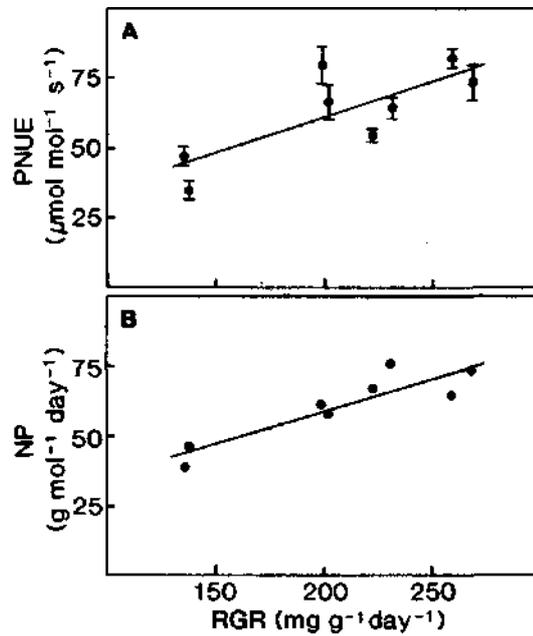


Fig. 7. A. Mean rate of photosynthesis per unit reduced nitrogen in the leaves (PNUE, Photosynthetic Nitrogen Use Efficiency) for eight species plotted against mean RGR. B. *idem* for the Nitrogen Productivity (NP, eq 8).

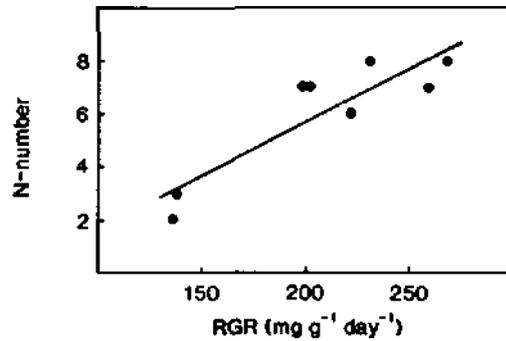


Fig. 8. N-number of Ellenberg (1979) for 8 species plotted against mean RGR.

7. Ecological significance of RGR

Having discussed how interspecific variation in RGR is brought about under identical, close to optimum conditions, we may now ask the question 'What is the ecological significance of a certain potential RGR?' For the eight species investigated there was a clear positive relation between the soil fertility in their natural habitat, indicated by the N-value of Ellenberg (1979) and their RGR (Fig. 8), in accordance with the observations of Grime & Hunt (1975). The survival value of a high RGR has been discussed in the introduction: Fast growth may imply a higher capture of resources in a dense vegetation or a rapid completion of the life cycle. However, the ecological advantage of a low RGR is less clear. In temperate climates, slow growing species are found on less fertile soils. Grime & Hunt (1975) and Chapin (1980) have suggested 3 reasons for this. (1) Slow growing species have low demands and therefore will not exhaust resources very rapidly. However, this is not likely to be an evolutionarily stable strategy: A neighbouring species with a higher RGR may easily capture most of the limiting resource, thus outcompeting the slower growing species. (2) A species with a low RGR functions closer to its optimum growth rate in an unfavourable situation than a fast growing species. But this does not necessarily mean that the fast growing species will be outperformed by the slow growing species. Plants often have a high physiological and/or morphological plasticity (Grime *et al.* 1986, Poorter & Lambers 1986), enabling adaptation to a wide variety of environmental conditions. (3) Slow growing species could have lower rates of incorporation of photosynthates and minerals into structural material, thus forming a reserve for later growth. But photosynthates do not seem to be a factor limiting growth in a nutrient-poor environment as accumulation of starch is often observed (Hofstra *et al.* 1985, Waring *et al.* 1985, McDonald *et al.* 1986). As far as nutrients are concerned, given that a plant will need a certain amount of nutrients to reach a certain size and construct a minimum amount of reproductive material, the time to incorporate these minerals into structural compounds seems of minor importance.

The alternative explanation is that the components of RGR, and not RGR itself, have been the target of selection under adverse conditions (Lambers & Dijkstra 1987). I would like to extend this thesis, suggesting that not only for stress tolerators, but also for ruderals and competitors the factors underlying the RGR have been the

subject of selection. This focuses attention on the physiological functioning of the plant. Which demands are made upon plants in different environments? Let us consider plant growth in two distinct habitats, differing in soil fertility, all other environmental conditions being equal. For simplicity's sake, further conditions are a seasonal climate with a distinct growing period and the absence of woody species.

7.1 The components of RGR in a nutrient-rich environment

In the nutrient-rich habitat a dense vegetation will develop in the course of a season, with a high leaf area index (Fliervoet & Cortenraad 1989). As the supply of light is uni-directional, light intensity in the lower parts of such a vegetation will be low. For an individual plant growing in this dense vegetation it is essential to develop a large area of leaves in the top layer of the vegetation (*cf.* Berendse & Elberse 1989; This Volume). This will ensure both high light interception and shading of neighbouring plants. Thus, selection favours a high biomass investment in leaves (LWR) and also in stems (Hara 1984). Another characteristic of this type of vegetation is fast development of a new strata of leaves. The period a certain leaf receives full light is relatively short. Thereafter another top layer of leaves develops and light intensity will eventually drop to such low levels that the carbon balance of the lower leaves is hardly positive (Pons *et al.* 1989, This Volume). Given these kind of conditions, a successful strategy for a plant will be to rapidly develop leaves which intercept as much light as possible, but with low construction costs per unit leaf area, thus ensuring a high return of carbon. This is exactly what fast growing species do. They form thin (Fig. 4B), large leaves, with a low investment in structural material per unit area (Fig. 3A). Simulations have shown that a higher SLA may have a tremendous positive effect on the outcome of competition of isogenic maize cultivars (Spitters & Aerts 1983). Biere (1989) determined the growth parameters of several lines of *Lychnis flos-cuculi*. A competition experiment was then carried out between these lines and *Anthoxantum odoratum*. He found that the differences in LAR between the lines determined the relative performances of *Lychnis* more than differences in RGR, in spite of the close correlation between these two parameters.

A consequence of a low amount of cell wall material per leaf area is frailness of the leaf. How do these fast growing species achieve rigidity? It is hypothesized that they have solved this problem by accumulating a high amount of water per unit leaf weight (*cf.* Fig. 4A), thus inflating each cell with water. If correct, this implies that plants have to invest in solutes to maintain the osmotic value of the cell. By using ions, which are relatively easily available in this habitat, the cost of maintaining rigidity is much lower than either the use of sugars as an osmotic or by investing in cell wall material.

Another consequence of a high SLA is its effect on the carbon economy. Leaves with a low investment of dry weight per unit area will almost automatically have a low investment in photosynthetically active compounds (Fig. 6B). As a result, photosynthetic activity per unit area will be relatively low (Fig. 5A). It is therefore not likely that these plants have a high NAR.

7.2 The components of RGR in a nutrient-poor environment

In a nutrient-poor habitat biomass and leaf area index of the canopy will remain low (Fliervoet 1989). Compared with the fertile habitat, nutrient acquisition gains importance, whereas light interception is less critical (Tilman 1984). In such an environment plants will invest relatively more in root biomass. In general, plants have a high plastic ability to adjust biomass allocation to the nutrient supply. However, Grime *et al.* (1986) found that this morphological plasticity is higher for fast growing than for slow growing species. This explains why, even under optimal conditions slow growing species invest relatively more in roots (*cf.* Fig. 3B).

As leaf area index remains rather low during the growing season, leaves continuously experience high light intensities. Leaf longevity therefore may be higher. As stated above, species growing in a nutrient-poor environment are not limited by carbon but only by nutrients. Thus emphasis should be laid not only on acquisition of nutrients, but also on conservation of the acquired nutrients (Monk 1966, Small 1972, Berendse & Aerts 1987). Losses of nutrients in the shoot may occur by leaching out of the leaves, through grazing and by dying off of leaves. Leaching may be diminished by wax layers, which limit contact between the interior and exterior of the leaf (Mulroy 1979, Marschner 1986). Losses by herbivory may be counteracted by accumulation of lignin, phenolics or other C- or N-based secondary compounds (Coley 1987). Dying off of leaves may be prevented provided their tolerance to less favourable weather conditions, like frost or drought is increased. This may be achieved by leaf hairs, a thick cuticle, increase in cell solute concentration, increase in lipid concentration and possibly small cell sizes (Jones 1983). However, all of the above-mentioned actions to prevent nutrient losses require accessory investment in the leaves, implying a lower SLA (Fig. 3A), a higher dry matter percentage (Fig. 4A) and/or a lower conversion factor (eq 3).

In itself a low SLA may result in a high N concentration per unit leaf area (Fig. 6B) and consequently a higher photosynthetic capacity. However, this does not necessarily result in a high NAR. Firstly, due to a high root weight per unit leaf area, respiration will increase and lower NAR. Moreover, secondary compounds may require high construction costs, also decreasing NAR. Thirdly, investment of N in compounds not involved in photosynthesis may decrease PNUE (*cf.* Fig. 7A) and NAR. Lastly, lowering of PNUE may also be caused by shading within these rather thick leaves.

7.3 The components of RGR in other adverse environments

Plant species may be adapted to all kinds of suboptimal environments. Have these adjustments led to alterations in the components of RGR? Mooney *et al.* (1978) grew 5 *Eucalyptus* species from habitats differing in water availability under identical conditions. No differences in NAR were found, but the SLA of desert species was lower than that of species from mesic habitats. Sclerophylly, often observed for evergreen leaves in the dry Mediterranean habitats also results in a low SLA (Gray 1982). Woodward (1975) and Körner & Pelaez Menendez-Riedl (1989, This Volume) found a negative correlation between altitude and SLA. Woodward (1983) tested the hypothesis that adaptation to high wind velocities at higher altitude could play a role.

Indeed he found that a species originating from higher altitude and with a lower SLA resisted high wind velocities better than a species from lower altitude, possibly due to a higher amount of supporting tissue in the leaf.

An inherently lower LAR may be the result of adaptation to frost or chilling. Warren Wilson (1966b) reported an inherent difference in LAR, but not in NAR, in a growth analysis of two arctic and a temperate species. It is expected this is at least partly caused by a difference in SLA. Small cell sizes and a low water content may increase the frost tolerance of a species. Moreover, a low water content can decrease the digestibility of leaf material for predators, as shown by Scriber (1977). Cell size and thickness of the cell walls could also play a role in the difference in trampling resistance between two *Plantago major* subspecies. The subspecies with the highest trampling resistance had the lowest SLA and the highest NAR (Dijkstra 1989, This Volume).

In all of the above-mentioned environments a stress factor led to an inherent decrease in SLA and/or LWR. A clear contrast is formed by species from environments with low light intensities. Here selection has led to species with a high SLA, to enable maximum light interception. As a consequence, maximum NAR is low for these species, even when grown under high light conditions (Pons 1977).

7.4 Other aspects of plant functioning

It should be borne in mind that not only the components of RGR are relevant for a plant's functioning in the field. An important feature like plant size is not solely determined by RGR. Factors like seed size, germination time, ontogenetic development and duration of growth may play an important role in determining the ultimate weight of a plant. A clear example is the growth of trees. Despite a low RGR, trees are capable of attaining a large size due to their longevity. Neither is competition solely dependent on plant size. Features like the architecture of the plant (Küppers 1985, Roush & Radosevich 1985) and production of allelopathic compounds (Rice 1974) may have a decisive influence on competition. This applies as well to a plant's ability to adapt to (temporary) sub-optimal conditions (Bradshaw 1965).

8. Conclusions

Leaf area per unit plant weight (LAR) is an important factor in explaining inherent differences in relative growth rate between species, whereas NAR is only of secondary importance. It is postulated that this is a reflection of selective pressures in the natural environment: in highly productive environments a high LWR and a high SLA will be of paramount importance to survive in a dense vegetation. In low productive environments high biomass allocation to the roots (low LWR) and a set of traits ensuring physiological integrity and leaf longevity (lignin, secondary compounds, waxes, hairs, small vacuoles) and consequently a low SLA will enable survival. If correct, and apart from other factors influencing competition, this implies that not the potential RGR of a species determines its occurrence, but rather factors determining specific leaf area and allocation.

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