

- Introduction
- The Concept of Growth
- The Components of RGR
- Variation in RGR between Species
- Environmental Influences on Growth: the Shoot Environment
- Environmental Influences of Growth: the Root Environment
- Ecological Significance of Variation in RGR

# Plant Growth and Carbon Economy

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Plant growth can be defined as the increase in biomass over time. The rate of growth depends on the daily amount of carbon fixed in photosynthesis, the amount of carbon used for respiration as well as the carbon concentration of the newly formed material.

## Introduction

In the period between seed germination and onset of senescence, plants may increase in mass by a factor one thousand to more than a million. This process has intrigued people ever since Aristotle, who wondered how plants – unlike animals – were growing without visibly consuming food. The first scientific experiment on this topic was probably carried out in the sixteenth century by Jan van Helmont. He tested the hypothesis that the increase in plant mass was balanced by a similar decrease in mass of the soil. Based on sequential data for plant and soil mass, he could clearly dismiss this idea. However, it was not until the discovery of the processes of photosynthesis and respiration that the factors underlying plant growth could be properly studied.

in plant size, which necessarily requires a relatively larger investment in support structure. However, since in most cases the increase in biomass will be to a large extent proportional to the biomass already present, it remains appropriate to use RGR as the descriptor of growth. The concept of proportional growth is less suitable when plants grow in competition, or enter the generative phase. Under these conditions, where growth levels off quite quickly because of light interception by neighbours or even stops because of developmental triggers, it is more appropriate to use other growth functions, such as an exponential or sigmoid function (**Figure 1a**; Causton and Venus, 1981; Goudriaan and Monteith, 1990).

## The Concept of Growth

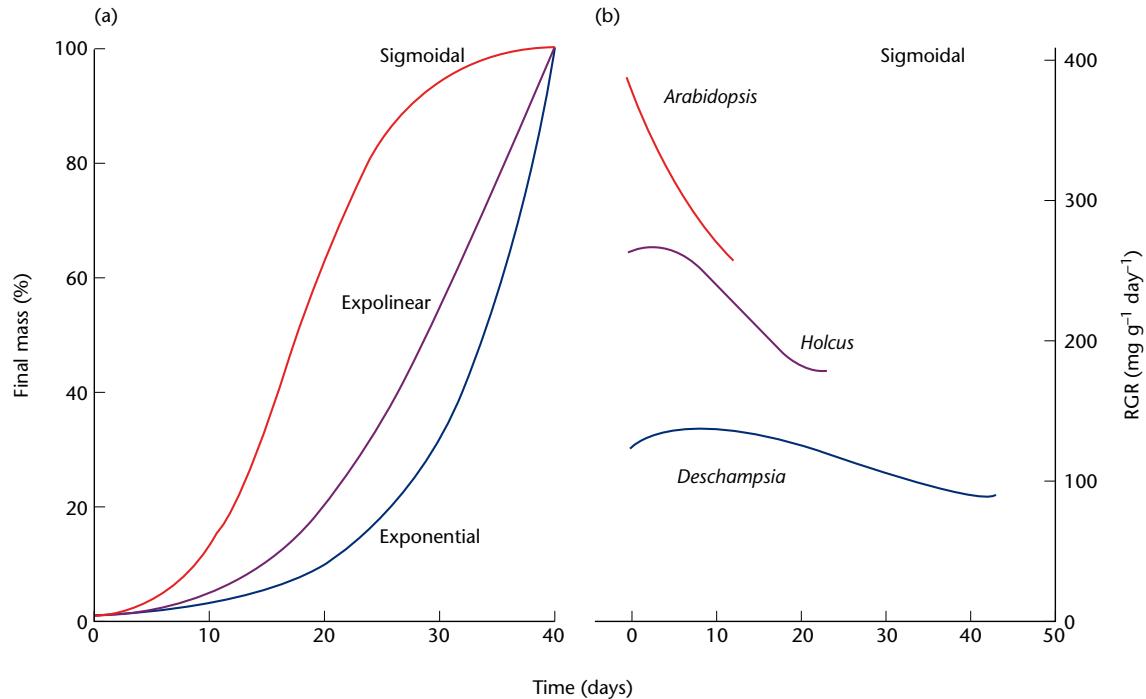
The basis for the analysis of plant growth was laid in the 1920s, when it was realized that the increase in biomass of a seedling is more or less proportional to the amount of biomass already present. This is similar to money accumulating in a bank account, and economic theory was used to describe growth in mathematical terms. In this approach, the rate of plant growth is similar to the concept of interest rate, and is given as ‘relative growth rate’ (RGR). In eqn [1]

$$M_2 = M_1 \cdot e^{\text{RGR}(t_2 - t_1)} \quad [1]$$

where  $M_1$  and  $M_2$  are the mass of the plants at time  $t_1$  and  $t_2$ , respectively, and RGR is defined as the rate of increase in biomass per unit plant mass already present. If RGR is constant over time, then plants will increase in mass in an exponential way (**Figure 1a**). Strictly speaking, plant growth is never truly exponential. As the increase in mass depends on the rate of photosynthesis, which in turn is affected by light intensity, growth will inevitably fluctuate over the day due to changes in solar radiation. At night, RGR will even be negative, as plants lose weight because of respiration. During plant development, RGR will gradually decrease (**Figure 1b**) due to self-shading and/or because of an increase

## The Components of RGR

The main driving factor for growth is the process of photosynthesis, in which atmospheric carbon dioxide is reduced to sugars with the help of light energy. Part of the photosynthetically fixed carbon (C) will be respired, providing the energy (ATP) and reducing equivalents (NADH, NADPH) to power the processes of nutrient uptake, transport, growth and maintenance of biomass. Apart from respiration, plants may also physically lose organic compounds due to volatilization, exudation, the death of leaves, branches or roots, and consumption by herbivores. Under the assumption that these latter processes are quantitatively of no importance, RGR could be factorized into five components. The first is the rate of whole plant photosynthesis per unit leaf area, integrated over the day ( $\text{PS}_A$ ; mol C fixed  $\text{m}^{-2}$  leaf area  $\text{day}^{-1}$ ). The second component is the fraction of the daily fixed carbon that is not respired by the various organs of the plant but is incorporated in the ‘structural’ biomass of the plant (FCI, mol C incorporated  $\text{mol}^{-1}$  C fixed). The third component is the specific leaf area (SLA;  $\text{m}^2$  leaf area  $\text{kg}^{-1}$  leaf mass), by which the amount of fixed C available for growth can be converted from a leaf area to a leaf biomass basis. The fourth factor is the leaf mass fraction (LMF;  $\text{g leaf g}^{-1}$



**Figure 1** (a) Time course of plant mass following growth in an exponential, an expolinear or sigmoidal way. The curves are hypothetical examples, for which the mass after 40 days is set to 100%. (b) Time course of RGR for different species grown in conditions of unlimited water and nutrient supply (*Arabidopsis thaliana* (unpublished data from D. Tholen), *Holcus lanatus*, *Deschampsia flexuosa*). Day 0 indicates the first harvest of the seedlings.

total plant mass), by which the amount of fixed C available for growth can be converted from a leaf mass to a total plant mass basis. The last component is the carbon concentration of the plant ( $[C]$ ,  $\text{mol C g}^{-1}$  dry weight), which has to be known in order to calculate how much new biomass can be formed with 1 mol of available carbon. In eqn [2]

$$\text{RGR} = \frac{\text{PS}_A \text{ FCI SLA LMF}}{[C]} \quad [2]$$

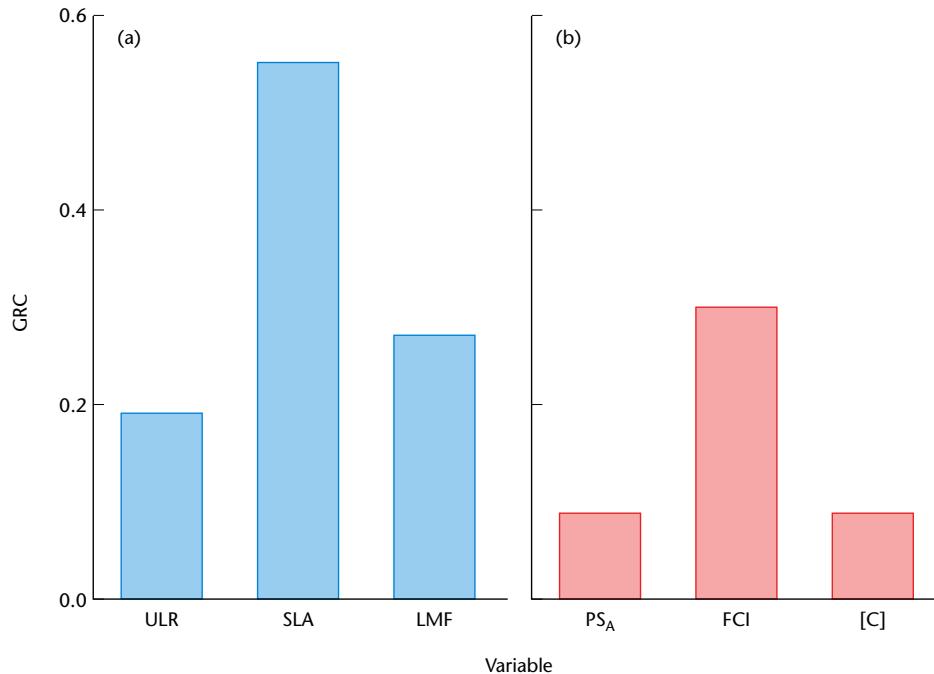
Generally, photosynthesis measurements are carried out on a specific leaf during only part of the day period, and often under close to light-saturating conditions. These are not necessarily the right data to evaluate the factors underlying eqn [2], as other leaves may be in another physiological stage and/or another environment because of shading. Similarly, it is not easy to assess the daily respiration of the plant, especially as it comes to below-ground organs. A simplified approach is to harvest plants over the period of interest and to calculate the increase in biomass per unit leaf area and per unit of time. This factor is called the unit leaf rate (ULR;  $\text{g dry mass increase m}^{-2}$  leaf area  $\text{day}^{-1}$ ), and depends on  $\text{PS}_A$ , FCI and  $[C]$ . The formula for RGR then becomes:

$$\text{RGR} = \text{ULR} \cdot \text{SLA} \cdot \text{LMF} \quad [3]$$

Differences in ULR between species or treatments often correlate well with differences in the rate of whole plant photosynthesis per unit leaf area, but there will be cases in which the fraction of daily fixed carbon not respired by the plant, as well as the C concentration of the plant biomass may play an additional role.

## Variation in RGR between Species

Plant species differ in the rate of growth they can achieve, even when they are all grown under optimal conditions. Some species grow fast and double in biomass within a period of 2–3 days. Others, notably tree seedlings, grow much slower and may have doubling times of 50 days or more. What are the causes behind this inherent variation in maximal growth rate? This can best be analysed using a parameter termed ‘growth response coefficient’ (GRC). GRCs indicate the proportional change in one of the growth parameters underlying RGR relative to the proportional change in RGR itself. The sum of the GRCs for the parameters of eqn [2] as well as eqn [3] add up to 1, and each of the GRC values indicates the relative importance of a growth parameter in explaining the variation in RGR. **Figure 2a** shows for a specific experiment



**Figure 2** Growth response coefficients (GRC) for the C-budget variables that underlie interspecific variation in relative growth rate (RGR). Each GRC value indicates to what extent a change in the parameters of eqns [2] and [3] scales with the relative change in RGR. Data in (a) are for measured growth parameters, data in (b) for the factors underlying unit leaf rate (ULR). Derived from Poorter *et al.* (1990). SLA, specific leaf area; LMF, leaf mass fraction; PS<sub>A</sub>, daily whole plant photosynthesis per unit leaf area; FCI, fraction of daily fixed carbon that is incorporated in the plant; [C], carbon concentration.

**Table 1** Average growth response coefficients for 60 growth experiments in which different herbaceous species or genotypes were analysed for growth components underlying relative growth rate (after Poorter and Van der Werf, 1998)

	GRC
ULR	0.26
SLA	0.63
LMF	0.11

in which all parameters of eqns [2] and [3] were measured for a range of herbaceous species, that SLA and LMF explain most of the variation in growth between the species, and ULR least. For the components underlying ULR, it is not so much the difference in PS<sub>A</sub> that explains the variation, but rather the fact that fast-growing species spend less of their daily fixed C in respiration and therefore retain more for growth (**Figure 2b**).

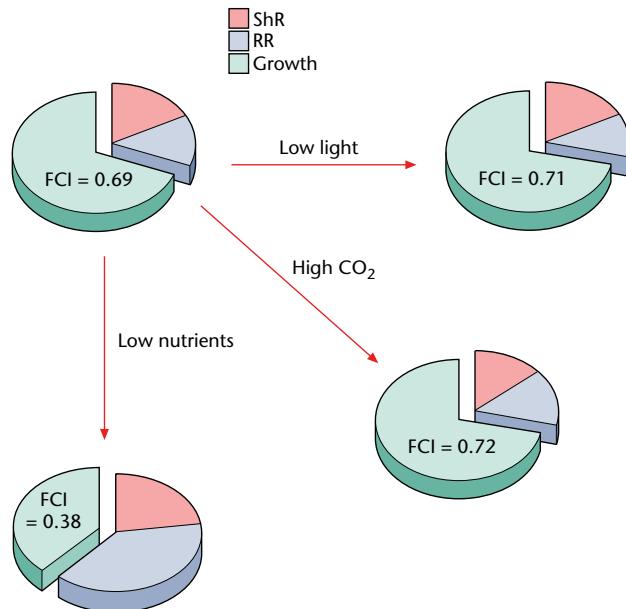
How general are these results? In a survey of 60 published experiments with herbaceous plants, it was found that, on average, species differed most in SLA and less in ULR and LMF (**Table 1**). Thus the fastest growing species under optimal conditions were those that had the highest SLA. Similar results have been found for tree species. However, when shade species – plants that

generally grow in places with low light intensities – are compared with sun species, it turns out that species-specific differences in RGR are determined more by ULR than by SLA or LMF, at least for plants that are grown at higher light intensities. It should be kept in mind that these are general rules, with considerable variability depending on species and experimental conditions.

## Environmental Influences on Growth: the Shoot Environment

Quite often analyses comparing species have been carried out under close-to-optimal conditions. These are generally not the conditions that prevail in the natural environment. As plants are sessile organisms, they only have a limited ability to avoid (temporarily) unfavourable environmental conditions. Therefore, it could be expected that they have a genetic programme that enables them to acclimate to a sub- or supra-optimal environment.

One of the most dynamic environmental factors is light. It may not only differ between habitats, but also strongly vary in a period of seconds, over the diurnal period as well as over seasons. The momentary effect of a decrease in irradiance is a decrease in the rate of photosynthesis per unit leaf area. When plants remain in low light over a



**Figure 3** Carbon budgets of plants grown under various environmental conditions. The upper left panel indicates what fraction of the daily fixed C is spent in shoot (ShR) and root respiration (RR), and what fraction is used for growth (FCI), for a plant grown at a daily quantum input of  $16 \text{ mol m}^{-2} \text{ day}^{-1}$ , a  $\text{CO}_2$  concentration of  $350 \mu\text{L L}^{-1}$  and an unlimited nutrient and water supply (hydroponics). The other three panels indicate how the carbon budget changes in plants grown with less light ( $8 \text{ mol m}^{-2} \text{ day}^{-1}$ ), a higher  $\text{CO}_2$  concentration ( $700 \mu\text{L L}^{-1}$ ) or a lower N supply. Data based on various observations for *Holcus lanatus* and *Plantago major*.

longer period of time, the rate of respiration will decrease as well, the net result being that the fraction of the daily fixed C incorporated in the plant biomass (FCI) remains largely similar to that of high-light grown plants (Figure 3, top right panel). The carbon concentration will marginally decrease. The net result of these changes is a large decrease in the ULR. Interestingly, at the same time the SLA increases. Note that the changes in ULR and SLA are not fully independent of each other: an increase in SLA implies that leaves invest less biomass per unit area. This will come, at least partly, at the expense of the photosynthetic machinery. Therefore a lower rate of photosynthesis per unit leaf area can be expected, especially at high light intensities where C fixation is determined by the amount of the photosynthetic enzyme Rubisco per unit area. The third growth parameter affected by low light is the allocation of biomass to leaves (LMF), which increases slightly. These shifts in SLA and LMF counterbalance the decreased carbon fixation per unit leaf area by increasing the total leaf area at a given size and therefore conserve to some extent the rate of carbon dioxide fixation per unit plant biomass. In general, a decrease in irradiance will not affect RGR as long as the daily quantum input exceeds  $20 \text{ mol m}^{-2} \text{ day}^{-1}$ . If the daily irradiance drops below that value, the SLA cannot fully compensate for the

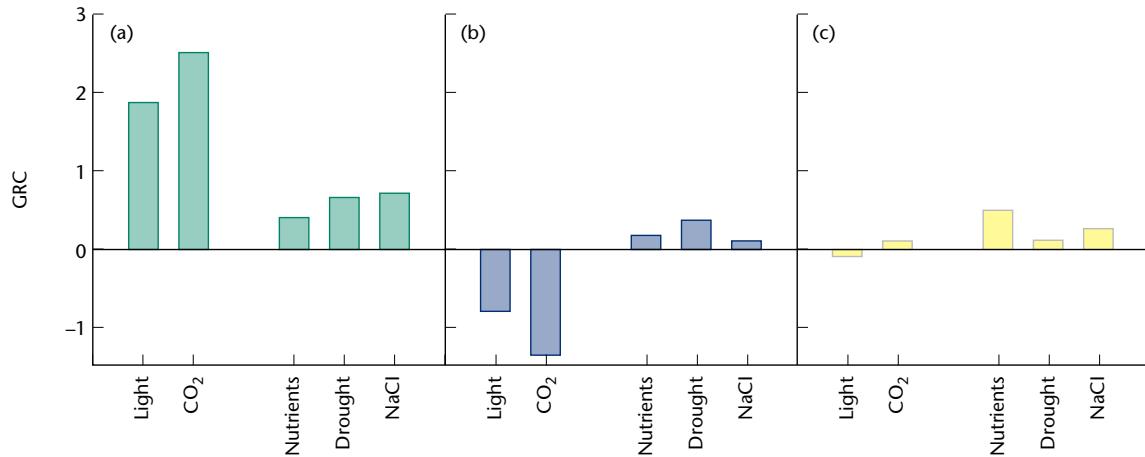
decrease in ULR, and RGR declines. Expressed quantitatively over a range of experiments, a 10% decrease in RGR due to a decreased daily irradiance was brought about by a 22% decrease in ULR, but at the same time there was an 11% increase in SLA and a 1% increase in LMF (Figure 4).

The case for carbon dioxide ( $\text{CO}_2$ ) is a bit more complicated. Seen from an evolutionary time scale, plants have experienced much higher atmospheric  $\text{CO}_2$  concentrations in the past than at this moment. However, with atmospheric  $\text{CO}_2$  concentrations currently rising again due to anthropogenic causes, it is appropriate to analyse how increases in  $[\text{CO}_2]$  will affect plant growth, using current levels as a baseline. Analysing the growth parameters as ratios between the value at  $700$  and  $350 \mu\text{L L}^{-1}$ , it turns out that RGR is only marginally affected (0–10%). The increase in growth rate is primarily due to an increase in the rate of photosynthesis. The FCI is hardly affected (Figure 3; lower right panel) and so is the C concentration. Consequently ULR increases, but similar to the light factor the increased ULR is balanced by a decrease in SLA (Figure 4a,b). The decrease in SLA in this case is not so much caused by a change in leaf morphology, but is mainly due to the increase in nonstructural carbohydrate levels, such as starch. This accumulation of starch can be seen as evidence that it is not so much the carbon gain itself that is limiting growth at elevated  $\text{CO}_2$ , but rather that there are not enough sinks (such as meristems or growing fruits) to fully utilize all the extra fixed carbon for growth.

## Environmental Influences of Growth: the Root Environment

The most widespread soil-related stresses are nutrient shortage and drought. Plants that experience nutrient stress, for example a decreased N availability, will have a hampered uptake, and also decreased production of photosynthetic enzymes. Consequently, a decrease in the rate of photosynthesis can be expected. Moreover, there is a strong biomass allocation away from leaves (Figure 4c) and towards roots. This implies that the fraction of the daily fixed C that is spent in root respiration increases dramatically. Consequently, the FCI decreases markedly (Figure 3, lower left panel), which is at variance with what happens at low light or high  $\text{CO}_2$ . Remarkably, at the same time an accumulation of starch takes place, indicating that reduced photosynthesis is not the primary cause of the hampered growth. It is as yet not known what exactly is the prime limiting factor in this case.

Drought and salt stress do have a number of effects in common. In both cases a reduced growth goes with a reduction in ULR, most likely due to a decrease in photosynthesis. However, in the case of sodium chloride, part of the reduction is due to damage of the photosynthetic apparatus, whereas the primary effect of drought will

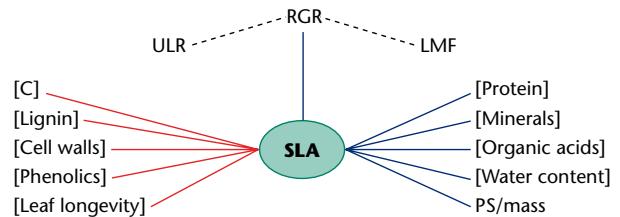


**Figure 4** Summary of growth response coefficient (GRC) data for plants that differed in growth due to differences in light, CO<sub>2</sub>, nutrients, water or salt. (a) GRC values for unit leaf rate (ULR); (b) specific leaf area (SLA); (c) leaf mass fraction (LMF). Data are averages from a meta-analysis for the factors light ( $n = 71$ ), CO<sub>2</sub> ( $n = 113$ ), nutrients ( $n = 75$ ) and water ( $n = 15$ ) (for more information see Poorter and Nagel, 2000), as well as 15 experiments on salt stressed plants. Note that a positive GRC indicates that an increase in RGR goes with an increase in a given parameter, and a decrease in RGR with a decrease in that parameter.

be closure of the stomata. It could be derived from **Figure 4** that biomass allocation is affected more by salt, whereas SLA changes more strongly in the case of drought. However, as growth data for both environmental factors are scarce, this awaits better evidence. The general conclusion that can be drawn is that, quite unlike the effects of light and CO<sub>2</sub>, for all three soil-related stresses, decreased growth accompanies a decrease in all three growth parameters of eqn [3].

## Ecological Significance of Variation in RGR

It has been noted that species with an inherently low RGR occur more often in nutrient-poor environments, whereas inherently fast-growing species are found in nutrient-rich, less stressful environments, or in ruderal habitats (Grime, 2001). This may be true for habitats with other types of stress as well, although evidence is not always strong. Does this imply that (potential) RGR has been the trait selected for during evolution? In a ruderal environment, with a high supply of nutrients and a low intensity of competition, a plant may come close to its maximal RGR. A high RGR may be advantageous in such cases since it enables a plant to quickly achieve a high biomass and complete its life cycle. In general, however, plants in their natural habitat will never achieve a growth rate close to their potential RGR and it may be questioned to what extent selection has been for a high RGR *per se*. Alternatively, the observed correlation between RGR and natural habitat may be due to a selection of one or more traits underlying RGR. Given the strong correlation between RGR and SLA, this is likely



**Figure 5** Diagram showing differences between plants that are inherently fast- and slow-growing. Red lines indicate variables with highest values for low-SLA plants, blue lines indicate variables with highest values for high-SLA plants.

to be a key factor. Inherent differences in SLA are generally well preserved over habitats, the most notable example being the leaves of evergreens, which have an SLA considerably lower than that of deciduous species under all growth conditions. Moreover, SLA correlates strongly with a suite of physiological and chemical traits (**Figure 5**): high-SLA species have high concentrations of cytoplasmic/vacuolar compounds such as protein, minerals and organic acids, whereas low-SLA species have more cell wall compounds, especially lignin, and accumulate more soluble phenolics. Such leaves are tougher and less attractive for herbivores. Therefore, they have a longer lifespan. Most likely, these characteristics will be mirrored below-ground, with lower root turnover for slow-growing species. As a consequence, these plants lose less of their nutrients accumulated in the leaves and roots. In nutrient-rich habitats this may be of little importance. In nutrient-poor habitats, however, plants that retain their nutrients for a prolonged time have a higher competitive ability than plants that shed their leaves more frequently (Aerts and

Chapin, 2000). This is a likely reason that low-SLA species, such as evergreens, occur under these conditions.

There are other environments where a low SLA seems to be of survival value. Some desert plants show a considerable investment in leaf hairs, which reflect a large part of the incoming irradiance and thus avoid excessive transpiration. Plants with tough, leathery leaves containing a large amount of lignin and other cell wall material will be more resistant to the physical damage of trampling and wind. Under these conditions, conservation of the existing biomass will be more important than a quick increment in biomass. Thus, it may well be that under these circumstances traits related to a low SLA have been selected for, rather than selection for a given growth rate.

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## Further Reading