

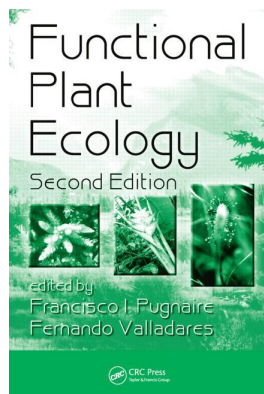
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3 Ecological Significance of Inherent Variation in Relative Growth Rate and Its Components

Hendrik Poorter and Eric Garnier

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INTRODUCTION

An amazing number of higher plant species are present on earth, with estimations greater than 250,000 (e.g., Wilson 1992). These species are not randomly distributed, but often can be

found in rather specific habitats. What is the reason that some species flourish in a desert and others in the tundra? Clearly, a certain degree of specialization must have taken place. It is the one major aim of functional ecology to explain the distribution of species (or genotypes within a species) from their functional attributes. These attributes can be related to the physiological, morphological, anatomical, and chemical characteristics of a plant species, but they could also depend on life history characteristics such as seed longevity, flowering time, life form, and so on. Since the question is why an individual of species A performs better in a given environment than an individual of species B, a comparative approach is needed (Bradshaw 1987). The strength of such an approach is that we not only gain insight into the processes that determine a plant's success or failure in a given habitat, but it also enables us to categorize the wide variety of species into a more limited number of functional groups. This may be an avenue toward simplification of a complex reality, with a great number of species in a given habitat. On the basis of functional groups we are probably better able to predict effects of environmental changes on vegetations (Hobbs 1997).

This chapter uses the comparative approach to analyze the characteristics and distribution of species varying in the maximum relative growth rate (RGR_{max} ; see the next section for a definition and Table 3.1 for a listing of abbreviations and units used throughout this chapter) they can achieve. Plant species grown under uniform and more or less optimum conditions in the laboratory differ several-fold in RGR_{max} (100–400 $mg\ g^{-1}\ day^{-1}$ for herbaceous species; 10–150 $mg\ g^{-1}\ day^{-1}$ for woody species). Over the last four decades, evidence has accumulated that RGR_{max} is linked to the characteristics of the habitat from which the species originated (Parsons 1968, Chapin 1980, Lambers and Poorter 1992, discussed on pp. 73–76). This linkage is intriguing, and leads to a number of questions, which are addressed in this chapter. After introducing the different analytical concepts that are used and providing evidence of a relationship between RGR_{max} and habitat characteristics, the physiological, morphological, and anatomical attributes that lead to variation in RGR_{max} between

TABLE 3.1
Terms, Abbreviations, and Units Used in This Chapter

Abbreviation	Meaning	Preferred Units	Normal Range
LAR	Leaf area ratio	$m^2\ leaf\ kg^{-1}\ plant$	5–50
LD	Leaf density	$kg\ m^{-3}$	100–400
LTh	Leaf thickness	μm	100–600
LMF	Leaf mass fraction	$g\ leaf\ g^{-1}\ plant$	0.15–0.60
LR _m	Rate of leaf respiration	$nmol\ CO_2\ g^{-1}\ leaf\ s^{-1}$	5–50
MRT	Mean residence time	Year	0.2–20
NUR	Net nitrogen uptake rate	$mmol\ N\ g^{-1}\ root\ day^{-1}$	1–8
NP	Nitrogen productivity	$g\ increase\ mol^{-1}\ N\ day^{-1}$	20–100
NUE	Nitrogen use efficiency	$kg\ increase\ mol^{-1}\ N\ taken\ up\ or\ lost$	0.5–15
PCC	[C] in the plant	$mmol\ C\ g^{-1}\ plant$	25–33
PNC	[N] in the plant	$mmol\ N\ g^{-1}\ plant$	1–4
PS _a	Rate of photosynthesis	$\mu mol\ CO_2\ m^{-2}\ leaf\ s^{-1}$	3–30
PS _m	Rate of photosynthesis	$nmol\ CO_2\ g^{-1}\ leaf\ s^{-1}$	100–600
RGR	Relative growth rate	$mg\ increase\ g^{-1}\ plant\ day^{-1}$	40–400
RMF	Root mass fraction	$g\ root\ g^{-1}\ plant$	0.15–0.60
RR _m	Rate of root respiration	$nmol\ CO_2\ g^{-1}\ root\ s^{-1}$	10–80
SLA	Specific leaf area	$m^2\ leaf\ kg^{-1}\ leaf$	8–80
SMF	Stem mass fraction	$g\ stem\ g^{-1}\ plant$	0.05–0.30
SR _m	Rate of stem respiration	$nmol\ CO_2\ g^{-1}\ stem\ s^{-1}$?
ULR	Unit leaf rate	$g\ increase\ m^{-2}\ leaf\ day^{-1}$	2–20

Note: Normal ranges found in herbaceous species. All mass-based parameters are expressed per unit dry mass.

species are explored. We show that, whatever the evolutionary forces have been, fast- and slow-growing species grown under laboratory conditions show consistent suites of traits. To have an ecological meaning, these sets of traits should not only be found in the laboratory, but also in the field. After testing whether this is indeed the case, we analyze the ecological implications of interspecific differences in growth rate and of variation in the underlying parameters. This leads us to suggest that selection has acted on components of RGR, rather than on RGR itself.

ASSESSING THE GROWTH POTENTIAL OF A SPECIES

This section focuses on the analysis of inherent differences in RGR (Box 3.1). The concept of RGR was first introduced by Blackman (1919), who recognized that the increase in plant biomass over a given period of time was proportional to the biomass present at the beginning of this period. He saw a parallel with money in a bank account accumulating at compound interest. In the case of plants, newly formed biomass is immediately deployed to fix new carbon and take up extra nutrients and water, thus leading to an accelerated biomass increase. Borrowing from economic theory, he derived the following equation:

BOX 3.1 Relative Growth Rate

The problem of how to express the growth rate of a plant can best be illustrated by the following example. Suppose there are two plants, A and B, whose dry masses are 0.1 and 1.0 g, respectively. Given that both increase in biomass by 0.1 g in 24 h, can they be considered to grow at the same rate? One way to express growth is to consider the absolute growth rate (AGR), which is defined as the increase in plant mass M over a period of time t

$$\text{AGR} = \frac{dM}{dt}. \quad (3.1)$$

Plant mass M_2 at time t_2 can be calculated for a given AGR when mass M_1 at time t_1 is known

$$M_2 = M_1 \text{AGR}(t_2 - t_1). \quad (3.2)$$

In the above, example plants A and B have the same AGR. However, A achieved this increase with far less starting material than B. To take this into account, the rate of biomass increase can be defined relative to the mass of the plant already present. This is the RGR

$$\text{RGR} = \frac{1}{M} \frac{dM}{dt}. \quad (3.3)$$

For a given RGR and plant mass M_1 at time t_1 , M_2 at time t_2 can be calculated by

$$M_2 = M_1 e^{\text{RGR}(t_2 - t_1)}. \quad (3.4)$$

By taking the natural logarithm of both sides of Equation 3.4, and a little rearranging, we obtain a formula by which RGR can be calculated from experimental data

$$\text{RGR} = \frac{\ln M_2 - \ln M_1}{t_2 - t_1}. \quad (3.5)$$

(continued)

BOX 3.1 (continued) Relative Growth Rate

Note that RGR can be interpreted graphically as the slope of the line that connects the ln-transformed dry masses of plants at several harvesting times (Figure 3.1b). Because of the ln-transformation, the numerator has no dimension; therefore RGR has the unit 'day⁻¹'. As RGR values were based on plant masses, rather than on leaf area or another parameter of plant size, units could be expressed as g g⁻¹ day⁻¹ (gram increase per gram dry mass present and per unit of time). These numbers are generally low, and therefore we use 'mg g⁻¹ day⁻¹' as the unit of expression.

In the previously given example, plant A has an RGR of 693 mg g⁻¹ day⁻¹, whereas B has an RGR of 95 mg g⁻¹ day⁻¹. We thus conclude that plant A is more efficient in terms of growth than B. (It may be surprising at first sight that plant A, that doubles its mass in 24 h, has an RGR less than 1000 mg g⁻¹ day⁻¹. The reason for this is that the assumption underlying Equation 3.4 is that extra biomass, produced during the beginning of the day, is immediately deployed to fix new C and minerals, leading to compounding growth.)

There are two additional points to which we want to draw attention. First, the dry mass of the whole plant is generally taken as the basis for the RGR calculation. However, RGRs have also been calculated on the basis of fresh weight, shoot weight, leaf area, or leaf number. As long as plant growth is in steady state, that is, as long as there are no changes in the dry mass: fresh mass ratio, allocation, morphology, leaf size, and so on, the RGR values expressed in several ways should be equal. Second, plants with a low RGR can still achieve a large biomass when they start with a high seed mass or grow over prolonged periods of time (see Equation 3.4). For a discussion on various approaches for the experimental design in growth analysis and details on calculations see Causton and Venus (1981), Hunt (1982), Poorter and Garnier (1996), Hoffmann and Poorter (2002).

$$M_2 = M_1 e^{\text{RGR}(t_2 - t_1)},$$

where M_1 and M_2 are the plant masses at time t_1 and t_2 , respectively. The RGR in this equation indicates the dry mass increment per unit dry mass, which is already present in the plant per unit time. For a more detailed discussion on the background of RGR see Box 3.1.

Originally, Blackman thought of RGR as a physiological constant, which would be characteristic for a given species under given conditions. However, a constant RGR implies that plants grow exponentially throughout their life (Figure 3.1). In reality, plants hardly ever show a true exponential growth phase, as RGR changes continuously with ontogeny (Hunt and Lloyd 1987, Robinson 1991, Poorter and Pothmann 1992). During germination there is a gradual transition from growth dependent on seed reserves to complete autotrophy. When plants get older and larger, the upper leaves start to shade lower leaves. Moreover, larger plants have to allocate more resources away from the assimilating parts of leaves and roots and invest more in support tissue, especially in stems. Consequently, RGR decreases with size and time (Figure 3.1). Does this imply that the concept of RGR can only be used in the seedling stage, during what is often termed the "exponential growth phase?" Mathematically, there is no requirement for RGR to be constant, because it is a parameter that can be used as a quantification of growth at any point in time, even if growth is not strictly exponential. It can also be used as an average over a given time period (Evans 1972) or a given mass trajectory. Therefore, as long as one is convinced that the growth of the plants under study is somehow proportional to the plant biomass already present, RGR is the most appropriate parameter to use. However, it is not a parameter fully independent of plant size!

In the field, where plants experience a fluctuating environment, growth is restricted by a continuously changing array of abiotic factors (light, temperature, nutrients, and water) and affected by biotic interactions (competitors, herbivores, pathogens, but also

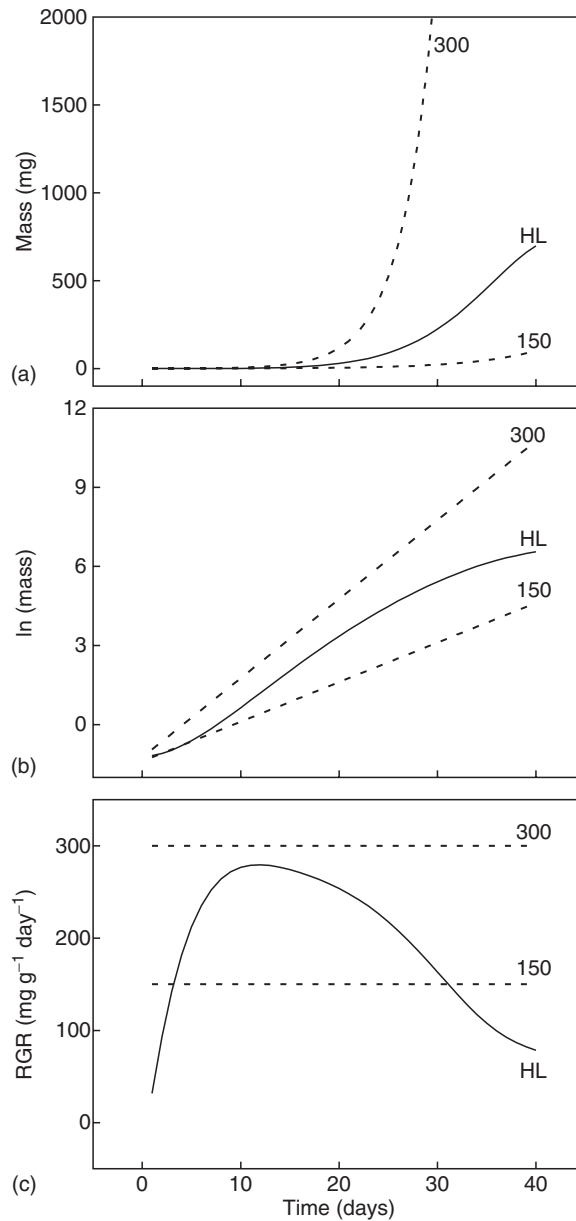


FIGURE 3.1 Time course in (a) total plant mass, (b) ln-transformed values of total plant mass, and (c) RGR of a theoretical plant population growing continuously with an RGR of 150 or 300 (dashed lines) $\text{mg g}^{-1} \text{day}^{-1}$, and experimental data on a population of *Holcus lanatus*. (Continuous line marked HL; adapted from Hunt, R. and Lloyd, P.S., *New Phytol.*, 106, 235, 1987.) All populations had a similar starting mass at day 0.

symbionts). In comparing species (or genotypes) it is of interest to know their genetic potential or growth achieved in the absence of constraining factors. Such a goal is difficult to achieve. It would require knowledge about the exact combination of factors that enables fastest growth for each species. Even if such a goal could be technically achieved, it would have the drawback of comparing species that had been grown in more or less different environments. The practical solution has been to choose a set of conditions that is close to

optimal for growth of most species and technically achievable (Grime and Hunt 1975). Growth rate is then measured for relatively small and young plants over rather short time intervals (10–20 days), and without interference from other plants. The RGR value obtained in this way is considered to be RGR_{max} . These values are not absolute, because they depend on ontogeny as well as growth conditions. However, with the exception of very low nutrient levels (Shipley and Keddy 1988) or light levels (Mahmoud and Grime 1974), RGR ranking remains rather similar (see Poorter et al. 1995, Biere et al. 1996 for nutrients; Hunt and Cornelissen 1997, Poorter and Van der Werf 1998 for light). Therefore, ranking of species for RGR_{max} does not change strongly across experiments and can be used in a relative way to order species on the fast–slow continuum. However, there is variability in such relative rankings across experiments, with correlation coefficients approximately 0.6 (Table 3.2). Part of this variation is probably caused by imprecisions related to RGR determinations, especially in larger screening programs with a limited number of plants harvested per species (Poorter and Garnier 1996).

What do RGR_{max} values obtained in the laboratory tell about plant growth in the field? With respect to light, field-grown plants generally experience stronger fluctuations in instantaneous irradiance, and higher levels of total quantum input, when considered over the whole growing season (Garnier and Freijnsen 1994). However, RGR does not strongly depend on the total daily quantum input above $20 \text{ mol m}^{-2} \text{ day}^{-1}$ (Poorter and Van der Werf 1998), a value quite often reached in growth chambers. Temperature is often lower in the field, especially during vegetative growth in temperate climates. With respect to nutrients, conditions are generally far more limiting in the field. Moreover, plants in the field encounter competition

TABLE 3.2
Correlation Coefficients

	G75	P89	P and O	H97	V98
G75	–	0.77	0.55	0.66	0.57
P89	8	–	0.98	–	–
P and O	23	7	–	0.73	0.76
H97	30	–	13	–	0.62
V98	33	–	13	13	–

Sources: Data are from Grime, J.P. and Hunt, R., *J. Ecol.*, 63, 393, 1975. (G75; 130 species), Poorter, H., *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*, H. Lambers, M.L. Cambridge, H. Konings, and T.L. Pons, eds, SPB Academic Publishing, The Hague, 1989 (P89; 9 species), Poorter, H. and Remkes, C., *Oecologia*, 83, 553, 1990 supplemented with data from Van der Werf, A., van Nuenen, M., Visser, A.J., and Lambers, H., *Physiol. Plant.*, 89, 563, 1993; Den Dubbelden, K.C. and Verburg, R.W., *Plant Soil*, 184, 341, 1996 and van Arendonk, J.J.C.M. (unpublished results), which were all grown under identical conditions (P&O; 47 species), Hunt, R. and Cornelissen, J.H.C., *New Phytol.*, 135, 395, 1997 (H97; 43 species), and from Van der Werf, A., Geerts, R.H.E.M., Jacobs, F.H.H., Korevaar, H., Oomes, M.J.M., and de Visser, W., *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences*, H. Lambers, H. Poorter, and M. van Vuuren, eds, Backhuys Publishers, Leiden, 1998 (V98; 71 species).

Note: RGR_{max} values of herbaceous species shared by some larger-scale comparative experiments (*upper right part*) and number of species in common on which the correlation coefficient is based (*lower left part*). Only those correlations are given when seven or more species were in common.

and other biotic interactions. Consequently, there is a large difference between the RGR_{max} , as measured in the lab, and RGR of plants in the field (reviewed by Garnier and Freijisen 1994, see also Villar 1998, 2005). Although we expect some relationship between the relative ranking in laboratory and field, data are too scarce for a proper evaluation. In this chapter, we treat RGR_{max} more as a representation of a complex of traits than as a predictor of growth rate under natural conditions. This aspect is discussed further in the sections on pages 73–76 and 84–90.

RGR_{MAX} AND PLANT ECOLOGY

RGR_{MAX} AND PLANT DISTRIBUTION

Bradshaw et al. (1964) were among the first to establish a relationship between the RGR_{max} of wild species, as measured under laboratory conditions, and the characteristics of the habitat they originated from. Others followed, but generally the number of species was rather low (less than 10) to infer strong conclusions. Grime and Hunt (1975) determined RGR_{max} of 130 species from England and classified them according to habitat. Fast-growing species were found relatively more often in fertile habitats, whereas species with a low potential growth rate tended to occupy infertile habitats. It is not always easy and straightforward to quantitatively classify a specific habitat along a fertility scale. A semiquantitative approach has been used by Ellenberg, who assigned so-called “ N -numbers” to a wide range of species from Central Europe (Ellenberg 1988). The higher the value, the higher the fertility of the habitats in which such a species would generally occur. Plotting RGR_{max} data of herbaceous perennials against the N -number of Ellenberg generally yields positive relationships (Figure 3.2a). A positive relation between RGR_{max} and nutrient availability is also likely for woody species (Cornelissen et al. 1998). However, annuals seem to have a high RGR_{max} independent of soil fertility (Fichtner and Schulze 1992).

Is inherent variation in potential RGR of species also related to other environmental gradients? Evidence is less well-documented than in the case of nutrient availability. Alpine species have lower RGR_{max} under laboratory conditions than lowland species (Figure 3.2b). Dry (Rozijn and Van der Werf 1986, Figure 3.2c) or saline habitats (Figure 3.2d) harbor species that grow more slowly under optimal conditions, and the same relation between RGR_{max} and plant occurrence was found for sites with heavy metal pollution (Wilson 1988, Verkleij and Prast 1989). Disturbance regime may also be a source of variation in RGR_{max} : annuals that have to complete their life cycle in periodically disturbed habitats, display a higher RGR_{max} than congeneric perennials from more stable habitats (Garnier 1992), and species from early stages of secondary succession tend to have higher RGR_{max} than those from more advanced stages (Gleeson and Tilman 1994, Vile et al. 2006). The intensity of trampling has also been identified as selecting for species with different RGR_{max} : plants from trampled places have a lower RGR_{max} than those from nontrampled sites (Figure 3.2e). Finally, when determined at relatively high-light levels, species from strongly shaded habitats have a lower RGR than those from light-exposed environments. In most of the cases shown in Figure 3.2b through Figure 3.2f, however, it seems that differences in RGR_{max} between species from favorable and unfavorable habitats are not as clear as in the case of species adapted to habitats differing in fertility.

RGR_{MAX} AND ECOSYSTEM PRODUCTIVITY

Most of this chapter focuses on the comparison between plant species. However, in recent years there has been much attention for ecosystem functioning and a possible link with species composition. The fact that inherently fast-growing species are more often found in

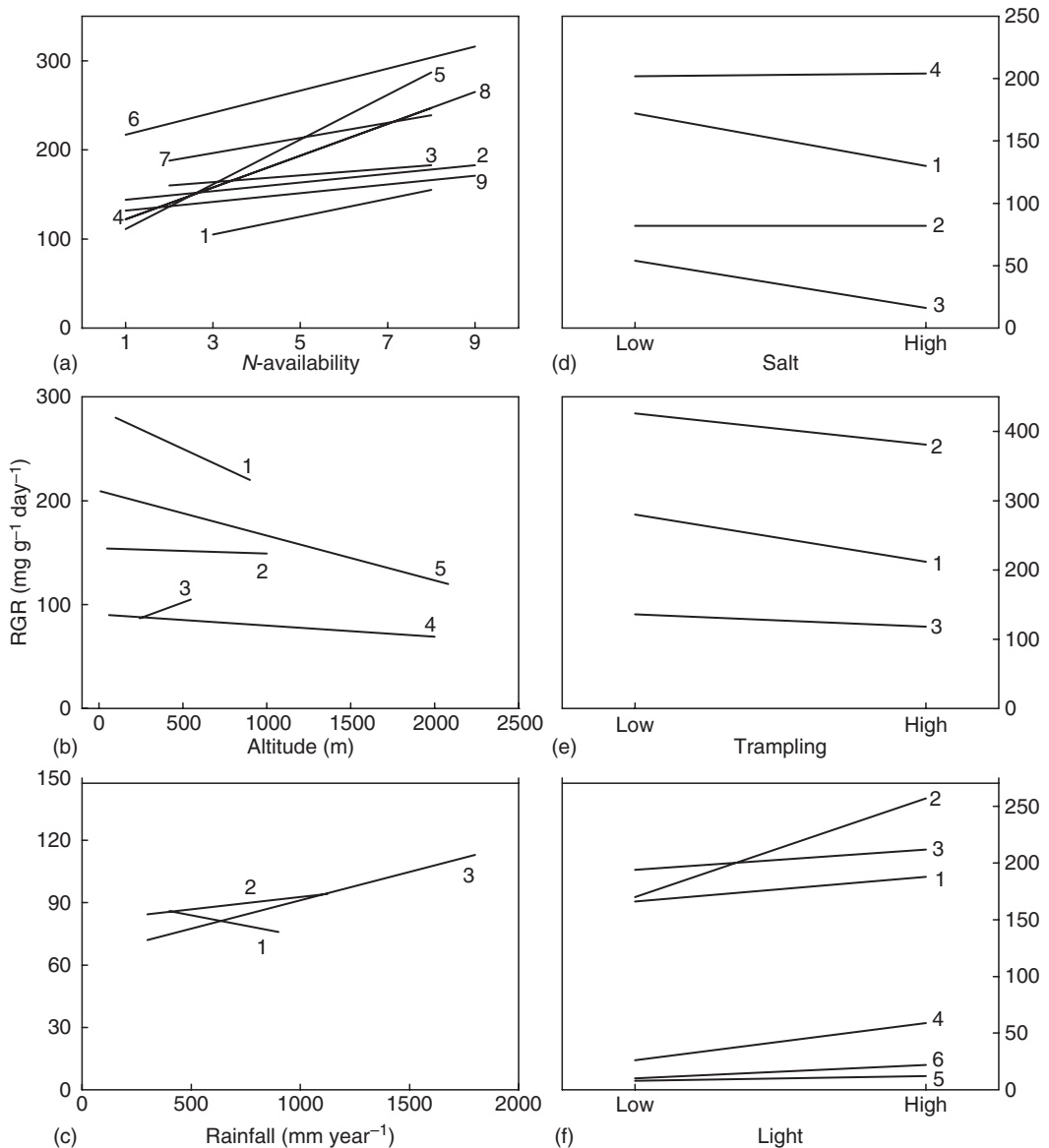


FIGURE 3.2 RGR_{max} of species originating from habitats differing in: (a) Nutrient availability, as indicated by the N-number of Ellenberg; (b) Altitude, in meters above sea level; (c) Rainfall; (d) Salt concentration; (e) Trampling intensity; and (f) Light intensity. Each study is represented by a regression line. Numbers refer to the following studies: A: data from (1) Rorison, I.H., *New Phytol.*, 67, 913, 1968; (2) Grime, J.P. and Hunt, R., *J. Ecol.*, 63, 393, 1975; (3) Boorman, L.A., *J. Ecol.*, 70, 607, 1982; (4) Poorter, H., *Causes and Consequences of Variation in Growth Rate and Productivity of Higher Plants*, H. Lambers, M.L. Cambridge, H. Konings, and T.L. Pons, eds, SPB Academic Publishing, The Hague, 1989; (5) Poorter, H. and Remkes, C., *Oecologia*, 83, 553, 1990; (6) Reiling, K. and Davison, A.W., *New Phytol.*, 120, 29, 1992; (7) Stockey, A. and Hunt, R., *J. Appl. Ecol.*, 31, 543, 1994; (8) Van der Werf, A., Geerts, R.H.E.M., Jacobs, F.H.H., Korevaar, H., Oomes, M.J.M., and de Visser, W., *Inherent Variation in Plant Growth. Physiological Mechanisms and Ecological Consequences*, H. Lambers, H. Poorter, and M. van Vuuren, eds, Backhuys Publishers, Leiden, 1998; and (9) Schippers P. and Olf, H., *Plant Ecol.*, 149, 219, 2000; B: data from (1) Woodward, F.I., *New Phytol.*, 82, 385, 1979; (2) Woodward, F.I., *New Phytol.*, 96, 313, 1983; (3) Graves, J.D. and Taylor, K., *New Phytol.*, 104, 681, 1986; (4) Atkin, O.K. and Day, D.A., *Aust. J. Plant Physiol.*, 17, 517, 1990; and

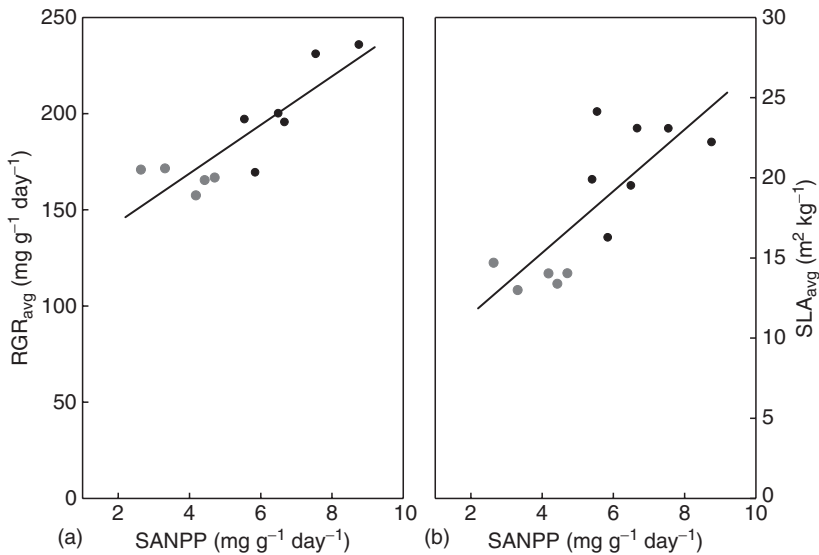


FIGURE 3.3 (a) Aggregated RGR_{max} and (b) aggregated SLA of plant species grown in the field plotted as a function of the specific aboveground net primary productivity (aboveground RGR) of 12 abandoned vineyards at different stages of secondary succession. Laboratory-derived data of the species present in the succession were averaged according to the proportion of biomass they represented in the field. (From Vile, D., Shipley, B., and Garnier, E., *Ecol. Lett.*, 9, 1061, 2006 and Garnier, E., Cortez, J., Billés, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellman, A., Neill, C., and Toussaint, J.-P., *Ecology*, 85, 2630, 2004.)

nitrogen-rich habitats (*sensu* Ellenberg 1988), and nitrogen-rich habitats often show a higher productivity, makes it likely that there is in this case a positive correlation between ecosystem behavior and the RGR of the composing species as determined in the laboratory. Vile et al. (2006) tested this correlation in a Mediterranean habitat, following secondary succession in abandoned vineyards. The aboveground net primary productivity, expressed per gram of biomass present at the beginning of the growing season, varied fourfold between sites and was negatively correlated with field age. The decrease in productivity was correlated with a change in species composition, such that species more abundantly present at later successional stages were those that were showing lowest RGR_{max} in growth room experiments (Figure 3.3a).

FIGURE 3.2 (continued) (5) Atkin, O.K., Botman, B., and Lambers, H., *Funct. Ecol.*, 10, 698, 1996a; C: data from (1) Mooney, H.A., Ferrar, P.J., and Slatyer, R.O., *Oecologia*, 36, 103, 1978; (2) Wright, F.I. and Westoby, M., *J. Ecol.*, 98, 85, 1999; and (3) Warren and Adams, *Oecologia*, 144, 373, 2005; D: data from (1) Ball, M.C., *Aust. J. Plant Physiol.*, 15, 447, 1988; (2) Van Diggelen, J., *A Comparative Study on the Ecophysiology of Salt Marsh Halophytes*, PhD Thesis, Free University, Amsterdam, 1988; (3) Schwarz and Gale, *J. Exp. Bot.*, 35, 193, 1984 and (4) Ishikawa S.I. and Kachi, N., *Ecol. Res.*, 15, 241, 2000; E: data from (1) Dijkstra, P. and Lambers, H., *New Phytol.*, 113, 283, 1989; (2) Meerts, P. and Garnier, E., *Oecologia*, 108, 438, 1996; and (3) Kobayashi, T., Ikeda, H., and Hori, Y., *Plant Biol.*, 1, 445, 1999; F: data from (1) Pons, T.L., *Acta Botanica Neerl.*, 26, 29, 1977; (2) Corré, W.J., *Acta Botanica Neerl.*, 32, 49, 1983a; (3) Corré, W.J., *Acta Botanica Neerl.*, 32, 185, 1983b; (4) Kitajama, K., *Oecologia*, 98, 419, 1994; (5) Osunkoya, O.O., Ash, J.E., Hopkins, M.S., and Graham, A.W., *J. Ecol.*, 82, 149, 1994; and (6) Poorter, L., *Funct. Ecol.*, 13, 396, 1999.

RGR_{max} AND PLANT STRATEGIES

We have shown earlier that in a variety of cases, there is a link between the potential growth rate of a species and its occurrence in a given habitat. As such, RGR_{max} forms one of the cornerstones in the plant strategy theory formulated by Grime (1979). According to this theory, plant strategies are shaped by the possible combinations of two factors experienced by plants: stress and disturbance. Stress in this sense is defined as the extent to which a combination of environmental variables retards growth (e.g., low nutrient availability, low or high temperature, low water availability). Disturbance is defined as the degree of physical disruption of the plant’s biomass (e.g., grazing, trampling). Species from habitats with a high degree of stress and a low degree of disturbance are called “stress-tolerators.” They are generally perennials with a low RGR_{max} (Figure 3.4). Species from sites with a high disturbance but with low stress are called “ruderals”. They are mostly annuals that have a high RGR_{max}, enabling them to complete their life cycle quickly. This would ensure that seeds are produced before a disturbance event takes place, which kills the plant. Habitats in which both stress and disturbance are low are favorable for plant growth. According to the plant strategy theory, these are sites where a strong competition between plants is expected; consequently species that thrive here are called “competitors”. They are generally perennials, and also have a high RGR_{max}. Sites with a high level of both stress and disturbance (volcanoes, nutrient-poor and strongly drifting sand dunes) do not bear plants, because there is no feasible strategy to cope with such an environment.

Given the importance that is generally attached to biomass gain and the relative fitness of a plant (discussed in McGraw and Garbutt 1990), it may be hypothesized that there has been a selection pressure in fertile (and favorable, even if only temporarily) habitats toward plant species with a high RGR, and toward a low potential RGR in places which are unfavorable (Grime 1979, Chapin 1980). However, RGR is a parameter that is the result of a combination of many physiological, morphological, anatomical, and biochemical traits. Alternatively, it could well be that it is one or more of these traits underlying RGR that has been the target of selection, rather than RGR itself (cf. Grime 1979, Coley 1983, Lambers and Dijkstra 1987). RGR would then merely be a by-product of selection. Before evaluating these contrasting hypotheses, we first have to investigate the components underlying RGR.

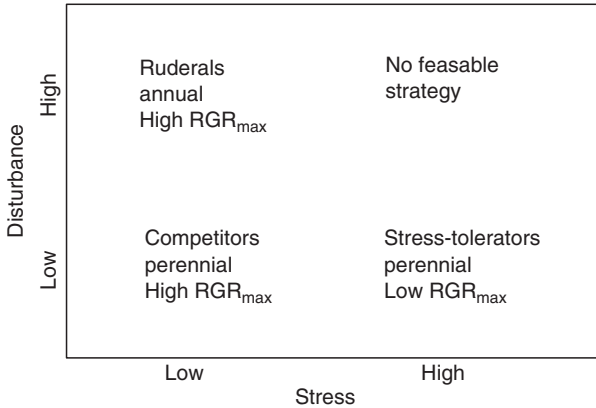


FIGURE 3.4 Relation between stress and disturbance and the growth strategy, life form, and RGR of the three types of strategies. (Adapted from Grime, J.P., *Plant Strategies and Vegetation Processes*, John Wiley & Sons, Chichester, 1979.)

COMPONENTS UNDERLYING RGR_{MAX}

GROWTH PARAMETERS

Growth is more than photosynthesis. It is the balance between the carbon gain per unit leaf area (ULR) and the carbon losses in the plant (which depend on the respiration rate but also on the relative proportion of the assimilatory and nonassimilatory organs, and in the longer run on biomass turnover), corrected for the C-concentration of the newly formed biomass. Evaluating the relative importance of each of these factors requires a top-down approach, in which RGR is broken down into components. A common way to do so is factorizing RGR into the increase in mass per unit leaf area and time (ULR) and the leaf area per unit plant mass (LAR, leaf area ratio). LAR can be factorized further into the components leaf area: leaf mass (SLA, specific leaf area) and leaf mass: plant mass (LMF, leaf mass fraction). A definition of these components of RGR, as well as an explanation of the concept of growth parameters underlying RGR is given in Box 3.2.

BOX 3.2

Components of RGR

A simple framework to factorize RGR was developed at the beginning of the twentieth century (Blackman 1919, West et al. 1920). The basic assumption underlying this framework is that plant growth is dependent on photosynthesis and that leaf area is the plant variable driving total C-gain. RGR is then factorized into two components: ULR and LAR (Hunt 1982). ULR is defined as the increase in biomass per unit time and leaf area

$$ULR = \frac{1}{A} \frac{dM}{dt}, \quad (3.6)$$

where A is the total leaf area of the plant, dM the increase in mass over period dt . LAR is defined as the total leaf area per unit total plant mass

$$LAR = \frac{A}{M} \quad (3.7)$$

and consequently

$$ULR \cdot LAR = \frac{1}{A} \frac{dM}{dt} \frac{A}{M} = RGR. \quad (3.8)$$

By determining leaf mass and stem and root mass separately, one is also able to break down LAR into two components: specific leaf area (SLA) and leaf mass fraction (LMF). SLA is the amount of leaf area per unit leaf mass (M_L):

$$SLA = \frac{A}{M_L} \quad (3.9)$$

and LMF is the fraction of total plant mass that is invested in the leaves

$$LMF = \frac{M_L}{M} \quad (3.10)$$

and consequently

(continued)

BOX 3.2 (continued)
Components of RGR

$$\text{SLA.LMF} = \frac{A}{M_L} \frac{M_L}{M} = \text{LAR}. \quad (3.11)$$

The advantage of this approach is that it requires only data on progressions in leaf area and plant mass to obtain a good indication about the causes of variation in growth rate. This is because differences in ULR are often due to differences in the area-based rate of photosynthesis. However, ULR is, in fact, the net balance of total plant carbon gain and carbon losses, expressed per unit leaf area and corrected for the C-concentration of the newly formed biomass. If one really wants to obtain insight in the relation between the various C-fluxes and RGR, the following formula can be used

$$\text{RGR} = \frac{\text{PS}_a \text{FCI}}{\text{PCC}} \text{SLA LMF} \quad (3.12)$$

Poorter (2002), where PS_a is the total amount of C fixed per unit leaf area integrated over a 24 h period, FCI the fraction of that daily fixed carbon that is not respired in leaves, stems, or roots but invested in growth (so $1-\text{RE}/\text{PS}$). The first four terms in the right-hand side of Equation 3.12 determine the net amount of C fixed per unit of biomass and per day. The denominator (PCC) converts this net amount of C into a biomass increase.

There are slightly different approaches, in which Equation 3.12 is written as the difference between carbon gain in photosynthesis and daily rate of respiration in leaves, stems, and roots. However, by using the form currently presented in Equation 3.12, with FCI (also termed carbon use efficiency), the equation is the product of five entities, which makes it amenable to the GRC analysis explained in the ‘‘Physiological Parameters’’ section on the next page. Note that in this equation C-losses due to exudation, or leaf and root turnover are considered to be negligible.

To what extent is inherent variation in RGR_{max} caused by variation in the components ULR and LAR? A wide variety of results has been published; some experiments found ULR to be the factor determining growth, others found LAR to be the cause of variation in growth, whereas others found intermediate results. Variation may be due to the choice of the species as well as growth conditions used and the experimental procedure followed (e.g., duration of the experiment and number of harvests). To enable a quantitative analysis of the cause of variation in RGR within a given experiment, we use the growth response coefficient (GRC). This coefficient can be calculated after determining the linear regression between the growth parameter X (which can be ULR, LAR, SLA, or LMF) as the dependent variable and RGR as the independent variable. GRC_X then is defined as the relative increase in growth parameter X divided by the relative increase in RGR

$$\text{GRC}_X = \frac{dX/X}{d\text{RGR}/\text{RGR}}$$

The sum of GRC_{ULR} and GRC_{LAR} for any experiment should be 1, and this is also the case for the sum of GRC_{ULR} , GRC_{SLA} , and GRC_{LMF} . A value of 1 for GRC_{ULR} indicates that species variation in RGR within an experiment fully scales with variation in ULR, whereas a value of 0 indicates no effect of this parameter at all.

What is the overall picture that emerges from the literature? Poorter and van der Werf (1998) analyzed a total of 111 experiments on herbaceous C_3 species, and calculated the

TABLE 3.3
Growth Response Coefficients for ULR,
LAR, SLA, and LMF

	GRC
ULR	0.26
LAR	0.74
SLA	0.63
LMF	0.11

Note: Average values from a literature survey on causes of inherent variation in RGR. A total of 111 articles were compiled. Only those reports were considered where RGR differences between species or genotypes were at least 40 mg g⁻¹ day⁻¹. More details are given in Poorter and van der Werf, 1998.

average GRC for the various growth parameters. They found that, on average, variation in SLA is by far the most dominant factor explaining variation in inherent RGR. ULR is second, and LMF is, on average, the quantitatively least important variable (Table 3.3). For a more elaborate analysis on GRC and the literature compilation see Poorter and van der Werf (1998).

It is not all that clear how the above-mentioned relationship between RGR of different species and the underlying growth parameters depend on environmental conditions or functional types. There have been suggestions that at high irradiance growth variation between species is due more to ULR than to SLA (Shipley 2006). Comparing variation in RGR between C3 and C4 species, or between sun and shade species, this seems indeed the case (Poorter 1989, Poorter 1999). However, for other species there is no indication that the relative importance of ULR and SLA shift with light environment (Poorter and van der Werf 1998). Growth temperature affects the relationships such that in cooler environments GRC_{ULR} gains in importance, in warmer environments GRC_{SLA} plays a dominant role (Loveys et al. 2002).

PHYSIOLOGICAL PARAMETERS

The aforementioned technique of growth analysis has the advantage of being simple. Moreover, technical requirements to conduct such an experiment are low. A drawback is that ULR is a parameter that integrates various aspects of plant functioning (photosynthesis, respiration, chemical composition) and therefore cannot be related directly to a specific physiological process. One may assume that a considerable part of the variation in ULR is due to differences in the area-based rate of photosynthesis (Konings 1989). To obtain more insight into the physiological basis of variation in RGR, however, a more mechanistic approach has to be followed, in which growth is analyzed in terms of the plant's carbon (C) economy. This requires knowledge of the C-gain of the plant in photosynthesis, and C-losses in leaf, stem, and root respiration, all integrated over the day. The net increase in C over the day can be converted into a dry mass increase, if the C-concentration of the newly formed material is known. A formula to relate the C-fluxes to RGR is presented in the second part of [Box 3.2](#).

Given that 85%–95% of plant dry matter is composed of carbon-based compounds (for a review see Poorter and Villar 1997), it is beyond doubt that almost all newly formed biomass

is fixed during the photosynthetic process. However, that does not necessarily imply that variation in RGR must be due to variation in the rate of photosynthesis, measured per unit leaf area and per unit of time (PS_a). Only few attempts have been made to quantify both whole shoot photosynthesis at growth conditions (rather than determining photosynthetic capacity for the youngest expanded leaf) and RGR. In a number of cases no relationship at all has been observed (Dijkstra and Lambers 1989, Poorter et al. 1990, Van der Werf et al. 1993, Atkin et al. 1996a), but in others a positive relation was found (Garnier et al., unpublished). If indeed the growth parameter ULR is correlated well with the rate of photosynthesis per unit leaf area (Konings 1989, Poorter and van der Werf 1998), we might derive from the GRC_{ULR} value in Table 3.3 that, in the average experiment, there is a modestly positive relationship between PS_a and RGR.

It may well be that PS_a (and ULR) is not the best variable to consider if one seeks to understand the physiological basis of growth. Traditionally, in physiological research, the rate of photosynthesis is expressed per ULR. In this way the flux of C can be related to the flux of incoming photons and the efflux of water. In analyzing growth, however, it may be more relevant to consider how much C is fixed by 1 g of leaf biomass, which is the photosynthetic rate per unit leaf mass (PS_m). This would relate much better to RGR, which is the increase in biomass per unit of biomass and time. PS_m is the product of PS_a and SLA (Box 3.2), and this parameter is strongly associated with RGR (Poorter et al. 1990, Reich et al. 1992, Van der Werf et al. 1993, Walters et al. 1993, Atkin et al. 1996a, Garnier et al. unpublished results).

Both shoot and root respiration are generally positively correlated with RGR (Poorter et al. 1990, Van der Werf et al. 1993, Walters et al. 1993, see also Atkin et al. 1996a). This is partly a reflection of the higher rate of growth of the fast-growing species, which requires extra amounts of energy (ATP) and reducing power (NADH) per unit dry mass. As far as roots are concerned, the higher respiration rate is also a reflection of a much higher uptake rate of ions (Van der Werf et al. 1994).

An alternative approach to the carbon balance decomposition just described can be followed, focusing on the nitrogen economy of the plant. RGR can then be expressed as the product of the root mass fraction (RMF) and the nitrogen uptake rate divided by the mean plant nitrogen concentration (Garnier 1991, Lambers and Poorter 1992). Breaking down the RGR of fast- and slow-growing species in this way shows that faster growth is associated with a relatively lower allocation of biomass to roots, a higher plant nitrogen concentration, and a higher nitrogen uptake rate (NUR). In fact, NUR is the parameter that shows the widest variation and the strongest correlation with RGR in the fast-slow continuum (Garnier 1991).

CHEMICAL AND ANATOMICAL PARAMETERS

There is a wide range of other parameters for which fast- and slow-growing species differ under more or less optimal growth conditions. Most notably, fast-growing species have higher concentrations of reduced nitrogen in all organs, as well as higher amounts of minerals (Poorter and Bergkotte 1992, Reich et al. 1992, Van der Werf et al. 1993, Garnier and Vancaeyzeele 1994, Atkin et al. 1996b), observations that also hold for fast- and slow-growing tree species (Villar et al. 2006). They tend to have slightly lower concentrations of C (but see Garnier and Vancaeyzeele 1994 and Atkin et al. 1996a), but these differences are marginal for species within the same life form. Differences in C-concentration may become substantial when the growth differences between herbaceous and woody species are analyzed (Poorter 1989).

Given the importance of SLA in explaining variation in RGR_{max} (Table 3.3), it is appropriate to factorize this parameter further. SLA, or rather its inverse, $1/SLA$ (expressed in $g\ m^{-2}$), is the product of leaf thickness and leaf density (see Box 3.3). Generally, the

lower SLA of slow-growing species is due more to a higher leaf density (LD) than that it is caused by a higher leaf thickness (Van Arendonk and Poorter 1994, Garnier and Laurent 1994, but see e.g., Körner and Diemer 1987 and Shipley 1995). The density of a leaf or root is strongly related to its water content per unit dry mass (Garnier and Laurent 1994). This can easily be understood by envisaging a cell as a box. A higher density is often caused by an extra deposition of cell wall material (lignin, cellulose). A doubling of the amount of cell wall material hardly affects the cell size or the amount of water in the cell (the volume of the box). However, the amount of water relative to the dry mass decreases, whereas the density, the dry

BOX 3.3 Components of Specific Leaf Area

SLA, leaf area per unit leaf mass, is a parameter that scales linearly and positively with RGR and is, in this respect, an easy parameter to use in growth analyses. However, if one would like to analyze what factors play a role in determining SLA, it is more appropriate to consider its inverse, $1/\text{SLA}$, for which many other terms have been used (SLW, SLM, LMA). This is because components of the leaf, like leaf thickness, or anatomical and biochemical features, increase linearly with the inverse of SLA. Witkowski and Lamont (1991) factorized $1/\text{SLA}$ into two components: leaf thickness (LTh) and leaf density (LD). Leaf density is defined as the mass of a leaf per unit leaf volume:

$$\text{LD} = \frac{M_L}{\text{LTh } A} \quad (3.13)$$

and therefore,

$$\frac{1}{\text{SLA}} = \text{LD LTh} = \frac{M_L}{\text{LTh } A} \text{LTh} \quad (3.14)$$

A leaf can also be separated into its underlying anatomical tissues: epidermis, mesophyll, sclerenchyma, vascular tissue, and intercellular spaces. The $1/\text{SLA}$ is then the sum of the densities of the various tissues i , weighted by the volume per unit leaf area taken by each tissue (Garnier and Laurent 1994):

$$\frac{1}{\text{SLA}} = \sum_{i=1}^5 \frac{V_i M_i}{A V_i} \quad (3.15)$$

Leaf biomass can also be separated into its various biochemical fractions. A simple grouping of the wide range of compounds is: Lipids, lignin, soluble phenolics, protein, structural carbohydrates (cellulose, hemicellulose, pectin), nonstructural carbohydrates (glucose, fructose, sucrose, starch), organic acids, and minerals (for a review see Poorter and Villar 1997). $1/\text{SLA}$ is then the sum of the masses of each of the eight classes of compounds expressed per unit area:

$$\frac{1}{\text{SLA}} = \sum_{i=1}^8 \frac{M_i}{A} \quad (3.16)$$

The three ways of breaking down $1/\text{SLA}$ are interrelated: a high leaf density, for example, can be the result of a high proportion of sclerenchyma, which shows up in the biochemical analysis as a high concentration of cell walls (lignin and structural carbohydrates).

mass per unit volume increases. It can therefore be expected that fast-growing species, with a low density of tissues, will have a high water content per unit biomass. This turns out to be the case and not only applies to leaves but also to stems and roots (Garnier 1992, Ryser 1996). Another factor that strongly affects the density is the relative volume of intercellular spaces.

RGR AND ITS COMPONENTS: A SYNTHESIS

It is quite clear from the previous section that inherent differences in RGR_{max} among species are associated with differences in a large array of plant traits (Lambers and Poorter 1992; Chapin et al. 1993). To what extent are these parameters related to each other? To answer this question, a principal component analysis (PCA) was conducted on two sets of data obtained from wild herbaceous species for which a large number of variables were measured. The first one (*Herbs*) concerns 11 grasses and 13 dicotyledonous species, the second (*Grasses*) is for 12 wild grasses. The results are shown in Figure 3.5.

The patterns confirm the differences between the fast- and slow-growing species as presented in the previous section: in both data sets a high RGR is strongly related to a high uptake capacity of both leaves (photosynthesis, PS_m) and roots (NUR) expressed per unit mass of leaves and roots. The correlation between RGR and PS_a (and ULR) is looser. Shoot respiration and root respiration (only available for Herbs) are also positively associated with RGR. Species with a high RGR also have a high SLA, a high nitrogen concentration in the leaves and a high concentration of minerals in their tissues (only available for Herbs). All these parameters can be found at the right-hand side of Figure 3.5. At the left-hand side are the variables associated with slow-growing species. They have a high density in leaves and roots and a high proportion of leaf biomass in cell walls. Moreover, a large fraction of the total C fixed daily in photosynthesis is spent in respiration (only available for Herbs). Similar results have been found for a range of *Hordeum spontaneum* genotypes differing in RGR_{max} (Poorter et al. 2005).

A PCA analysis can also be used to gain insight into how well the various other parameters of the plants are correlated with each other, and probably also mechanistically associated. For example, PS_a and ULR are strongly associated. The rates of shoot and root respiration (only available for Herbs) have a similar value in common for factor 1, but at the axis of factor 2 they are separated from each other. This may indicate that, although they are both highly correlated with RGR, the reason for correlation is—at least to some extent—different. Part of the respiration is necessary for growth and can be expected to be high in both organs for fast-growing species. Another part of the shoot respiration may have to do with a high transport of sugars to the sink, whereas part of the root respiration is related to nutrient uptake. It is this type of information we need if we want to understand the trade-offs that play a role in determining the functioning of the whole plant.

From the above analyses, suites of traits can be associated with fast and slow growth: high RGR_{max} is achieved in species exhibiting high rates of resource acquisition, made possible, among other things, through high-light interception per unit leaf mass (high SLA), high concentration of enzymatic machinery (reflected by a high nitrogen concentration) and low density of tissues (i.e., high water content). The latter two are an indication that fast-growing plants display a high concentration of protoplasmic elements (except for starch; see also Niemann et al. 1992). Opposite traits are found in slow-growing species, a low RGR_{max} associated with a high amount of cell walls and starch, which are metabolically inactive and lead to low acquisition rates per unit mass. In the section on pp. 90–93, we put forward the hypothesis that these contrasting suites of traits can be interpreted as a functional trade-off between high biomass productivity and efficient conservation of nutrients.

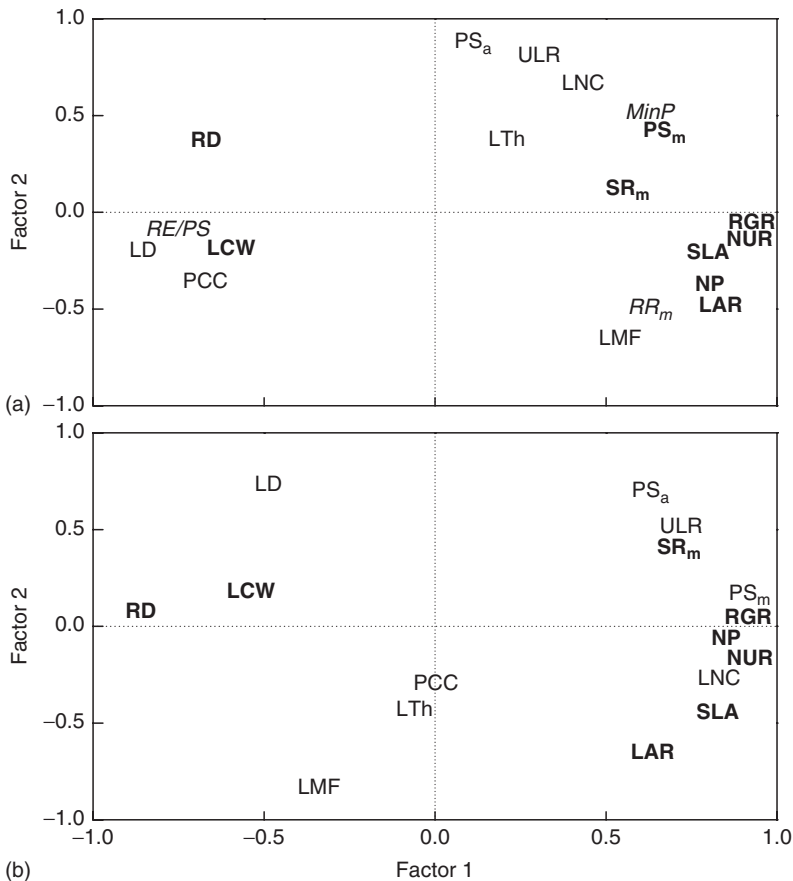


FIGURE 3.5 PCA plots for (a) Herbs and (b) Grasses. The first two axes explain 66% and 71% of the overall information for Herbs and Grasses, respectively. In both analyses, axis 1 can be interpreted as a biomass production axis; axis 2 appears to be mainly determined by gas exchange properties (photosynthesis and transpiration) per unit leaf area. Variables printed in bold are on similar places in the plane. Variables printed in italics were determined for Herbs only. Abbreviations not given in Table 3.1 are: LCW, proportion of cell walls in the leaves; LTh, leaf thickness; MinP, mineral concentration of the plant; RE/PS, the fraction of daily fixed photosynthesis that is respired again. In this analysis, two new variables (factor 1 and factor 2) are computed out of a combination of all original variables. For each of these variables it is calculated whether they contribute positively (close to 1.0), negatively (close to -1.0), or not (close to 0.0) to factor 1. The amount of variance thus explained is taken out of the data and the procedure is repeated with the remaining variance. The result is somewhat comparable to a two-dimensional electrophoresis. Variables that are close together (like RGR and NUR) are generally positively correlated, variables that are at opposite parts of the graph (like RGR and LCW) are negatively correlated, and variables that have values close to 1 or -1 for one factor and values close to 0 for the other axis [like RGR and PS_a in (a)] are generally not correlated at all. (Data for Herbs are from Poorter, H., Remkes, C., and Lambers, H., *Plant Physiol.*, 94, 621, 1990; Poorter, H. and Remkes, C., *Oecologia*, 83, 553, 1990; Poorter, H. and Bergkotte, M., *Plant, Cell Environ.*, 15, 221, 1992; and concern 11 grasses and 13 dicotyledonous species. Data for Grasses are from Garnier, E., *J. Ecol.*, 80, 665, 1992; Garnier, E. and Laurent, G., *New Phytol.*, 128, 725, 1994; Garnier, E. and Vancaeyzeele, S., *Plant, Cell Environ.*, 17, 399, 1994; and Garnier et al. (unpublished) and comprise 12 grass species.)

DO LABORATORY FINDINGS APPLY TO THE FIELD?

As stated earlier (see the second section on pp. 69–73), plants growing in the field certainly do not achieve their potential growth rate. However, to bear ecological significance, differences in the above-mentioned suite of traits between species, as found under laboratory conditions, should at least reflect to some extent the differences between the same species growing in their natural habitat. Is there evidence that this is the case? This question can be approached by comparing plant traits that have been measured for the same species both in the laboratory and in the field. This is done here for SLA and leaf nitrogen concentration on a leaf mass basis, which are positively related to RGR_{max} , and leaf density, which is negatively correlated with RGR_{max} for plants grown under optimum conditions in the lab (see the previous two sections, pp. 76–83). How are these attributes for plants growing naturally in the field, and is the ranking of species the same under both conditions?

Several data sets are available to address this question, comprising both herbaceous and woody plants. For the 86 species for which such data are available, SLA is on average 50% lower in the field than in the lab. Nonetheless, there is a good relationship between SLA measured in the field and in the laboratory for four of the five data sets taken individually (Figure 3.6a). Leaf nitrogen concentration is 34% lower in field grown plants, and the relationship between field and laboratory-grown plants is significant for three of the five data sets (Figure 3.6b). Finally, leaf density is approximately 40% higher in the field than in the laboratory, and the relationship between density measured in the field and in the laboratory is highly significant for the only data set with a substantial amount of data points (11 species: Figure 3.6c). Differences between laboratory and field-measured leaf traits are probably caused by a combination of a higher light intensity, higher wind speed, and lower nutrient availability in the latter environment.

Although there are differences in plant traits measured under field and lab conditions, these results show that the ranking of species for such important traits as SLA and leaf density are maintained under a wide range of growing conditions. This is further corroborated by the fact that the relationships between ecosystem productivity and community-averaged RGR_{max} on the one hand and ecosystem productivity and community-averaged SLA measured in the field on the other hand compare well (Figure 3.3). This may be less so for leaf nitrogen concentration. We may therefore expect that the suite of traits discussed in the previous section is likely to be maintained, at least partially, under field conditions.

SELECTION FOR RGR OR UNDERLYING COMPONENTS?

SELECTION FOR RGR

As discussed in the previous section, RGR is a parameter that is associated with a suite of traits. Based on the negative correlations between RGR_{max} and the harshness of the environment (Figure 3.2), it has been suggested that RGR was the target of selection (Grime 1977, Chapin 1988). Alternatively, it may have been one or more of the components of RGR that has been selected for (Grime 1977, Coley 1983, Dijkstra and Lambers 1987).

What are the arguments in favor of selection for a high RGR? For ruderals and other annual species, a fast completion of the life cycle seems of paramount importance (Grime 1979). A high RGR may be of help to reach the size required for high seed production (discussed by Benjamin and Hardwick 1986, McGraw and Garbutt 1990, and Garnier and Freijssen 1994). Competitive species, be it woody or herbaceous, seem to have an advantage by occupying quickly the available space within the vegetation. The acquisition of resources,

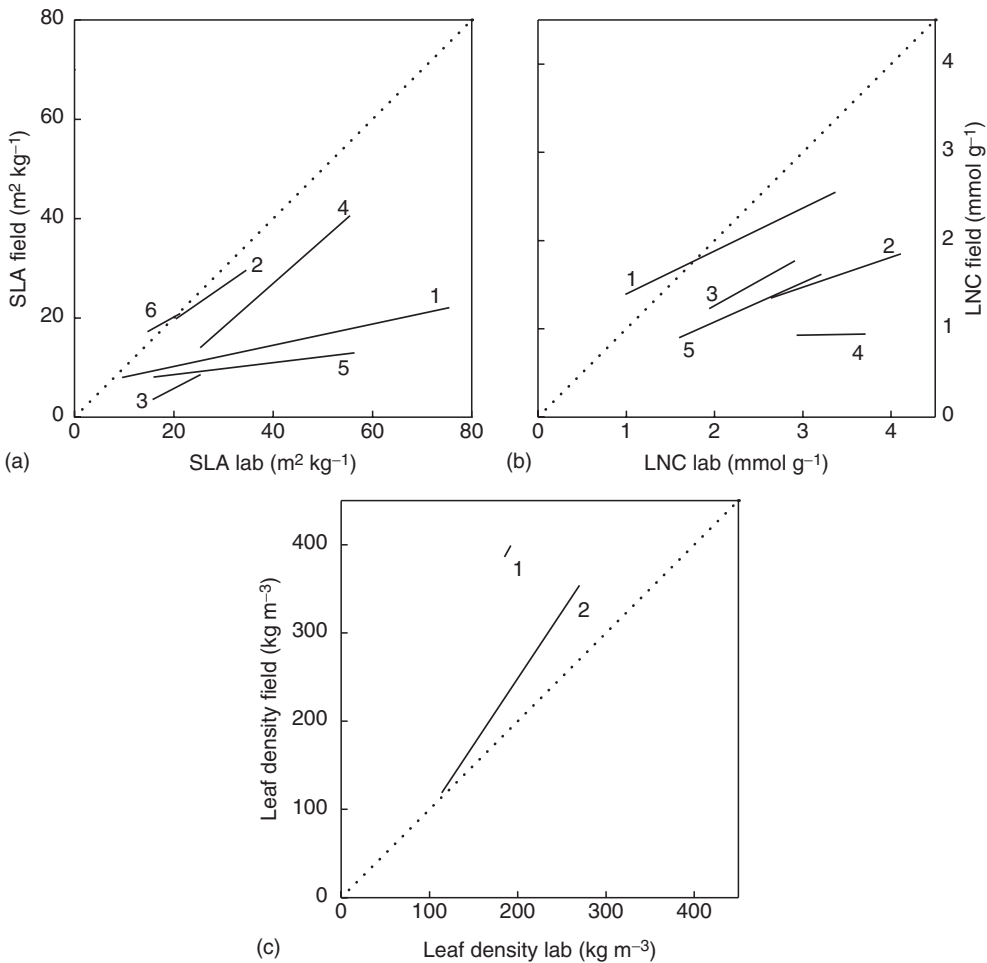


FIGURE 3.6 (a) SLA; (b) leaf nitrogen concentration, and (c) leaf density measured on the same species in field and laboratory conditions. Each study is represented by a regression line and contains several species. (Data from: a: (1) Cornelissen, J.H.C. et al. (unpublished, laboratory, and field); (2) Garnier, E. and Laurent, G., *New Phytol.*, 128, 725, 1994 (laboratory) and Garnier, E., Cordonnier, P., Guillermin, J.-L., and Sonié, L., *Oecologia*, 111, 490, 1997 (field); (3) Mooney, H.A., Ferrar, P.J., and Slatyer, R.O., *Oecologia*, 36, 103, 1978 (laboratory and field); (4) Poorter, H. and Remkes, C., *Oecologia*, 83, 553, 1990 (laboratory and Poorter, H. and de Jong, R., *New Phytol.*, 143, 163, 1999 (field); (5) Walters, M.B., Kruger, E.L., and Reich, P.B., *Oecologia*, 96, 219, 1993, and P.B. Reich (unpublished) (laboratory) and Reich, P.B., Walters, M.B., and Ellsworth, D.S., *Ecol. Monogr.*, 62, 365, 1992 (field); (6) Bloor J.M.G., *J. Trop. Ecol.*, 19, 163, 2003; b: (1) Cornelissen, J.H.C., Werger, M.J.A., Castro-Diez, P., van Rheeunen, J.W.A., and Rowland, A.P., *Oecologia*, 111, 460, 1997; (2) Garnier, E. and Vancaeyzeele, S., *Plant, Cell Environ.*, 17, 399, 1994 (laboratory) and Garnier, E., Cordonnier, P., Guillermin, J.-L., and Sonié, L., *Oecologia*, 111, 490, 1997 (field); (3) Hull, J.C. and Mooney, H.A., *Acta Oecologica*, 11, 453, 1978 (laboratory and field); (4) Mooney, H.A., Ferrar, P.J., and Slatyer, R.O., *Oecologia*, 36, 103, 1978 (laboratory and field); (5) P.B. Reich (unpublished, laboratory) and Reich, P.B., Walters, M.B., and Ellsworth, D.S., *Ecol. Monogr.*, 62, 365, 1992 (field); c: Garnier, E. and Laurent, G., *New Phytol.*, 128, 725, 1994 (laboratory) and E. Garnier and J.-L. Cordonnier (unpublished); (2) Poorter, H. and Bergkotte, M., *Plant, Cell Environ.*, 15, 221, 1992 (laboratory) and Poorter, H. and de Jong, R., *New Phytol.*, 143, 163, 1999 (field).)

both above and belowground, depends on how much of the volume of soil and air is occupied by roots and leaves. A high RGR may enable this.

What would be the adaptive value of a low RGR? Some explanations have been offered, focusing on plant species from nutrient-poor habitats (Chapin 1980, 1988). However, these suggestions are questionable (Poorter 1989, Lambers and Poorter 1992):

1. *If plants grow slowly, they are less likely to deplete the available nutrient resources early in the season.* This does not seem to be an evolutionarily stable strategy. As soon as one species or genotype starts to take up as much nutrients as possible early in the season, the others miss out.
2. *Plants in nutrient-poor areas will never grow fast. If they have a low potential RGR, they will be closer to their optimum in the field.* For all plants it applies that their physiological optimum differs from the conditions they experience in the field (see the second section, pp. 69–73). However, a clear difference between physiological and ecological optimum does not necessarily imply a disadvantage. Fast- as well as slow-growing species have a large flexibility, morphological as well as physiological, to cope with varying conditions (Reynolds and d'Antonio 1996). At low nutrient supply, for example, it is found that species with a high RGR_{max} still grow faster or at similar rates than those with a low RGR_{max} (Shipley and Keddy 1988, Poorter et al. 1995).
3. *If plants grow slowly, they can accumulate sugars and nutrients during favorable times, so as to enable growth in later times when nutrients are less easily available.* As far as sugars are concerned this explanation does not hold. Plants experiencing nutrient stress are limited more in growth than in photosynthesis. They fix more C than can be used in growth, resulting in accumulation of nonstructural sugars (mainly starch; Poorter and Villar 1997). Therefore, it does not seem necessary to store sugars for times with a low-nutrient availability. For nutrients however, this reasoning could be valid. A prerequisite is that nutrients become available in flushes. Such flushes have been shown, for example during freeze-thaw events that lyse microbial cells or during drought–wet cycles (for discussion see Bilbrough and Caldwell 1997). However, although these processes have been shown to occur, there is at present not enough evidence to conclude that species found in sites of different nutrient availability (or those with contrasting RGR_{max}) differ in this respect. For plants grown hydroponically in the laboratory at a nonlimiting nutrient supply, we found fast-growing species to accumulate 4–5 times more NO_3^- than slow-growing species.
4. A last hypothesis does not explain why plants in low-resource environments do have a low RGR, but rather why they do not have a high potential RGR: *A high RGR cannot be realized in low-resource environments and therefore RGR is a selectively neutral trait.* Although a very high RGR would not be reached, a genotype with a slightly higher RGR could still occupy some extra space and consequently would be able to acquire some extra nutrients. Thus, in those cases RGR would not necessarily be a selectively neutral trait.

SELECTION FOR COMPONENTS OF RGR

Is there evidence that components of RGR have been selected for, rather than RGR itself? This is not a question that can be easily answered. If all of the components scale positively with RGR, it becomes impossible to separate between the two alternatives. Moreover, it is difficult to single out one component if the different traits have not been selected independently, or if they are functionally related. For example, a high rate of photosynthesis is achieved with a high concentration of protein. A high concentration of protein may imply a

high rate of protein turnover, and therefore a high maintenance respiration. In addition, a high rate of photosynthesis may result in a high rate of export to the phloem, which also causes an increase in shoot respiration (cf. Figure 3.5). Given these mechanistic interrelations, it is not easy to break the correlation between photosynthesis and respiration.

Nevertheless, we believe that there are good reasons to think that selection in a low-resource environment has been for components related to a low SLA, rather than for RGR per se. Generally, SLA is the most important growth parameter associated with inherent variation in RGR_{max} (pp. 76–83). Moreover, differences in SLA observed in the laboratory are preserved in the field (p. 84), and in the case of the old-field succession described in the “RGR_{max} and Ecosystem Productivity,” pp. 73–75, the correlation between the RGR of the vegetation and the aggregated SLA of the composing plant species, which was determined in the field, was almost as good as the correlation with the aggregated RGR derived from lab measurements (Figure 3.3b). What are the arguments in favor of this alternative hypothesis?

SELECTION FOR SLA-RELATED TRAITS IN ADVERSE ENVIRONMENTS

Plants from extremely nutrient-poor environments are often evergreens, with a high leaf longevity. As has been previously discussed, availability of photosynthates is not a growth-limiting factor in these environments, but the availability of nutrients is. A first problem of plants in a low-nutrient environment is to acquire nutrients; a second problem is to use them efficiently. Berendse and Aerts (1987) showed that an efficient use of, for example, N [nitrogen use efficiency (NUE); gram of growth per unit N taken up or lost by the plant] depends on two components: the biomass increase per unit N and per unit of time (NP, the mean annual nitrogen productivity) and the average time that a unit of N stays in the plant (MRT, mean residence time of nitrogen; see Box 3.4). They argue that there is a trade-off between these two components: a plant cannot achieve both a high NP and a high MRT (Figure 3.7). Such a trade-off has indeed been shown in several cases (e.g., Eckstein and Karlsson 1997; Figure 3.7), but is less evident in other experiments (reviewed by Garnier and Aronson 1998). The putative trade-off between NP and MRT is most likely due to the suite of characters discussed on pp. 82–83: a high nitrogen productivity is strongly correlated with both a high SLA and a low density of organs (characteristics found at the right-hand side in Figure 3.5). Plants with those characteristics are mainly directed toward attaining a high rate of resource capture (carbon, nutrients). This strategy is further discussed on p. 90. The other extreme is formed by the species with a high MRT. Species with such a strategy can be found in nutrient-poor environments. Why is this so? In nutrient-poor environments, it may be a disadvantage for an individual plant to lose acquired nutrients, as it is very questionable whether that individual is able to take them up again once they have entered the nutrient cycling process. Therefore, there is a premium to increase the residence time of nutrients. Theoretically, this can be achieved in two ways (Box 3.4): either a plant resorbs nutrients from senescing organs very efficiently, or it restricts the turnover of organs and thus the loss of biomass per unit of biomass present (Aerts 1990, Garnier and Aronson 1998). Although there is variation in resorption efficiency among species, it does not differ strongly among life-forms or species originating from habitats differing in fertility (reviewed by Aerts and Chapin 2000). Thus, the way species from nutrient-poor habitats achieve a high MRT is by a long life span of both leaves and roots (Aerts 1995, Ryser 1996, Eckstein and Karlsson 1997, Garnier and Aronson 1998, Hikosaka 2003).

BOX 3.4 Components of Nitrogen Use Efficiency

In Box 3.2, RGR was factorized into components based on the assumption that leaf area is the important plant variable driving photosynthesis, and thus growth. An alternative approach is to consider plant (organic) N as the driving variable, as proteins play a vital role in C-fixation, nutrient uptake, and in most other physiological processes of the plant. RGR is then factorized into the components NP (Nitrogen Productivity) and PNC (Plant Nitrogen Concentration; preferably restricted to organic nitrogen, as NH_4^+ and NO_3^- play less of a physiological role). NP is defined as the increase in biomass per unit time and plant nitrogen (Ingestad 1979):

$$\text{NP} = \frac{1}{N} \frac{dM}{dt}, \quad (3.17)$$

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

$$\text{PNC} = \frac{N}{M} \quad (3.18)$$

and consequently

$$\text{NP PNC} = \frac{1}{N} \frac{dM}{dt} \frac{N}{M} = \text{RGR} \quad (3.19)$$

Considered over a short and fixed period of time, plants use their internal nitrogen efficiently if they have a high NP. Considered over a longer time scale, an alternative way to make efficient use of a unit of nitrogen taken up is to increase the time this unit remains in the plant. This time span is called the mean residence time (MRT, expressed in years). Under steady-state conditions (i.e., when the amount of nutrients taken up by the plant equals that lost by leaf and root shedding, herbivory, etc.), MRT is equal to the ratio between the average amount of nitrogen in the plant (N) and that taken up or lost over a given period of time (dN/dt ; see, e.g., Frissel 1981). Berendse and Aerts (1987) have proposed that it is the product of NP and MRT that determines the nutrient use efficiency (NUE)

$$\text{NP.MRT} = \frac{1}{N} \frac{dM}{dt} N \frac{dt}{dN} = \frac{dM}{dN} = \text{NUE} \quad (3.20)$$

NUE is therefore the total amount of biomass produced per unit N taken up or lost. Note that in Equation 3.19, NP is generally determined over a short time scale (days to weeks), whereas in Equation 3.20 it is determined on an annual basis.

Under steady-state functioning MRT depends on two parameters in the following way (Garnier and Aronson 1998):

$$\text{MRT} = \frac{1}{1 - R_{\text{eff}}} \frac{1}{e}, \quad (3.21)$$

where R_{eff} is the nitrogen resorption efficiency during senescence (defined as the reduction in the amount of nutrient between mature and senesced organs, relative to the amount in mature organs: Aerts 1996, Killingbeck 1996), and e is the rate of biomass lost by the plant, which depends on the life span of organs. These two parameters are central to the definition of the nutrient conservation strategy of the various species.

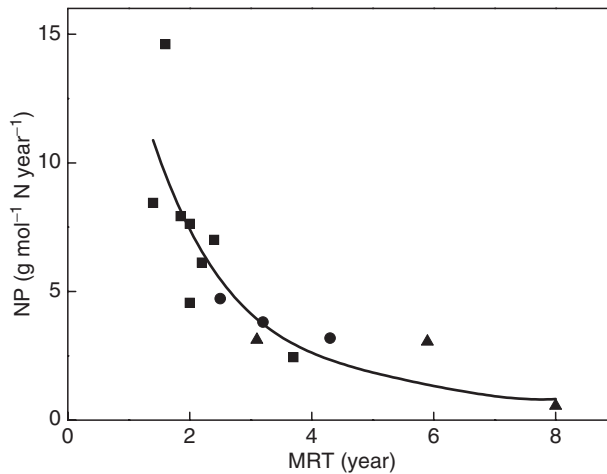


FIGURE 3.7 The relation between Nitrogen Productivity (NP; on an annual basis) and the MRT of nitrogen of 14 species grown in the field. Squares, herbaceous species; circles, deciduous shrubs; triangles, evergreen shrubs. (Data from Eckstein, R.L. and Karlsson, P.S., *Oikos*, 79, 311, 1997.)

What determines the life span of a leaf or root? For perennial species, there is an effect of the environment, with increases in leaf life span under relatively predictable low-resource conditions (low temperature, low irradiance). However, most of the variation in leaf life span is due to inherent differences between species (Reich 1998). Leaves of some species live for less than 2 months, whereas leaves of others have been reported to function for more than 20 years (Ewers and Schmid 1981). The physiological mechanism determining the life span of a leaf is unknown. However, it is evident that a leaf can only become long-lived if it can withstand adverse periods. Therefore, compared with a leaf with a short life span extra investments have to be made to survive periods of drought or coldness. It should also be less attractive to herbivores, and not be so frail that it is damaged in storms. Finally, in a nutrient-poor environment one could expect extra investments of plants to prevent nutrients leaching out of the leaf. Drought tolerance may be achieved by leaf hairs, a thick cuticle, an increase in lipid concentration and possibly small cell sizes (Jones 1983). Cold resistance may be acquired by increases in osmotic solutes. Herbivory may be counteracted by the accumulation of phenolics or other secondary compounds. In all these cases extra lignification may occur. Extra lignification and thicker cell walls can also be expected for plants that have adapted to a high degree of mechanical disturbance, such as trampling or strong winds. Nutrient leaching could be prevented by extra investment in wax layers.

Compared with a basic leaf with a short life span, all of these additional investments increase the biomass per unit leaf area and thus decrease SLA. Therefore, we might expect a negative relation between SLA (and the suite of traits positively associated with SLA) and leaf life span. This has indeed been shown in an analysis of plant species across a wide range of habitats (Reich et al. 1992, Wright et al. 2004, Figure 3.8). Data on the life span of roots are far less abundant (Eissenstat and Yani 1997). As far as data are available, they seem to indicate that species with a higher density of root tissue may have longer life spans (Ryser 1996). It is this connection between the nutrient economy (in the form of a high MRT through a long leaf or root life span) and the carbon economy (in the form of a low SLA) that may explain the success of species with a low RGR_{max} in nutrient-poor environments.

Up to now, we have focused discussion on RGR components of plants from habitats low in nutrients. Basically, similar considerations could work for plants in other environments

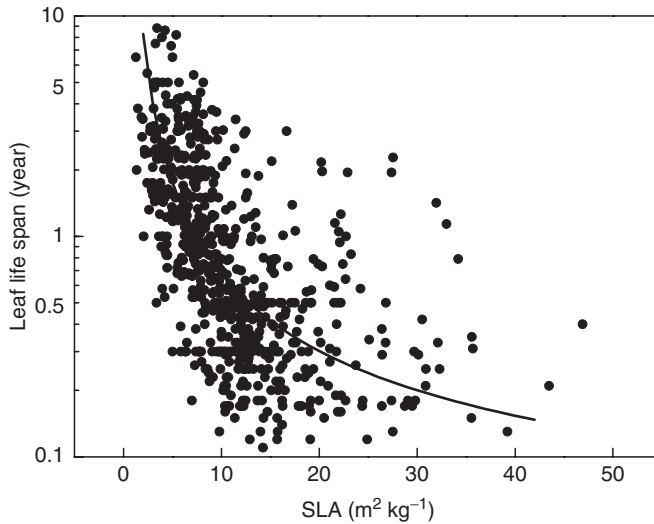


FIGURE 3.8 Leaf longevity as a function of SLA for a wide range of trees, shrubs, and herbaceous C_3 species found across a range of contrasting climates. (Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., +26 others, *Nature*, 428, 821, 2004.)

adverse to growth. In all cases where the production of biomass is difficult, one may expect a premium on maintaining existing biomass rather than replacing lost leaves or roots.

SELECTION FOR SLA-RELATED TRAITS IN FAVORABLE ENVIRONMENTS

What about a possible selection for RGR components in an environment favorable for plant growth? Vegetation is dense there, with a fast leaf area development during the growing season. Consequently, there is a strong competition for light, necessitating a fast increase in stem height and an efficient light interception per unit leaf biomass. In simulations of competition under agricultural conditions, it has been shown how important SLA is during the period before canopy closure: high-SLA plants have a higher light-interception per unit leaf biomass and therefore faster growth than competing plants with a low SLA (Spitters and Aerts 1983, Gutschick 1988). In a closed canopy, maximum photosynthetic carbon gain of the vegetation as a whole is highest at lower values of SLA (Gutschick 1988). However, also under those conditions there may be a selection pressure towards an increase in SLA. Using game theory, Schieving and Poorter (1999) analyzed mathematically the total carbon gain of two putative genotypes, which were similar in all traits, except for SLA. Simulating competition in a dense stand on the basis of functions for the distribution of light, nitrogen and leaf area, they found that the genotype with the higher SLA always replaced the lower SLA genotypes.

EVIDENCE FOR THE IMPORTANCE OF SLA-RELATED TRAITS

As outlined in the previous section, it is difficult to really prove that selection has been for SLA-related traits rather than for RGR itself. At best we can show that SLA and the suite of leaf and root characteristics associated with it, vary along environmental gradients, or that high-SLA species that have been introduced in new continents displace low-SLA species in favorable habitats, but not in harsher environments. In analyzing these data, one should realize that SLA of a given species is not very sensitive to differences in nutrient availability, but rather sensitive to light.

NUTRIENT AVAILABILITY

The most obvious difference in SLA is between woody deciduous and woody evergreen species. Evergreens have much lower SLAs (Villar and Merino 2001) and are generally found in nutrient-poor habitats (Monk 1966, Small 1972). Comparing productivity of various woody deciduous and evergreen species at the stand scale, a positive correlation has been found between SLA and annual productivity per unit leaf mass (Reich et al. 1997). Additionally, for herbaceous vegetations, there is a general trend that productive sites bear species with a higher SLA (Poorter and de Jong 1999). However, there is considerable variability around this trend, as only half of the total variation in SLA between species was explained by differences between sites, the other half due to differences in species within sites. This is in line with data of Van Andel and Biere (1989), who found a large variation in RGR_{max} and SLA for species co-occurring in the same habitat.

Species replacement has been observed in Venezuela, where two introduced C_4 grasses have outcompeted the original C_4 grass in most areas, but not in drier sites with low fertility (Baruch et al. 1985, Baruch 1996). Conforming to our expectations, the native species has a lower SLA, a higher proportion of sclerenchyma, and a lower concentration of N (Table 3.4).

A controlled experimental test to analyze the relation between growth parameters and field performance was carried out by Biere et al. (1996). They selected a range of families of *Lychnis flos-cuculi* and performed a growth analysis for each of these families in the glasshouse. At the same time, seeds of these families were sown in the field, along a fertility gradient. The aboveground biomass of all field plants at the end of the growing season, a good predictor of next year's fecundity, was estimated and correlated with the growth parameters determined in the glasshouse. At the poorest site, families with a high RGR_{max} , LAR, and SLA fared worst (Table 3.5). However, the higher the site fertility, the more these parameters gained importance, and in the most productive site families with a high SLA (and LAR) were those that attained the highest biomass. These results were confirmed in an experiment where early plant growth characteristics were correlated with fitness in *H. spontaneum* accessions (Verhoeven et al. 2004). At high, but not at low nutrient supply, high SLA accessions had the highest seed mass output. RGR itself was not correlated with fitness.

TABLE 3.4
Differences in Leaf Characteristics between Introduced and Native Species

	<i>H. rufa</i> Introduced	<i>T. plumosus</i> Native	<i>A. stolonifera</i> Introduced	<i>A. magellanica</i> Native
SLA ($m^2 kg^{-1}$)	34	21	33	13
Leaf thickness (μm)	140	190	170	330
Leaf density ($kg m^{-3}$)	210	250	180	235
Volume (%)				
Epidermis	36	38	24	20
Mesophyll	53	39	72	62
Vascular	11	17	3	3
Sclerenchyma	1	5	2	16
Concentrations ($mg g^{-1}$)				
N	20	13	21	16

Note: The first comparison is a C_4 grass introduced in Venezuela (*Hyparrhenia rufa*) with a native C_4 grass species (*Trachypogon plumosus*; Data from Baruch, Z., Ludlow, M.M. and Davis, R., *Oecologia* 67, 388, 1985.) The second comparison is an *Agrostis* species introduced on sub Antarctic islands (*A. stolonifera*) with a native species from the same genus (*A. magellanica*; Data from Pammenter, N.W., Drennan, P.M., and Smith, V.R., *New Phytol.*, 102, 143, 1986.)

TABLE 3.5
Correlations between Plant Mass in the Field, Determined at Four Sites Differing in Productivity, and a Number of Growth-Related Parameters, Determined in the Glasshouse

Site Productivity	Seed Mass	Emergence	RGR	ULR	LAR	SLA	LMF
Low	0.77	0.07	-0.70	0.11	-0.70	-0.76	0.49
Low-intermed	0.25	-0.02	-0.06	0.15	-0.15	-0.11	-0.09
Intermed-high	0.12	-0.27	0.04	0.03	0.02	-0.02	0.12
High	-0.10	-0.45	0.21	-0.27	0.38	0.41	-0.02

Source: After Biere, A., *Plant Soil*, 182, 313, 1996, slightly simplified and reworked for this table.

Note: Data are family means ($n = 56$) of above-ground plant mass (in-transformed) of plants of *Lychnis flos-cuculi* sown in the field and seed mass, time to emergence and growth parameters as determined in the glass house. Values in bold are significant at $P < 0.05$.

WATER AVAILABILITY

Mooney et al. (1978) investigated *Eucalyptus* species along a rainfall gradient, and showed that, both for plants growing in the field and in the laboratory, the SLA of the low-rainfall species was lower than those of species growing at sites with higher rainfall. The high SLA species had the highest concentration of N per mass. In this case, the correlation between seedling RGR and rainfall was not very tight, whereas the correlation with SLA was tight. Similarly, the SLA of sun-lit leaves from *Eucalyptus* canopies, sampled along a climatic gradient in Australia was found to be inversely related to the potential evaporation at the various sites studied (Specht and Specht 1989). These results are not supported by Warren and Adams (2005) though, who showed a relationship between rainfall and biomass allocation, rather than with SLA for nine *Eucalypt* species. *Encelia farinosa* plants from dry places are reported to have lower SLA than those from wetter places, and lower SLA than *Encelia frutescens* plants growing close-by but tapping in on deeper water (Ehleringer and Cook 1984, Ehleringer 1988). The lower SLA of *E. farinosa* from the driest sites is completely due to a thick layer of leaf hairs, which reflect the sunlight and may take up 50% of the biomass of the leaf. Finally, Tsialtas et al. (2004) found low-SLA species to be more abundant in dry Mediterranean sites than high-SLA species.

TRAMPLING AND WIND DAMAGE

A very clear case in which a low SLA is of survival value is trampling. Dijkstra and Lambers (1989) studied two subspecies of *Plantago major*. One is an annual, growing on occasionally flooded river banks, whereas the other is a perennial, occurring in frequently mown and trampled lawns. The leaves of the first subspecies have a high SLA and are erect. Those of the second are prostrate and have a low SLA, as well as a higher proportion of biomass in cell walls. An experiment showed that the subspecies with the low SLA survived trampling better (Table 3.6). Similarly, Meerts and Garnier (1996) found that *Polygonum aviculare* genotypes from trampled habitats show a lower SLA under laboratory conditions than those from nontrampled places, and so did Kobayashi et al. (1999) for trampling-resistant forbs and grasses.

Leaf destruction can also take place by strong winds. Pammenter et al. (1986) analyzed differences in leaf anatomy between two *Agrostis* species that occur at sub-Antarctic islands. *Agrostis magellanica* is native to these islands, *Agrostis stolonifera* has been introduced recently. The latter species has displaced *A. magellanica* in wind-sheltered areas, but not in

TABLE 3.6
Leaf Characteristics, Chemical Composition, and Trampling Survival, Determined for Lab-Grown Plants of Two Subspecies of *P. major*

	<i>P. major</i> River Bank	<i>P. major</i> Trampled Lawn
SLA ($\text{m}^2 \text{kg}^{-1}$)	39	29
Leaf thickness (μm)	280	280
Leaf density (kg m^{-3})	90	125
Concentrations (mg g^{-1})		
N	42	42
Minerals	190	130
Cell walls	200	240
Trampling survival (%)	6	45

Source: Dijkstra, P. and Lambers, H., *New Phytol.*, 113, 283, 1989.

Note: One subspecies is an annual, occurring on irregularly flooded riverbanks; the other is perennial from a frequently mown and trampled lawn.

more open terrain. This is most likely explained by the fact that the leaves of the introduced species are relatively thin and fragile. *A. magellanica*, with an unusual high fraction of the leaf volume occupied by sclerenchyma, a high leaf thickness, and a much lower SLA (Table 3.4), seems better able to withstand wind damage.

Alpine species have been found to have lower SLA than lowland species, both in the field (Körner and Diemer 1987) and in the laboratory (Atkin et al. 1996a). Under both sets of conditions, this was at least partly due to thicker leaves. It has been suggested that the increased wind speed measured at higher elevations could play a role here as well. In an experiment with an upland, low-SLA species and a lowland high-SLA species grown in a wind tunnel at high wind speed, Woodward (1983) found much greater leaf damage in the high-SLA species.

HERBIVORY

Herbivory by insects and mammals may have a large impact on the vegetation and strongly damage individual plants. Species that have a low attractivity to herbivores are those with a low water content, a low organic nitrogen concentration, high concentrations of lignin and other cell wall components, a high concentration of secondary compounds like tannins and tough leaves in general (Scriber 1977, Grubb 1986, Coley and Barone 1996). These are all traits associated with a low SLA.

An interesting case where species with an inherently high SLA perform less is in the understorey of tropical forests. Plants generally acclimate to a low light environment by an increase in SLA, enabling to capture more light per unit leaf biomass. Therefore, one might expect at first to find high-SLA species in the understorey. Indeed, high-SLA pioneer species have a higher RGR at low light intensities than shade-tolerant species (Veneklaas and Poorter 1998). Notwithstanding their initially higher growth rate, these plants suffer from a high mortality rate under these conditions compared with the shade-tolerant seedlings with low SLA (Kitajima 1994). Susceptibility to herbivory may play a role here as well.

CONCLUSIONS

We have shown that there is a relationship between the potential RGR of a species, as measured under optimal conditions in the laboratory, and the distribution of species in the

field. Fast-growing species are found in habitats favorable for plant growth, either on the short term (annuals, ruderals) or in the longer term (competitors according to the classification of Grime). Species found in harsh environments generally have a lower potential RGR. These interspecific differences in RGR_{max} are largely due to inherent differences in SLA. We have shown evidence that selection in the field may have acted, at least partly, on parameters related to SLA. An inherently low SLA (and the suite of traits associated with it) diminishes losses of nutrients or biomass due to grazing, trampling, or leaf turnover and may be advantageous for plants growing in harsh environments. If correct, this implies that a low RGR_{max} is merely a side effect of the low SLA.

Up to now, we have focused on the average fast- and slow-growing species, as representatives of two groups of functional types of species. However, it would be naive to think that any categorization into functional types can account for more than a modest amount of the variation that we encounter in the field. Moreover, it is evident that the plant traits discussed here are not the only ones that are shaped by evolution. To capture more of the variability, it would be desirable to include some other plant characteristics that are to a large extent independent of SLA and RGR. Westoby (1998) presented an interesting scheme, proposing to categorize species on the basis of SLA, seed mass, and maximum height achieved in the canopy. Seed mass is an important predictor of seed output per square meter of canopy cover, and a good indicator of seedling survival (Westoby 1998). The maximum height a plant can achieve is important for the type of vegetation in which it can survive. Westoby et al. (2002) further added leaf size and its relationship with twig size to this scheme. Such characterization across a wide range of species could be a promising avenue to further increase our understanding of the success or failure of species in a given habitat.

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