IS INHERENT VARIATION IN RGR DETERMINED BY LAR AT LOW IRRADIANCE AND BY NAR AT HIGH IRRADIANCE? A REVIEW OF HERBACEOUS SPECIES.

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Abstract

In this review we analysed inherent differences in Relative Growth Rate (RGR) between herbaceous species or genotypes in terms of variation in the growth parameters Net Assimilation Rate (NAR), Leaf Area Ratio (LAR), Specific Leaf Area (SLA) and Leaf Mass Ratio (LMR). We did so after introducing the 'Growth Response Coefficients' (GRCs), which indicate how a proportional difference in any of the growth parameters scales with the observed proportional difference in RGR. A GRC_{NAR} value of 1 indicates that a given proportional difference in RGR is accompanied by a proportional difference in NAR of the same magnitude; a GRC_{NAR} of 0 indicates that a difference in RGR is not accompanied by any systematic difference in NAR. Averaged over all literature on herbaceous species the GRC_{NAR} was 0.26 and the GRC_{LAR} was 0.74, indicating that LAR is by far the most important factor in explaining inherent variation in RGR. The differences in LAR were mainly due to variation in SLA, GRC_{SLA} being 0.63 and GRC_{LMR} 0.11. We tested in both a direct and an indirect way whether the relative importance of LAR was highest in experiments with low-light grown plants, with variation in NAR being more important in experiments conducted at highlight. In none of the two ways did we find any support for this hypothesis.

1. Introduction

Plant species vary widely in their potential growth rate. That is, when plants are grown under standardised, 'close to optimal' conditions, Relative Growth Rate RGR, the increase in plant mass per unit of mass present and per unit of time) varies threefold or more (Grime & Hunt 1975, Poorter & Remkes 1990, Gamier 1992, Hunt & Cornelissen 1997, Van der Werf *et al.* 1998, this volume). The technique of growth analysis can be used to analyse the causes of inherent variation in growth rate. To this end, RGR is factorised into the growth parameters NAR (Net Assimilation Rate, biomass increase per unit leaf area and time) and LAR (Leaf Area Ratio, leaf area per unit plant mass). LAR can be further analysed as the product of SLA (Specific Leaf Area, leaf area per unit leaf mass) and LMR (Leaf Mass Ratio, leaf mass:total plant mass). LAR, SLA and LMR are simple ratios that can be easily measured. NAR is a more complex parameter, being the net balance of C-gain in photosynthesis and C-losses in shoot and root respiration, divided by the C-concentration of the plant's newly formed biomass (Lambers *et al.* 1989). Generally, variation in NAR is determined most by variation in the rate of photosynthesis per unit leaf area (A_a, Konings 1989; Fig. la). This is because shoot and root respiration often represent a more or less fixed proportion of photosynthesis (Ludwig *et al.*

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1975, Poorter *et al.* 1990; Fig. 1b), and the C-concentration of the plant varies only marginally between species within the same life form and between treatments (Poorter & Villar 1997; Fig. 1c). Therefore, NAR can be interpreted as a fairly good indicator of the rate of photosynthesis per unit leaf area, not measured over the short term on the youngest fully developed leaf and under saturating light conditions as is often done in gas-exchange measurements, but integrated over the growth period for all leaves on the plant under the prevailing growth conditions.

In the following sections we analyse variation in RGR in terms of the growth model discussed above. The four parameters in this model summarise the carbon economy of the plant in a simple, but useful way. However, three points have to be borne in mind. First, variables like A_a and NAR are not only dependent on external conditions, such as light intensity, but may be under control of processes within the plant as well such as the demand for photosynthates. Thus, where variation in A_a may be the cause of variation in growth rate at one integration level, it can still be merely the result of an array of processes at a lower integration level *(cf.* Lambers *et al.* 1998, this volume). Second, growth parameters are not necessarily independent of each other. As will be discussed in section 5.2, an increase in NAR is often associated with a decrease in LAR. Third, in seeking generalisations we search for main patterns, which does not exclude that for a specific pair of species relations may be different.

In this chapter we first present a case study on the causes of variation in growth rate of a wide range of herbaceous species. We then describe the tools by which we will be able to generalise across different experiments to what extent inherent variation in RGR is due to the various components. Subsequently, we will update previous compilations of the literature (Poorter 1989, Lambers & Poorter 1992) and calculate quantitatively to what degree variation in RGR is due to variation in the underlying components in the 'average' experiment. It turns out that LAR is the main factor, but that there is quite some variability around these average values. It remains to be seen to what extent this variation can be ascribed to the specific taxonomic group of species under investigation, as well as the conditions under which the plants were grown. It has been suggested that LAR is the main factor explaining variation in RGR at low light, and that NAR is the dominant factor at high light. As light intensity varies substantially between experiments, we analyse how this affects the conclusions in the above compilation. In the second half of the paper we focus on the effect of light intensity *per se* on the various growth parameters and the consequence of the differences in light climate between growth chambers and glass houses for the outcome of growth analyses. Finally, we use the scarce data for fast- and slow-growing plants determined at various light intensities to test whether they support our conclusion, that LAR is in general the main factor determining inherent differences in growth rate between herbaceous species.

2. Inherent variation in RGR: a case study

Most comparative studies on interspecific variation in RGR and its underlying components require harvesting of large numbers of plants. To divide workload and avoid space limitations, experiments are carried out in several parts separated in time. This necessitates the use of growth rooms, where conditions can be kept constant through-

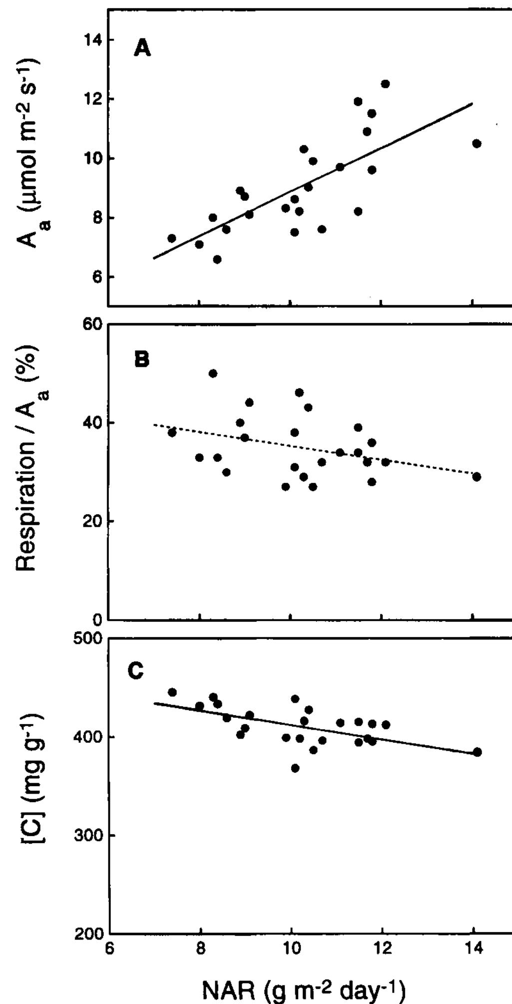

Fig. 1. (a) The rate of photosynthesis of whole shoots as determined under growth conditions; (b) daily whole plant respiration as a percentage of daily photosynthesis; and *(c),* the concentration of *C* in the plant, plotted against the growth parameter NAR for 24 species differing in relative growth rate. Lines are the regression lines (for A_a: $p < 0.001$, $r^2 = 0.54$, for Respiration/A_a: $0.05 < p < 0.10$, $r^2 = 0.13$, for [C]: $p < 0.01$, $r^2 = 0.34$). Data of Poorter & Remkes (1990) and Poorter *et al* (1990).

out the experiment. Nevertheless, the number of species that can be analysed will strongly depend on the detail and precision required and the experimental lay-out chosen. Most studies use an experimental design with two harvests *(e.g.,* Hunt & Cornelissen 1997), resulting in the largest number of species that can be compared for a given time investment. However, using such a design implies that changes in growth rate due to ontogenetic drift (Hunt & Lloyd 1987, Poorter & Pothmann 1992) cannot be accounted for (but see Van der Werf *et al.* 1998, this volume). A relatively large study where such an ontogenetic correction was made by calculating growth

parameters over a given plant mass trajectory was that of Poorter & Remkes (1990), comprising 24 herbaceous species. Subsequently, the same experimental design and growth conditions have been used to compare 12 climbing and non-climbing dicots (Den Dubbelden & Verburg 1996), and 7 herbaceous monocots (J.J.C.M. Van Arendonk & A. Van der Werf, unpublished). In total, 43 herbaceous species were analysed over the dry mass trajectory of 30-100 mg, at the stage after germination but before plants had reached a size where self-shading would occur.

An analysis of the relative growth rate and its components for these 43 species is shown in Figure 2, by plotting NAR and LAR against RGR. There is quite some variability in each of the parameters, with NAR and LAR showing up to a twofold difference at an intermediate RGR. Such variation implies that results from small-scale experiments, where just 2-4 species are compared, can be quite variable depending on the specific species selected. Taking all 43 species together, clearly the main variable determining variation in RGR is the LAR. NAR is not significantly correlated with RGR. Both components of LAR contribute to the positive correlation with RGR, with SLA being more important than LMR (Fig. 3). On average dicots have a higher LMR than monocots.

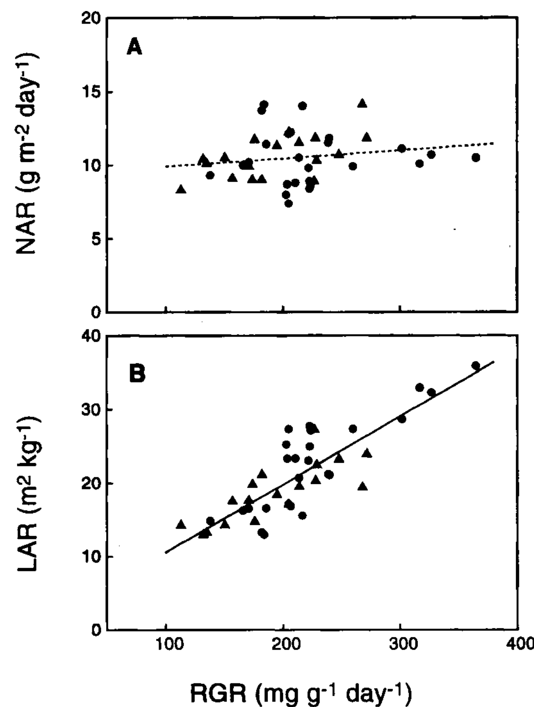

Fig. 2. (a) NAR; (b) LAR of 43 herbaceous species plotted against their RGR, determined during the time that plants weighed 30-100 mg. Triangles indicate monocotyledonous species, circles dicotyledonous ones. Lines are the regression lines through all data points (for NAR: n.s., $r^2 = 0.03$, for LAR: $p < 0.001$, $r^2 = 0.69$). All plants were grown hydroponically in a growth chamber at a light intensity of 315 µmol m^{-2} s^{-1} at mean plant height. Data from Poorter & Remkes 1990, Den Dubbelden & Verburg 1996 and J.J.C.M. Van Arendonk & A. Van der Werf, unpublished results on *Carex flacca, Festuca arundinacea, Holcus mollis, Poa alpina, Poa compressa, Poa pratensis,* and *Poa trivialis.*

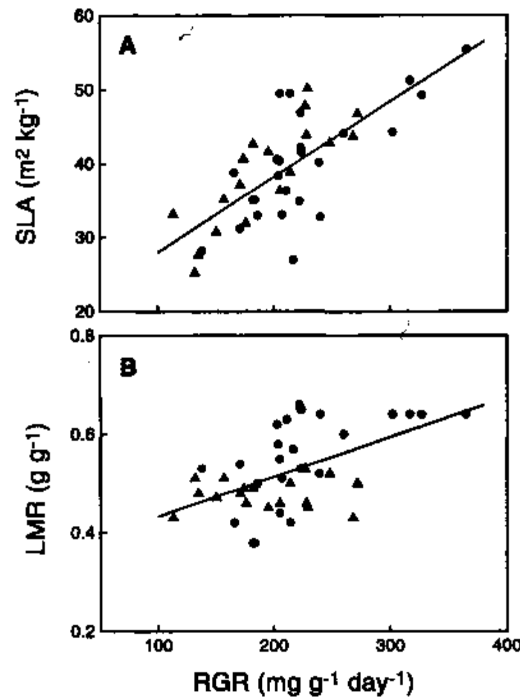

Fig. 3. (a) SLA; (b) LMR of 43 herbaceous species plotted against their RGR, determined during the time that plants weighed 30-100 mg. Lines are the regression lines through all data points (for SLA: $p < 0.001$, $r^2 = 0.53$, for LMR: $p < 0.001$, $r^2 = 0.27$). For more information see the legend of Figure 2.

3. An approach to generalise across experiments

The case study presented in the previous section has been carried out with herbaceous species from Western-Europe, under a specific combination of environmental conditions. Many more experiments have been published in which differences in RGR between specific groups of species or genotypes were analysed. To enable a generalisation across these individual experiments, several approaches are possible. First, one could plot all data on, say, NAR and LAR against the corresponding RGR values in one graph, similar to Figure 2. However, interpretation is a problem because experiments have been carried out under different conditions. Most species grow faster at high irradiance, with a concomitantly higher NAR but a lower LAR (*cf.* section 5.2). Mixing these phenotypic responses with genotypic differences will result in a bias, overestimating the importance of NAR and underestimating the importance of LAR. Therefore, one needs a parameter that is calculated for the data within each experiment and that can subsequently be used for comparisons across experiments. A possibility would be to compute correlation coefficients between RGR on the one hand, and parameters like NAR and LAR on the other hand. A high correlation coefficient would imply that variation in RGR (in terms of deviation from the overall mean) scales well with variation in, say, deviations from the

mean in NAR. The use of correlation coefficients has two drawbacks. First, in the case where only 2 species are analysed, the correlation coefficient will always be 1. Second, the correlation coefficient considers relative variation around the mean, but does not take into account the absolute size of the variation. That is, if RGR varies between 100 and 400 mg g^{-1} day^{-1} and NAR varies between 10 and 13 g m^{-2} day^{-1}, correlation between RGR and NAR can be as high as when NAR varied between 10 and 40 g m^{-2} day^{-1} (Fig. 4). In the first case, however, NAR would only marginally contribute to variation in RGR, whereas NAR would be the sole component responsible in the second case. To allow for this we introduce the 'Growth Response Coefficient' (GRC). We define GRC_X as the proportional difference in a particular growth parameter X (NAR, LAR, SLA or LMR), scaled to the proportional difference in RGR. In formula:

$$GRC_X = \frac{dX}{X} \Big/ \frac{dRGR}{RGR} \quad (1)$$

Full details on GRC and its calculation are given in Appendix 1. GRC will have a value of 1 if the change in X is fully proportional to the increase in RGR. A value of 0 indicates that the difference in RGR is not accompanied by any systematic difference in X. Values below 0 and above 1 may occur also, for example if a higher RGR for a given species is accompanied by both a lower NAR and a more than proportionally higher LAR (see Table 1 for some examples). In the experiment described in Section 2, GRC_{NAR} equals 0.13 and GRC_{LAR} equals 0.91.

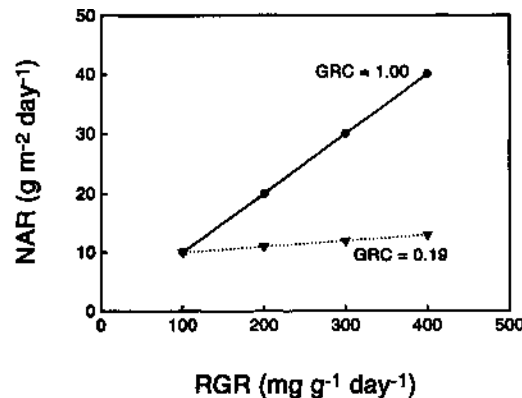

Fig. 4. A graphic example to show the concept of GRC. In hypothetical experiment A (triangles) the RGR of the 4 species is 100, 200, 300 and 400, respectively, and NAR is 10, 11, 12 and 13. The r^2 of the regression line is 1.0, GRC_{NAR} is 0.19. In hypothetical experiment B (circles) the fourfold difference in RGR is accompanied by a fourfold difference in NAR (10, 20, 30, 40). The r^2 of the regression line is still 1.0, GRC_{NAR} is now 1.0.

Table 1. Some hypothetical examples of RGR, NAR and LAR and the corresponding GRC values.

	RGR ($mg\ g^{-1}\ day^{-1}$)	**NAR** ($g\ m^{-2}\ day^{-1}$)	**LAR** ($m^2\ kg^{-1}$)	**GRC_{NAR}**	**GRC_{LAR}**
A	100	10	10	1.0	0.0
	200	20	10		
B	100	10	10	0.5	0.5
	200	14.1	14.1		
C	100	10	10	2.0	-1.0
	200	40	5		

This analysis is most fruitful if there is a simple, proportional relationship between RGR and parameter X. In the case, where RGR is the product of 2 or more variables (like NAR and LAR), the sum of the GRCs will be 1 or at least close to it (see Appendix 1). This enables a simple and straightforward evaluation of the relative importance of each parameter in 'explaining' variation in RGR.

4. How do fast-growing species achieve a higher growth rate than slow-growing species? A meta-analysis

4.1 Compilation of growth experiments

To what extent can the results of the analysis in section 2 be generalised? Poorter (1989) and Lambers & Poorter (1992) have reviewed the literature on comparative growth analyses. In this section we update these reviews with the publications of the last 6 years, restricting ourselves to herbaceous species which were in the vegetative phase and for which both shoots and roots were harvested. For woody species the reader is referred to Cornelissen *et al.* (1998) and Veneklaas & Poorter (1998, this volume). We arrived at a total of 111 experiments, ranging from a comparison of two rather similar genotypes up to a contrast of 68 widely different species. Given the difficulties in assessing RGR and NAR precisely (Evans 1972, Poorter & Gamier 1996), and the need to have species that differ in growth rate at least to some extent we decided to consider only those publications where variation in RGR between genotypes or species was at least 40 mg g^{-1} day^{-1}. The 57 experiments meeting this criterion are listed in Appendix 2. For each of these, GRCs for NAR, LAR, SLA and LMR were calculated as outlined in Appendix 1. Average GRC_{NAR} and GRC_{LAR} values over all experiments of appendix 2, after exclusion of the 5% highest and 5% lowest observations, are 0.26 and 0.74, respectively (Fig. 5). Those of SLA and LMR are 0.63 and 0.11, respectively. Thus, based on the averages for all experiments, we conclude that LAR, and more specifically SLA, is the most important factor explaining variation in RGR. NAR and LMR are of secondary importance. Given the strong correlation between NAR and A_a, the implication of these results is that the rate of photosynthesis per unit leaf area is not a dominant factor associated with inherent differences in growth rate.

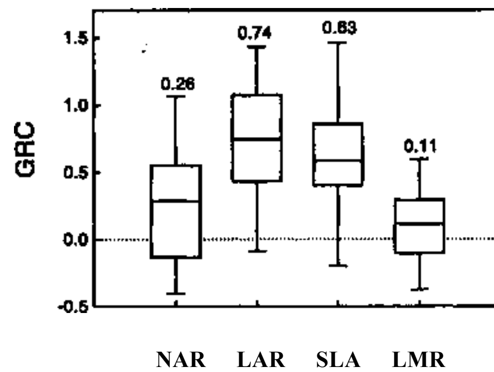

Fig. 5. Box plots of GRCs for NAR, LAR, SLA and LMR. Distributions are based on a compilation of 57 experiments, in which species or genotypes are compared, listed in Appendix Only those experiments were included where vegetative, whole plants were measured and the difference in RGR between the fastest- and the slowest-growing species was more than 40 mg g^{-1} day^{-1}. Boxes indicate the 10th, 25th, 50th, 75th and 90th percentiles, the numbers the 10%-trimmed mean values.

Two caveats of the above analysis should be mentioned. First, results are as general as the range of species investigated in the literature, which shows a dominance for crop species and wild plants from Western Europe. Second, some experiments consist of just a few species and a relatively small range in RGR. As mean GRCs were calculated by simply averaging GRC data over all experiments, small-scale experiments could distort the analysis. Taking these differences into account, however, by weighing large-scale experiments with widely ranging RGRs stronger in the calculations than others does not affect the above conclusion.

4.2 Variation in GRCs

Although the differences in average GRC_{NAR} and GRC_{LAR} are clear, there is considerable variation around the mean (Fig. 5). Is this just random variation, or does it vary systematically depending on the experimental conditions and the taxononomic group of species under investigation? We explore five possible explanations. First, it may be that the finding that NAR (and presumably A_a is quantitatively not important in explaining variation in growth rate is a consequence of the low light intensities used in most studies. At low irradiance, there would hardly be any possibility for variation in A_a between species, whereas at high light variation in A_a could be more pronounced. Thus, it would be possible that low values of GRC_{NAR} were found in experiments with a low light intensity, whereas the high values were observed in experiments with a high irradiance. Second, light intensity is generally fixed in growth chambers, whereas it may vary over the day from very low to intensities saturating for photosynthesis in glasshouses. Therefore, we analysed whether GRC_{NAR} would be more important under glasshouse conditions or in the field than in growth chambers. Third, it has been suggested that monocotyledonous species differ in GRC_{NAR} from dicots (Gamier 1991, Van der Werf *et al.* 1998, this volume). A fourth possibility is that across species (or genera) LAR would be important, but that within a species (or a genus) variation in NAR would be the dominant

factor. Fifth, there may be a difference between experiments where plants are grown in pots and those where plants are grown hydroponically. Although growing plants in hydroponics enables easy access to the roots, for most plants it is quite an unnatural rooting substrate. On the other hand, for plants growing in pots it may be difficult to ensure a non-limiting supply of water and nutrients. Moreover, plants in pots easily become pot-bound, which may also affect their growth (Dubik *et al.* 1992). As fast-growing species generally have a higher biomass after a given time, they are likely to suffer more from these size-related problems than slow-growing species. A last possibility we consider is that it could also be a combination of these factors that causes the variation in GRCs.

To investigate the extent to which GRC values are affected by the conditions in the experiments as well as the taxonomic group under investigation, we carried out four multiple regressions, in which each of the GRCs was in turn the dependent variable. Independent variables were the five attributes of the experiment mentioned above. For reasons explained later (section 5.1), we used the total daily quantum input to characterise the light environment for a given experiment. The multiple regression technique allowed us to examine variation in the five conditions between experiments simultaneously. Most striking result of this analysis is the very low proportion of variance explained by the regression, the r^2 for GRC_{NAR} and GRC_{LAR} being 0.04 and 0.05, respectively. This implies that only 5% of the variation in these GRC values is statistically explained by variation in the five parameters. Differences in GRC values between the different groups and for two different daily quantum inputs were calculated with the coefficients from the multiple regression, thus correcting for variation in each of the other factors separately (Table 2). Most contrasts do not differ significantly from each other, the only exceptions being GRC_{SLA} at low and high daily quantum input ($P < 0.05$) and for glasshouse *vs.* growth chamber experiments. This suggests less of an association between LAR and RGR at higher light intensities. However, no such indications are found for NAR and LAR, and as they are based on a larger sample size we conclude that there is no increasing role for NAR with increasing irradiance. None of the other four factors was able to account for variation in GRC_{NAR} and GRC_{LAR} either, so that we still can not explain the observed variability. Of course, differential outcome between experiments may simply be a matter of differences in species selection. Larger-scale experiments with species from different environments and from different continents will be the only avenue towards better-founded generalisations.

5. Effect of light on RGR and its components

In section 4.2, we concluded that differences in the light climate do not explain the observed variation in the outcome of the experiments. Nevertheless, we pay some more attention to this factor, as it is an environmental variable that can differ dramatically between experiments, and has by itself a profound effect on the growth of plants.

Table 2. Average GRC values for: A, experiments carried out with monocots or dicots; B, comparisons made within a given genus (or species), or with species from different genera; C, experiments with plants grown in pots on a solid substrate (with or without addition of nutrient solution) or hydroponically; D, growth chamber or glasshouse experiments; E, a daily quantum input (DQI) of 10 or 30 mol m^{-2} day^{-1}. For all 57 experiments listed in appendix 2 we scored the values for these attributes. For experiments where both monocots and dicots were included we calculated the GRC values for each group separately. Dummy variables were created with a score of 0 or 1 to discriminate between the two alternatives for each of the first 4 factors. The DQI values were calculated from data given by the authors. For glasshouse experiments where no DQI values were available, we assumed a value of 7.5 mol m^2 day^1 for experiments conducted in the northern hemisphere in November, December, January or February, a value of 15 mol m^{-2} day^{-1} for experiments in September, October, March or April, and a value of 25 mol m^{-2} day^{-1} for experiments in May, June, July or August. Experiments in the southern hemisphere were scored the other way around. Subsequently, we carried out a multiple regression with each of the GRC values as the dependent variable, and the 5 attributes as independent variables. Thereafter, mean differences between groups were calculated, while controlling for differences in the other 4 attributes by giving them an intermediate value (0.5 for A to D, 20 for E). Values in bold indicate significant effects ($P < 0.05$).

	GRC_{NAR}	GRC_{LAR}	GRC_{SLA}	GRC_{LMR}
A. Monocots	0.10	0.92	0.71	0.02
Dicots	0.14	0.87	0.57	0.19
B. Within a genus	0.04	0.97	0.70	0.13
Between genera	0.20	0.82	0.58	0.08
C. Pots	0.24	0.76	0.58	0.00
Hydroponics	0.00	1.03	0.71	0.21
D. Glasshouse	0.15	0.86	**0.85**	0.11
Growth chamber	0.09	0.92	**0.44**	0.10
E. DQI = 10	0.19	0.82	**1.02**	0.05
DQI = 30	0.10	0.91	**0.69**	0.16
n	60	60	39	41
r^2	0.04	0.05	0.39	0.16

5.1 Is RGR determined by peak light intensity or daily light integral?

In nature, light intensity follows a sinusoidal pattern, with a maximum peak light intensity in the photosynthetically active spectrum around 2000 µmol m^2 s^{-1}. Compared to these values, irradiance in most experiments carried out in growth rooms is low, with values generally ranging between 125 µmol m^{-2} s^{-1} *(e.g.,* Grime & Hunt 1975) and 500 µmol m^{-2} s^{-1} *(e.g.,* Atkin *et al.* 1996). The reason for this is mainly a technical one, as very high light intensities often cannot be achieved in growth chambers. Another difference with the natural situation is that light in growth rooms is generally applied as a square wave, with a duration ranging mostly between 12 and 16 hours. Such a square wave has the advantage that environmental conditions are stable over the day and daily C-gain by photosynthesis can quite accurately be estimated from short-term measurements. One may wonder, however, if such differences in light climate invalidate experiments carried out in growth rooms. Clearly, 2000 µmol m^{-2} s^{-1} is a light intensity that - at sea level - can only be achieved in

summer, around noon and with a clear sky. Consequently, during most of the growing season, light intensity will be (far) less than the peak value. A variable that takes such diurnal variation into account is the total daily quantum input (DQI). During the growing season in the Netherlands (April - August) average DQI is 37.5 mol m^{-2} day^{-1} (Krijnen 1992). To achieve a similar quantum input in a growth room would require a quantum flux density of, for example, 650 µmol m^{-2} s^{-1} over 16 hours. Clearly, the 4- to 16-fold difference in peak light intensity between the field and the growth room is reduced to a 1.5- to 5-fold difference when the values integrated over the day are considered. This implies that the daily quantum input differs by far less than peak light intensity (Gamier & Freijsen 1994).
To what extent is RGR determined by (peak) light intensity and to what extent by total daily quantum input? To answer this question we carried out an experiment which we grew 2 species, *Hordeum vulgare* and *Helianthus annuus,* in a growth chamber at three light intensities (125, 250 and 500 µmol m^{-2} s^{-1}) and at three light periods (5, 10 and 20 h). Thus, we could analyse the effect of different light intensities at a given light period and of different light periods at a given light intensity. Moreover, due to the levels and durations used, we can compare for a given DQI whether it makes a difference to have a high light intensity over a short light period or a low light intensity during a long light period.
In Figure 6a, RGR of the two species is plotted against the daily quantum input. Lines connect observations for plants grown in the same light period. RGR is low at a low DQI, and shows an increase with higher levels, coming close to saturation around 20 mol m^{-2} day^{-1}. Similar experiments with different combinations of light intensity and duration have been carried out by Newton (1963), Hughes (1973) and Hurd & Thornley (1974), basically showing a comparable pattern of an increase in RGR up to a total quantum input of 20 (Fig. 6b). In fact, the observed patterns seem to be quite general. In all cases where RGR is determined for herbaceous species at various DQIs, RGR_{max} is realised around 20 mol m^2 day^1 (Fig. 6c). This is a somewhat different conclusion from that of Blackman & Black (1959), who stated that RGR continued to increase with increasing light levels, be it with the log of the light intensity. The reason for this is that in their experiments they did not arrive Is high enough to find complete saturation.

To what extent do different combinations of light intensity and duration at a given DQI yield different results? The main pattern for the 5 studies shown in Figures 6a and 6b is that results are almost independent of the light intensity used: generally a short light period with a high light intensity yields the same RGR as a long period with a low light intensity. Only in the case of tomato (Hurd & Thornley 1974) it seems that RGR is somewhat dependent on the light intensity as well: a high RGR is more readily achieved by a long period of low light than a shorter period of high irradiance.

A common characteristic in these studies is that they have been carried out in growth chambers, with fixed light intensities during the day. It has been shown by modelling exercises that for a given DQI there may still be a difference in A_a for leaves experiencing a constant light climate, or a variable one like in a natural day (Pons *et al.* 1994, Evans 1998, this volume). Would that imply that DQI is not a good descriptor for RGR in a variable light climate? Bula *et al.* (1959) and Hughes & Cockshull (1971) grew plants in growth cabinets with either a constant light

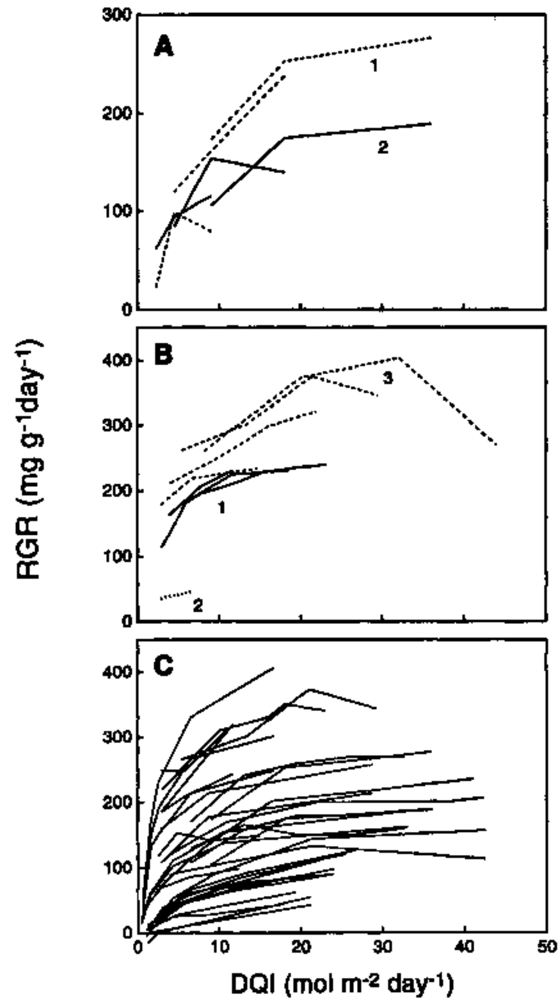

Fig. 6. (a) The effect of different combinations of light period and light intensity on the RGR of *Helianthus annuus* (1, dashed lines) and *Hordeum vulgare* (2, continuous lines). Values on the x-axis are the daily quantum input. The lines connect plants that were grown at a similar light period, but different light intensities, (b) *idem* for *Cucumis sativus* (1, Newton 1963), *Chrysanthemum morifolium* (2, Hughes 1973) and *Lycopersicon esculentum* (3, Hurd & Thornley 1974). (c) RGR as a function of DQI for a range of species, determined for at least 3 light intensities (Blackman & Black 1959, Evans and Hughes 1961, Friend *et al.* 1962, Hiroi & Monsi 1963, Rajan *et al.* 1973, Hurd & Thornley 1974, Pons 1977, Brewster & Barnes 1981, Hunt & Halligan 1981, Corré 1983a,b, Jeangros & Nößberger 1992, Ingestad *et al.* 1994).

level or with step changes in light intensity. They did not find any difference in biomass accumulation between treatments. In these cases, however, the maximum light intensity was still low and probably not sufficient to saturate photosynthesis. A difference was found for *Betula* seedlings, grown in an experimental garden in shade cages or in simulated forest gaps (Wayne & Bazzaz 1993), similar to that

observed by Hurd & Thornley (1974): long periods of lower light resulted in larger plants than shorter periods of bright light. Given the generally small differences in mass and the long period of growth, however, RGR differences were probably small. Bruggink & Heuvelink (1987) and Bruggink (1992) grew four crop species in a glasshouse, at various times of the year, with different amounts of shading and different amounts of supplemental lighting and determined shoot RGR. As with most other papers discussed above, the relationship between RGR and DQI was characterised by a simple, saturating curve. Therefore, we conclude that in studies on the RGR of plants, DQI is a much better descriptor of the light climate than (peak) light intensity. When short-term light flecks are involved, however, DQI is not necessarily the most appropriate parameter (Sims & Pearcy 1993).

5.2 Effect of light intensity on growth components

It has been known for long that light has opposing effects on NAR and LAR (Blackman & Wilson 1951, Hughes 1966, Pons 1977, Björkman 1981). That is, with an increase in quantum input, NAR increases, basically due to an increase in photosynthesis per unit leaf area. At the same time LAR decreases, however, resulting in a stimulation of RGR far less than expected from the A_a values. Some authors have noted that the decrease in LAR is mainly due to a decrease in SLA in their experiments (Hughes 1966, Pons 1977, Hunt & Halligan 1981). Others, *e.g.* Brouwer (1963, 1983) and Kuroiwa *et al.* (1964), have suggested an important role for biomass allocation in the response of plants to light. In the concept of Brouwer (the 'functional equilibrium') biomass allocation to the shoot increases with decreasing light intensity, because this is the organ that is closest to the most limiting factor, carbohydrates in the case of low irradiance. In this section we make a quantitative analysis of the literature, to assess how the different growth parameters respond. As a parameter for allocation we take LMR rather than the shoot:root ratio used by Brouwer, because LMR is a more appropriate parameter in the context of growth analysis. As various authors have used different degrees of shading, and different light intensities for their control, unshaded plants, we plotted all values against DQIs, as far as available. Trends in NAR and LAR are as expected (Figs 7a,b). The increased LAR is almost fully due to increases in SLA, whereas LMR remains constant (Figs 7c,d). It would be useful to have a parameter that summarises the various experiments by just one or two numbers, and to include those experiments where DQI was not determined. Therefore, we chose an approach, where we took the change in RGR as the basis of the comparison and calculated for each individual species to what extent and in which direction a change in RGR was accompanied by a change in the different growth parameters. In fact, this is the same analysis as that of the GRCs presented in section 3, with the differences in RGR now being caused by differences in irradiance rather than that by comparing faster- and slower-growing species. The relationships between NAR or LAR on the one hand and RGR on the other are partly curved and, consequently, the GRCs obtained represent average changes in growth parameters, approaching the real changes best at intermediate light intensities.

In total we analysed 24 reports with 49 growth *vs.* irradiance curves. A summary of the GRC values is given in Figure 8. An increase in RGR by a factor 1 is, on average, accompanied by an increase in NAR of a factor 2. This is compensated for

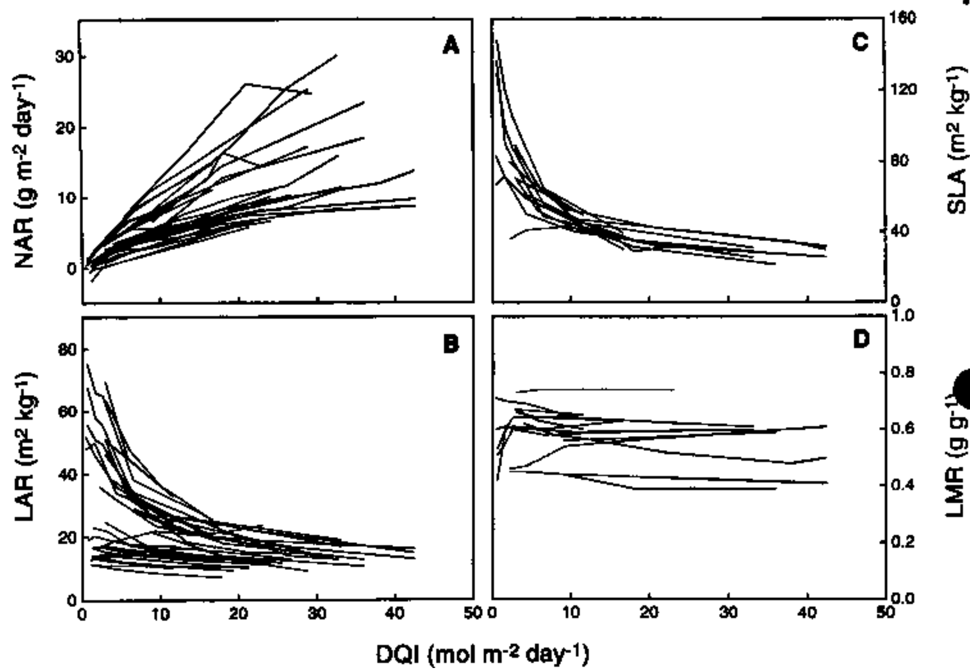

Fig 7. The effect of DQI on (a), NAR; (b), LAR; (c), SLA and (d), LMR for a range of species. Values were obtained from the experiments listed in the legend of Figure 6c, with the exception of Friend *et al.* (1962).

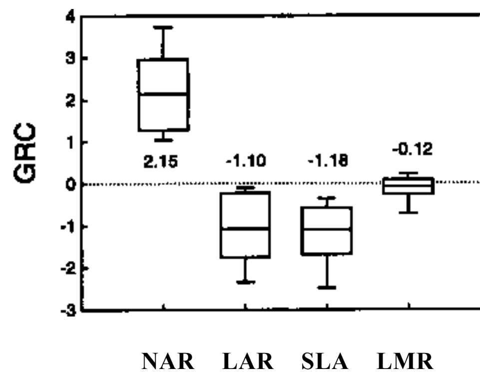

Fig. 8. The effect of DQI on the change in NAR, LAR, SLA and LMR, relative to the change in RGR. Values were calculated as GRCs for each individual species for the experiments listed in the legend of Figure 6c plus those from Pearce & Grubb 1982, Van Dobben 1984, Knight & Mitchell 1988, Grime *et al.* 1989, Brewster 1990, Poorter 1991, Mooney *et al.* 1995 and Van der Werf *et al.* 1996. Boxes indicate the 10th, 25th, 50th, 75th and 90th percentiles, the numbers the 10%-trimmed mean values.

by a decrease in LAR to half its low-light value. The decrease in LAR is mainly due to a change in SLA, whereas LMR is hardly affected. Thus, we conclude that, with the exception of some particular species *(cf.* Björkman 1981, Clabby & Osborne 1997), the evidence in the literature is contrary to the expectations by Brouwer with regard to the 'functional equilibrium'. That is, there are differences in allocation due to differences in irradiance, but they take place between roots and stems. Remarkably, allocation to the leaves is unaffected (Pons 1977, Hunt & Halligan 1981, Corré 1983a). Similar observations have been made for plants grown at elevated atmospheric CO_2 concentrations, where LMR is hardly affected either (Poorter *et al.* 1996). According to Brouwer's model, a decrease in the investment in leaves is expected because the carbohydrate availability of the plant increases, Therefore, we conclude that the so-called functional equilibrium does not adequate-ly cover the whole-plant responses after an environmental change affecting photosynthesis. A more appropriate parameter to use would be the LAR, as changes in this parameter follow Brouwer's concept of a functional equilibrium much better.

5.3 The negative relation between NAR and LAR

It is a key question what causes the strong negative relation between NAR (more specifically A_a and LAR (more specifically SLA). Such a negative relation can be found for plants grown at various irradiances or atmospheric CO_2 concentrations. Interestingly, it can also be observed in genotypes where a lower A_a is due to lower chlorophyll or Rubisco levels (Table 3). The simplest explanation is that high-light grown plants accumulate more photosynthetic compounds per unit leaf area, which increases photosynthetic capacity but at the same time decreases SLA. This is best illustrated by considering the inverse of SLA, the leaf mass per unit area. Suppose a low-light grown leaf would have a mass of 25 g per m^2 leaf area, 5 g of which are invested in 'photosynthetic compounds'. Let us also assume that photosynthetic capacity is proportional to the amount of photosynthetic compounds. Doubling photosynthetic capacity would then require an extra 5 g, resulting in a total leaf of 30 g m^{-2}. This would by itself suffice to cause a slight negative relation between A_a and SLA. However, the negative relation is stronger than that. In the hypothetical example, the concentration of photosynthetic compounds expressed on a leaf mass basis would increase from 20 to 33%. In reality, photosynthetic capacity per unit leaf mass is similar for low-light and high-light grown plants (Sims & Pearcy 1994, Evans 1998, this volume). This implies that the extra 5 g investment in photosynthetic compounds per m^2 is accompanied by 20 g of other constituents, resulting in a leaf mass per area of 50 g m^{-2}. Consequently, a 100% increase in photosynthetic capacity coincides with a reduction in SLA by 50%, which is in line with the data presented in Figure 8. The reason that the increase in investment of photosynthetic compounds coincides with an increased investment in non-photosynthetic material might be that larger and/or more mesophyll cells have to be formed to ensure good contact between chloroplasts and intercellular spaces (see Evans 1998, this volume, for a more extended discussion).

Table 3. Percentage increase in A_a of individual leaves, SLA, LMR and RGR, of low-light grown plants (200 µmol m^{-2} s^{-1}) compared to high-light grown plants (1000 µmol m^{-2} s^{-1}), plants grown at elevated CO_2 (700 µl l^{-1}) compared to control CO_2 levels (350 (µl l^{-1}), and of variegated (non-chlorophyllous for part of the leaves) and antisense Rubisco plants compared to wildtype plants, nd, not determined.

Species	A_a	SLA	LMR	RGR	Reference
Low light					
4 woody species	-69	59	1	nd	Poorter & Evans, (1998)
6 herbaceous species	-67	75	8	nd	Poorter & Evans, (1998)
Elevated CO_2					
10 species	20	-8	2	13	Poorter (1993)
Variegation					
Agonis flexuosa	-50	89	3	nd	Downton & Grant (1994)
Nerium oleander	-52	69	31	nd	Downton & Grant (1994)
Antisense Rubisco					
Nicotiana tabacum	-75	118	10	-32	Fichtner *et al.* (1993)
Nicotiana tabacum	-62	105	5	-10	Masle *et al.* (1993)

It has been suggested that plants respond to high irradiance by maximising photosynthetic capacity, whereas they respond to low light by maximising light interception. As discussed above, this would coincide with high-light grown plants having a low SLA and low-light plants having a high SLA. Following this strategy would enable a plant to maximise carbon gain at both high and low irradiance. Such a hypothesis does not fit, however, with experiments where light conditions are suddenly altered during growth. Plants grown at low light that are transferred to high-light conditions grow faster or have higher carbon gain than plants acclimated to high light (Blackman & Wilson 1954, Evans & Hughes 1961, Rice & Bazzaz 1989, Sims & Pearcy 1994). This might be explained by the results of modelling exercises by Pons *et al.* (1994) and Evans (1998, this volume). They show that high-SLA leaves with a low area-based photosynthetic capacity always gain more C per unit leaf mass than low-SLA leaves with a higher capacity. Remarkably, the low-light plants transferred to high light do not show this increased carbon gain for prolonged periods of time, as SLA of these plants drops quite quickly to values similar to high-light grown plants (Blackman & Wilson 1954, Evans & Hughes 1960). Might this be a consequence of a high rate of transpiration that coincides with a relatively high leaf area ratio and high light? In the experiment of Sims & Pearcy (1994), where low-light plants were measured at high-light conditions, transpiration rate per unit plant mass, as well as instantaneous water-use efficiency, were not different from plants that had been grown at high light. They suggest that protection from photoinhibition could cause plants to decrease SLA at high irradiance.

An alternative explanation for the temporarily faster growth of low-light plants at high light is that plants grown at high irradiance do not necessarily maximise carbon gain. In fact, such a conclusion could also be drawn from Figure 6c, where RGR was found to be relatively constant over a wide range of DQIs. Why are plants not able to grow faster when DQI increases beyond a value of 20 mol m^{-2}

day^{-1}? It is clear, for example from studies on CO_2 enrichment, that source:sink interactions may play a role in shaping the C-economy of the plant. An increased rate of photosynthesis due to a doubling in CO_2 concentration often results in a downward acclimation of photosynthesis and a decrease in SLA, mainly due to accumulation of non-structural carbohydrates. If growth would be constrained by internal factors, such as the formation of new sinks in the plants, the result could be that the increased photosynthetic rate, almost inevitably at high irradiance, has to be counterbalanced by a decrease in SLA. Although not easily testable, this is an alternative hypothesis that should be seriously considered. If found to be true, it would have important ramifications, not only for understanding the response of plants to light intensity, but also in the analysis of the causes of variation in growth rate between fast- and slow-growing species.

6. The effect of the daily quantum input on RGR and growth components of fast- and slow-growing species

In the meta-analysis of section 4.2, we found no indication that experiments carried out at high DQI result in a more important role for NAR in explaining inherent variation in RGR than those conducted at lower quantum input. This is only an indirect indication, however, as different species are compared in different experiments. A more direct test would be to grow different species at various light intensities, and assess in what direction and to what extent the underlying components are going to change. We carried out such an analysis with two grass species *(Holcus lanatus* and *Deschampsia flexuosa),* that were grown at a light intensity twice higher (630 µmol m^{-2} s^{-1}) or half that (150 µmol m^{-2} s^{-1}) of the experiment on the 43 species, described in Section 2. More details are given in the legend of Table 4. Growth parameters alter as expected from section 5.2, with an increase in RGR with increasing DQI, due to an increase in NAR and a decrease in LAR. For this specific case, a decrease in LMR was also observed. As far as the relative difference between the species is concerned, we conclude from this experiment that there is some support for the the-ory that NAR becomes more important in explaining variation in RGR when DQI increases. Even at the highest DQI, however, differences in RGR were explained more by LAR than by NAR, GRC_{NAR} being 0.27 only.

Table 4. The effect of low (160 µmol m^{-2} s^{-1}; DQI = 8 mol nr^{2} day^{1}) and high (630 µmol m^{-2} s^{-1}; DQI = 32 mol m^{-2} day^{-1}) irradiance on RGR and the components NAR, LAR, SLA and LMR of the slow-growing grass *Deschampsia flexuosa* (Df) and the fast-growing grass *Holcus lanatus* (Hl). Other conditions were as described by Poorter & Remkes (1990). Data from Poorter (1991).

Parameter	DQI = 8		DQI = 32	
	Df	Hl	Df	Hl
RGR (mg g^{-1} day^{-1})	104	197	170	286
NAR (g m^{-2} day^{-1})	6.5	5.5	15.4	17.7
LAR (m^2 kg^{-1})	19	38	11	16
SLA (m^2 kg^{-1})	38	70	24	38
LMR(g g^{-1})	0.56	0.54	0.47	0.42

To what extent are these observations supported by other experiments? To answer this question, we screened the literature on growth analyses on various species at different light intensities. Provided that the difference in RGR between the species at high light was at least 40 mg g^{-1} day^{-1} and DQIs were given, we calculated the GRC_{NAR} and GRC_{LAR} at each light treatment and plotted these values against the DQI (Fig. 9). From the scarce literature available, we conclude that there is no evidence for an increasing importance of NAR, and a decreasing importance of LAR in explaining inherent variation in RGR with increasing irradiance. On the con-trary, these data are fully in line with the conclusion drawn in the meta-analysis (section 4.2), that GRCs are independent of quantum input.

The analyses in this chapter have been confined to herbaceous species, with an emphasis on crop species and wild species occurring along a nutrient-poor to nutri-ent-rich gradient. Atkin & Lambers (1998, this volume), concluded that SLA could also explain RGR differences between alpine and low-land species. Differences in SLA were present even under high-light conditions in the field. Veneklaas & Poorter

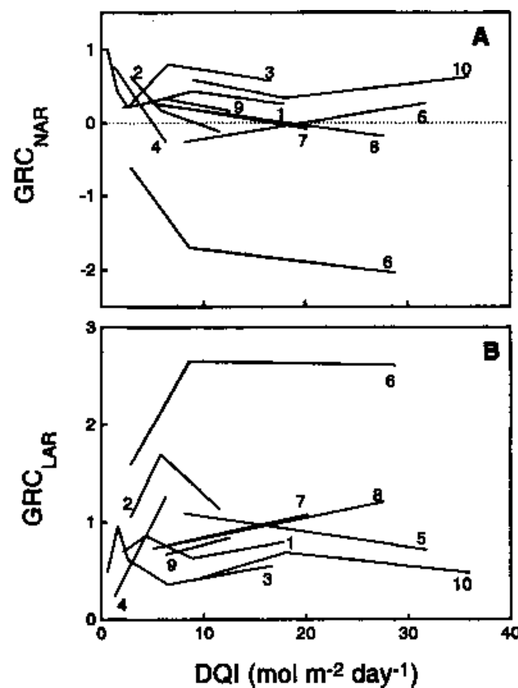

Fig. 9. (a) GRC_{NAR} and (b) GRC_{LAR} values for comparative experiments in which the growth of plants was studied at various daily quantum inputs. Only those experiments were included in which vegetative, whole plants were measured and in which RGR differed between the fastest- and the slowest-growing species at the highest irradiance by at least 40 mg g^{-1} day^{-1}. Lines connect the data for a given experiment. Data are from Blackman & Black 1959 (1 in the graph panels, n = 2 species), Corré 1983a (2, n=2), Corré 1983b (3, n=3), Grime *et al.* 1989 (4, n = 2), Poorter 1991 (5, n = 2), Jeangros & Nößberger 1992 (6, n=2), Mooney *et al.* 1995 (7, n=2), Van der Werf *et al.* 1996 (8, n = 2), Hunt & Cornelissen 1997 (9, n=29) and *Helianthus annuus* and *Hordeum vulgare* (H. Poorter, unpublished, 10).

(1998, this volume), however, found rather contrasting results when growth parameters of tropical tree seedlings were compared. In their study, LAR is the explaining factor for variation in RGR at low light, whereas NAR is the major component at higher light intensities. This is possibly due to the fact that they contrast fast-growing pioneer species and slow-growing, shade-tolerant climax species. If seedlings of climax species grow well in the shade, but saturate with respect to RGR and NAR at intermediate light levels due to a low photosynthetic capacity, GRC_{NAR} may become an important factor at high light in such comparisons. Clearly, we only begin to understand how variation in RGR between ecologically different groups of species is brought about.

7. Conclusions

In this chapter we described an approach to compare results across experiments, enabling generalisations on the causes of variation in RGR. Analysed from the perspective of the carbon economy, inherently fast-growing species achieve a higher growth rate mainly because they develop relatively more leaf area per unit plant mass. The main cause for this difference is the higher SLA of the fast-growing species. Differences in the physiological activity per unit leaf area are less important. It is therefore of main interest to analyse what factors cause the difference in SLA between species. These conclusions are basically independent of the daily quantum input during the experiment, the type of rooting substrate used, the order from which the plants are taken (monocots or dicots), and also independent of the fact whether species are from the same genus or not. Therefore, it remains unclear why different experiments may yield different results. A third topic that warrants more study is the strong negative relation between NAR and LAR. What are the mechanisms that cause SLA to increase if photosynthesis is decreased and *vice versa,* causing RGR to be relatively stable under varying conditions. Answers to these questions would greatly enhance our insight into the regulation of the growth of plants.

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Appendix 1. Calculation of Growth Response Coefficients

Suppose we have 2 species, A and B, for which there are observations on RGR (R_A and R_B), NAR (N_A and N_B) and LAR (L_A and L_B). Given that R = N * L, the relative difference in R between the species should equal the relative difference in N * L:

$$\frac{R_A}{R_B} = \frac{N_A * L_A}{N_B * L_B} \qquad \text{(A1)}$$

By ln-transformation, we arrive at:

$$(\ln R_A - \ln R_B) = (\ln N_A - \ln N_B) + (\ln L_A - \ln L_B) \qquad \text{(A2)}$$

Thus, the difference in In-transformed RGR values is the sum of the differences in ln-transformed NAR values and ln-transformed LAR values. This can be converted to:

$$1 = \frac{(\ln N_A - \ln N_B)}{(\ln R_A - \ln R_B)} + \frac{(\ln L_A - \ln L_B)}{(\ln R_A - \ln R_B)} \qquad \text{(A3)}$$

Consequently, the first part of the right-hand term gives the fraction of the RGR difference that is associated with variation in NAR, and the second part the fraction associated with variation in LAR. If the components in equation Al have been calculated correctly and RGR is indeed exactly the product of NAR and LAR, then these fractions, which we call the 'Growth Response Coefficients' (GRC), should add up to 1:

$$GRC_{NAR} + GRC_{LAR} = 1 \qquad \text{(A4)}$$

When growth parameters are calculated in the 'classical way' (Evans 1972) RGR foes not always exactly equal NAR * LAR and therefore, the sum of the GRCs will not exactly equal 1.0. However, generally deviations are within 10% and should not affect the analysis to a large extent. In a similar way as in eqn. Al, RGR can be defined as the product of NAR, SLA and LMR. Then, equation A4 becomes:

$$GRC_{NAR} + GRC_{SLA} + GRC_{LMR} = 1 \qquad \text{(A5)}$$

Basically, the components of equation A3 are the slopes of the In-transformed NAR and LAR values plotted against In-transformed RGRs. In experiments with more than two species (or treatments) these components can be replaced by the slopes estimated from a linear regression with ln(NAR) or ln(LAR) as the dependent variable, and ln(RGR) as the independent variable.

Consequence of this approach is that variability within the data that is not covered by the linear equation is ignored. For data with a low correlation coefficient this implies that some extra random variation is generated for GRC.

For a given growth component GRC can also be written as:

$$GRC_X = \frac{\ln X_A - \ln X_B}{\ln R_A - \ln R_B} = \frac{\Delta \ln X}{\Delta \ln R} \tag{A6}$$

If we assume that the In-transformed growth components are linearly related to the ln-transformed RGR values over the whole RGR trajectory under study, then the ratio of the differences holds for infinite small differences as well. In that case,

$$GRC_X = \frac{\Delta \ln X}{\Delta \ln R} = \frac{d \ln X}{d \ln R} = \frac{dX}{X} \bigg/ \frac{dR}{R} \tag{A7}$$

which equals the definition of GRC given in section 3. Note that GRC_X values represent the relative change in parameter X divided by the relative change in RGR, and, consequently, are without dimensions.

This concept was used before in a slightly different way by Poorter (1989) and Lambers & Poorter (1992) and denoted as 'Percentage Increase' or 'Degree of Association'.

Appendix 2.

List of 57 experiments and GRC values used in the compilation. Data presented by Tognoni *et al.* (1967), Stockey & Hunt (1984) and Atkin *et al.* (1996) were not included, because the sum of GRC_{NAR} and GRC_{LAR} deviated by more than 0.25 from unity. DQI values that could not be calculated from the data in the papers were estimated as high (H), intermediate (I) or low (L) according to the rules described in the legend of Table 2.

Reference	number of species/ genotypes	DQI (mol m^{-2} day^{-1})	RGR difference mg g^{-1} day^{-1})	GRC_{NAR}	GRC_{LAR}	GRC_{SLA}	GRC_{LMR}
Blackman & Wilson (1951)	3	I	88	0.41	0.63		
Blackman & Wilson (1951)	2		50	-0.66	1.71		
Tsunoda (1959)	11	I	161	0.38	0.62		
Warren Wilson (1966)	3	H	122	-0.09	1.08		
Thome et al. (1967)	2	15	70	1.28	-0.31		
Higgs& James (1969)	4	I	86	0.22	0.88		
Eze (1973)	2	39	97	0.82	0.26	-0.34	0.60
Rajan *et a/.* (1973)	3	49	109	0.89	0.19	0.31	-0.12
Smith & Walton	3	H	46	0.80	0.32		
Potter & Jones (1977)	6	23	92	0.46	0.54	0.70	-0.17
Patterson *et al.*	3	41	124	1.08	-0.09		
Elias & Chadwick (1979)	40	13	134				-0.08
Grime (1979)	15	11	271	-0.07	1.07		
Woodward (1979)	2	19	95	0.44	0.56		
Sionit *et al.* (1982)	3	60	83	-0.18	1.18		
Cook & Evans (1983)	41	H	54	0.43	0.57	0.38	0.19
Corré (1983a)	4	H	162	0.18	0.82	0.79	-0.19
Corré (1983a)	3	19	160	0.59	0.41	0.24	0.11
Corré (1983b)	4	4	52	0.35	0.45	0.94	-0.06
Corré (1983c)	2	I	94	0.63	0.39	0.42	-0.05
Woodward (1983)	2	19	60	0.51	0.49	0.86	-0.37
Kriedemann & Wong (1984)	2	I	75	0.19	0.81		
Paul *et al.* (1984)	5	35	40	0.28	0.77		
Roetman & Sterk (1986)	13	7	137	0.40	0.60	0.59	0.05
Bruggink & Heuvelink (1987)	3	H	105	-0.16	1.01		
Bunce (1989)	3	22	80	1.86	-0.86		
DeLucia *et* al. (1989)	2	40	70	-0.69	1.69		
Dijkstra & Lambers (1989)	2	13	68	-0.29	1.29	1.18	0.16
Grime *et al.* (1989)	2	6	44	0.31	0.71	1.86	-0.66
Poorter (1989)	8	11	132	-0.37	1.41	0.86	0.51
Muller & Gamier (1990)	2	20	55	-0.20	1.20	1.63	-0.50
Poorter & Remkes (1990)	24	16	252	0.18	0.87	0.56	0.28
Poorter (1991)	2	32	116	0.27	0.72	0.88	-0.22
Fichtner & Schulze (1992)	9	30	112	0.47	0.52	0.96	-0.40
Gamier (1992)	14	32	180	0.68	0.35	0.42	-0.07
Jeangros & Nößberger (1992)	2	29	44	-1.77	2.61	1.95	0.66

Reference	number of species/ genotypes	DQI (mol m^{-2} day^{-1})	RGR difference mg g^{-1} day^{-1})	GRC_{NAR}	GRC_{LAR}	GRC_{SLA}	GRC_{LMR}
Masle *et al.* (1992)	29	15	132	0.85	0.15		
Bowler & Press (1993)	2	32	65	-0.32	1.08		
Marañon & Grubb (1993)	27	17	199	-0.38	1.38	0.66	0.31
Van der Werf *et al.* (1993)	5	15	134	0.30	0.70	0.81	0.14
Wong (1993)	2	H	80	-0.11	1.11		
Nagel *et al.* (1994)	2	16	74	0.13	0.96	0.77	0.19
Poorter *et al.* (1995)	2	16	129	0.32	0.75	0.85	-0.10
Ryser & Lambers (1995)	2	H	71	0.52	0.48	0.55	-0.08
Ziska & Bunce	3	30	54	-0.50	1.53		
Den Dubbelden & Verburg(1996)	12	16	85	-0.01	1.03	0.50	0.57
Meerts & Gamier (1996)	11	30	73	-1.89	2.89	1.42	1.40
Roumet et *al.* (1996)	11	23	76	0.18	0.93	0.54	0.39
Van der Werf *et al.* (1996)	2	28	106	-0.18	1.21	0.82	0.40
Virgona & Farquhar (1996)	7	I	98	1.13	-0.14	-0.12	-0.06
Virgona & Farquhar (1996)	15	I	81	1.06	-0.10	-0.24	0.16
Hunt & Cornelissen (1997)	42	13	206	0.23	0.69	0.57	0.08
Visser(1997)	2	H	64	1.13	-0.13	-0.62	0.20
McKenna & Shipley (1998)	28	32	196	0.95	0.02	-0.19	0.24
Van der Werf *et al.* (1998)	68	15	232	0.26	0.75	0.49	0.25
J.G. Hamilton, unpublished	4	15	137	0.09	0.93	0.65	0.28
J.J.C.M. Van & A. Van der Werf, unpublished	7	16	97	0.28	0.75	0.57	0.08