

Inherent Variation in Growth Rate Between Higher Plants: A Search for Physiological Causes and Ecological Consequences

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I. SUMMARY

When grown under optimum conditions, plant species from fertile, productive habitats tend to have inherently higher relative growth rates (RGR) than species from less favourable environments. Under these conditions, fast-growing species produce relatively more leaf area and less root mass, which greatly contributes to their larger carbon gain per unit plant weight. They have a higher rate of photosynthesis per unit leaf dry weight and per unit leaf nitrogen, but not necessarily per unit leaf area, due to their higher leaf area per unit leaf weight. Fast-growing species also have higher respiration rates per unit organ weight, due to demands of a higher RGR and higher rate of nutrient uptake. However, expressed as a fraction of the total amount of carbon fixed per day, they use less in respiration.

Fast-growing species have a greater capacity to acquire nutrients, which is likely to be a consequence, rather than the cause, of their higher RGR. There is no evidence that slow-growing species have a special ability to

acquire nutrients from dilute solutions, but they may have special mechanisms to release nutrients when these are sparingly soluble.

We have analysed variation in morphological, physiological, chemical and allocation characteristics underlying variation in RGR, to arrive at an appraisal of its ecological significance. When grown under optimum conditions, fast-growing species contain higher concentrations of organic nitrogen and minerals. The lower specific leaf area (SLA) of slow-growing species is at least partly due to the relatively high concentration of cell-wall material and quantitative secondary compounds, which may protect against detrimental abiotic and biotic factors. As a consequence of a greater investment in protective compounds or structures, the rate of photosynthesis per unit leaf dry weight is less, but leaf longevity is increased.

In short-term experiments with a limiting nutrient availability the RGR of all species is reduced, but potentially fast-growing species still grow faster than inherently slow-growing ones. Therefore, the absence of fast-growing species from infertile environments cannot be explained by their growth rate *per se*. The higher leaf longevity diminishes nutrient losses and is a factor contributing to the success in nutrient-limited habitats. We postulate that natural selection for traits which are advantageous under nutrient-limited conditions has led to the low growth potential of species from infertile and some other unfavourable habitats.

Other examples indicating that selection for traits which allow successful performance under adverse conditions inevitably leads to a lower potential RGR are included. We conclude that it is likely that there are trade-offs between growth potential and performance under adverse conditions, but that current ecophysiological information explaining variation in RGR is too limited to support this contention quantitatively.

II. INTRODUCTION

Plants are distributed over a wide range of habitats varying from tundra to rain forests, from wetlands to deserts and from lowland to alpine regions. Coping with such contrasting, sometimes extreme, environments requires a certain degree of inherent specialization. One of the characteristics in which species of different habitats vary is their growth potential. Plants growing on nutrient-poor soils have a lower growth rate than those on fertile soils. But even when grown under optimum conditions, species which naturally occur on nutrient-poor soils still have a lower growth rate compared to plants characteristic of fertile sites (e.g. [Bradshaw](#)

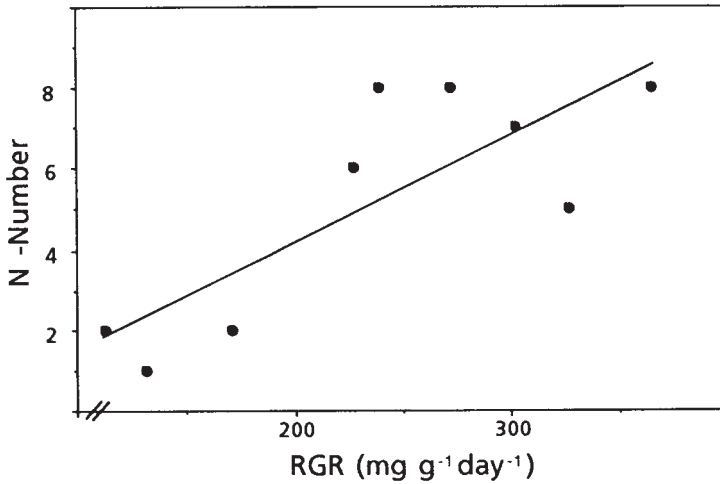


Figure 1 The relationship between the RGR of nine herbaceous C_3 species and the nitrogen index of the species' habitat according to Ellenberg (1979) (high values of the N number correspond to habitats of high nitrogen supply). RGR was determined at an optimum nutrient supply, moderate quantum flux density and fairly low vapour pressure deficit. The species described are, in order of increasing RGR *Corynephorus canescens*, *Festuca ovina*, *Pimpinella saxifraga*, *Phleum pratense*, *Anthriscus sylvestris*, *Poa annua*, *Scrophularia nodosa*, *Rumex crispus* and *Galinsoga parviflora*. (After Poorter and Remkes, 1990.)

et al., 1964; Rorison, 1968; Christie and Moorby, 1975; Grime and Hunt, 1975; Poorter and Remkes, 1990; Figure 1). In addition, species or ecotypes which naturally occur in shaded environments (Pons, 1977; Corré, 1983a), dry habitats (Rozijn and van der Werf, 1986), alpine regions (Woodward, 1979; Atkin and Day, 1990), arctic environments (Warren Wilson, 1966), saline conditions (Ball, 1988), sites which are rich in heavy metals (Wilson, 1988; Verkleij and Prast, 1989), or in other habitats adverse to plant growth all have a lower growth potential than comparable ones from favourable, fertile habitats.

This close association between a species' growth potential and the quality of its natural habitat raises two questions. First, how are the differences in growth rate between species brought about? And, second, what ecological advantage is conferred by a plant's growth potential? These two questions are in fact closely related. A plant is a complex of organs with contrasting functions and subject to conflicting demands. A low or a high potential growth rate may either be the basis or a by-product of adaptation to a certain set of environmental conditions. Hence there may be trade-offs between adaptation to adverse conditions and growth

potential. Therefore, the question on the ecological advantage of a potential growth rate cannot be answered until further ecophysiological information is available on the mechanisms explaining variation in growth potential.

Numerous plant characters contribute to a plant's absolute growth rate in its natural habitat, e.g. seed size, germination time, or plant size after overwintering. In this chapter we restrict ourselves to an analysis of the different traits that contribute to a plant's *relative growth rate* and discuss mechanisms which cause variation in any of these traits. We will treat the possible interdependence of various characteristics and try to quantify the importance of each of these in explaining interspecific variation in relative growth rate. Finally, we discuss the ecological implications of interspecific differences in the various traits and in the growth rate itself.

III. GROWTH ANALYSES

Growth analysis is often used as a tool to obtain insight into the functioning of a plant. Different types of analyses exist, depending on what is considered a key factor for growth (cf. *Lambers et al., 1989*). In the most common approach, leaf area is assumed to be a key factor. The relative growth rate (RGR) (see *Table 1* for a list of abbreviations), the rate of increase in plant weight per unit of plant weight already present, is then factorized into two components, the leaf area ratio and the net assimilation rate (*Evans, 1972*; see *Table 2* for a range of published values). The leaf area ratio (LAR) is the amount of leaf area per unit total plant weight. The net assimilation rate (NAR) is defined as the rate of increase in plant weight per unit leaf area. Thus:

$$\text{RGR} = \text{LAR} \times \text{NAR} \quad (1)$$

LAR and NAR can both be divided into a further set of components. The LAR is the product of the specific leaf area (SLA), the amount of leaf area per unit leaf weight, and the leaf weight ratio (LWR), the fraction of the total plant biomass allocated to leaves. Thus:

$$\text{LAR} = \text{SLA} \times \text{LWR} \quad (2)$$

Although termed the morphological component, LAR is affected by biomass allocation, chemical composition and leaf anatomy, as will be discussed later.

Table 1 Abbreviations used in this chapter and the preferred units in which they are expressed, listed in alphabetical order

Abbreviation	Meaning	Preferred units
CC	Carbon concentration	mmol C g ⁻¹
EXU _a (EXU _w)	Rate of exudation	mg m ⁻² (leaf area) day ⁻¹ (mg g ⁻¹ (plant wt) day ⁻¹)
LAR	Leaf area ratio	m ² kg ⁻¹
LR _a (LR _w)	Rate of leaf respiration	μmol CO ₂ m ⁻² (leaf area) s ⁻¹ (nmol CO ₂ g ⁻¹ (leaf wt) s ⁻¹)
LWR	Leaf weight ratio	g g ⁻¹
NAR	Net assimilation rate	g m ⁻² day ⁻¹
NIR	Net nitrogen uptake rate	nmol (g root) ⁻¹ s ⁻¹
PNC	Plant nitrogen concentration	mmol N g ⁻¹
PNUE	Photosynthetic nitrogen use efficiency	μmol CO ₂ (mol leaf N) ⁻¹ s ⁻¹
RGR	Relative growth rate	mg g ⁻¹ day ⁻¹
RWR	Root weight ratio	g g ⁻¹
SLA	Specific leaf area	m ² kg ⁻¹
SR _a (SR _w)	Rate of stem respiration	μmol CO ₂ m ⁻² (leaf area) s ⁻¹ (nmol CO ₂ g ⁻¹ (stem wt) s ⁻¹)
SRL	Specific root length	m g ⁻¹
SWR	Stem weight ratio	g g ⁻¹
PS _a (PS _w)	Rate of photosynthesis	μmol CO ₂ m ⁻² s ⁻¹
RR _a (RR _w)	Rate of root respiration	μmol CO ₂ m ⁻² (leaf area) s ⁻¹ (nmol C g ⁻¹ (root wt) s ⁻¹)
VOL _a (VOL _w)	Rate of volatile losses	mg m ⁻² (leaf area) day ⁻¹ (mg g ⁻¹ (plant wt) day ⁻¹)

The NAR is the net result of dry weight gain and dry weight losses and is largely the balance of the rate of photosynthesis, expressed per unit leaf area (PS), and the rate of leaf respiration (LR), stem respiration (SR) and root respiration (RR), in this case also per unit leaf area. If these physiological processes are expressed in moles of carbon, the net balance of photosynthesis and respiration has to be divided by CC, the carbon concentration of the newly formed material, to obtain the increase in dry weight. The balance is completed by subtracting losses due to volatilization (VOL) and exudation (EXU) per unit time, also expressed on a leaf area basis. Thus:

$$\text{NAR} = \frac{(\text{PS}_a - \text{LR}_a - \text{SR}_a - \text{RR}_a)}{\text{CC}} - \text{EXU}_a - \text{VOL}_a \quad (3)$$

Table 2 Interspecific variation in growth parameters. All values are expressed per unit dry weight. Species, grown in a controlled environment (glass house, growth room) are indicated with (C) in the specifications, references marked (F) are from plants grown in the field

Parameter	Range	Mean value	Specifications
RGR	31–151	74	(C) 15 tree species (seedlings), Grime and Hunt (1975)
	66–314	159	(C) 93 perennials; Grime and Hunt (1975)
	120–299	176	(C) 22 annuals, Grime and Hunt (1975)
	113–365	224	(C) 24 herbaceous species, Poorter and Remkes (1990)
NAR	19–386	158	(C,F) all species from Table 3
	8–14	10	(C) 24 herbaceous species, Poorter and Remkes (1990)
LAR	2–25	10	(C,F) all species from Table 3
	0.1–4.5	1.5	(F) 35 tropical trees, Ovington and Olson (1970)
SLA	13–36	23	(C) 24 herbaceous species, Poorter and Remkes (1990)
	2–65	18	(C,F) all species from Table 3
	6–37	15	(F) 35 tropical trees, Ovington and Olson (1970)
	25–56	41	(C) 24 herbaceous species, Poorter and Remkes (1990)
LWR	10–131	34	(C,F) all species from Table 3
	0.02–0.34	0.11	(F) 35 tropical trees, Ovington and Olson (1970)
SWR	0.43–0.64	0.54	(C) 24 herbaceous species, Poorter and Remkes (1990)
	0.26–0.81	0.53	(C,F) all species from Table 3
	0.52–0.86	0.70	(F) 35 tropical trees, Ovington and Olson (1970)
RWR	0.07–0.27	0.17	(C) 24 herbaceous species, Poorter and Remkes (1990)
	0.08–0.36	0.20	(F) 35 tropical trees, Ovington and Olson (1970)
	0.22–0.38	0.29	(C) 24 herbaceous species, Poorter and Remkes (1990)

where subscript *a* indicates that the rates are expressed on a leaf area basis. However, leaf, stem and root respiration are not expected to be directly related to leaf area, but rather to the biomass of the different organs. Equation (3) is therefore extended to include the relations between organ biomass and leaf area:

$$NAR = \frac{1}{CC} \left(PS_a - LR_w \cdot \frac{1}{SLA} - SR_w \cdot \frac{SWR}{LAR} - RR_w \cdot \frac{RWR}{LAR} \right) - EXU_a - VOL_a \tag{4}$$

where subscript w indicates that rates are expressed per unit dry weight; SWR and RWR are the stem weight ratio and the root weight ratio, the fraction of biomass allocated to stem and roots, respectively. From Eq. (4) it is clear that NAR is not purely a physiological component, as it is often termed, but rather a complex intermingling of a plant's physiology, biomass allocation, chemical composition and leaf area formation. Although NAR is relatively easy to determine, it is not the most appropriate parameter to obtain a clear insight into the relation between physiology and growth. Hence, we rewrite Eqs. (1) and (4) into:

$$\text{RGR} = \frac{(\text{PS}_a \times \text{SLA} \times \text{LWR} - \text{LR}_w \times \text{LWR} - \text{SR}_w \times \text{SWR} - \text{RR}_w \times \text{RWR})}{\text{CC} - \text{EXU}_w - \text{VOL}_w} \quad (5)$$

where EXU and VOL are expressed per unit total plant weight.

When plants are in a steady state, i.e. when there is a fixed ratio between the increment of nutrients (e.g. nitrogen) and biomass, growth can also be considered in relation to the acquisition of such nutrients;

$$\text{RGR} = \frac{\text{RWR} \times \text{NIR}}{\text{PNC}} \quad (6)$$

where NIR is the net rate of nitrogen absorption, the rate of nitrogen taken up per unit root weight, and PNC the total plant nitrogen concentration.

Factorizing RGR in its various components does not imply that these components are independent of each other (Hardwick, 1984). Often, an increase in one parameter affects another, either positively or negatively. In the next section we evaluate the importance of LAR and NAR in explaining variation in RGR.

IV. NET ASSIMILATION RATE AND LEAF AREA RATIO

A wealth of information is available on the comparison of growth of two or three species, but few authors have investigated the relation between RGR and growth parameters for a range of species. Potter and Jones (1977) compared nine crop and weed species, Mooney *et al.* (1978) investigated five *Eucalyptus* species and Poorter and Remkes (1990) analysed the growth of 24 wild species common in western Europe. In all of these cases the LAR was the predominant factor explaining the inherent variation in

Table 3 Degree of association between the growth parameters of Eqs. (1) and (2). Means of a compilation of 78 literature references on comparative growth analyses of herbaceous C_3 species. For each reference a linear regression was carved out with the mean of variable A for each species as the independent variable, and the mean of variable B over the experimental period as the dependent variable. Then the change in the predicted value of variable B associated with a 10% change in variable A was calculated, starting from the mean values of A and B . A value close to 10 indicates that a 10% increase in variable A , is associated with an almost equal increase in variable B , whereas a value close to zero indicates no association. Such an analysis is only fruitful provided the differences in variable A are large enough. Therefore, the degree of association was only calculated for pairs of variables in which the smallest and largest value of variable A differed at least 10% and 20 mg g⁻¹ day⁻¹ (RGR), 10% and 2 m² kg⁻¹ (LAR), 10% and 3 m² kg⁻¹ (SLA) and 10% (LWR). The values for all references were then averaged.

The literature references are those given in Table 2E of Poorter (1989), supplemented with the C_3 species of Table 2C, the sun species of Table 2D, and Tsunoda (1959), Enyi (1962), Tognoni *et al.* (1967), Khan and Tsunoda (1970a,b), Callaghan and Lewis (1971), Hughes and Cockshull (1971), Eze (1973), Ashenden *et al.* (1975), Smith and Walton (1975), Elias and Chadwick (1979), Grime (1979), Horsman *et al.* (1980), Cook and Evans (1983), Gray and Schlesinger (1983), Spitters and Kramer (1986), Campbell and Grime (1989), Garnier *et al.* (1989), and Muller and Garnier (1990). In each of these analyses root weight determinations were carried out and all species or genotypes were grown under identical conditions.

A	B	n	DOA	Sign.
RGR	NAR	46	2.4	*
RGR	LAR	46	7.5	***
RGR	SLA	21	7.8	***
RGR	LWR	22	2.0	ns
LAR	NAR	54	-4.3	***
LAR	SLA	27	7.3	***
LAR	LWR	27	3.1	*
SLA	NAR	28	-4.0	*
SLA	LWR	28	-0.7	ns
LWR	NAR	25	-4.8	*

A , variable A ; B , variable B ; n , number of references; DOA: averaged value of the degree of association between variable A and variable B ; Sign.: t-test of the H_0 hypothesis DOA = 00. ns, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

RGR. Poorter (1989) arrived at the same conclusion after a review of 45 literature sources. An extended compilation is given in Table 3. On average, a 10% increase in RGR is associated with an 7.5% increase in LAR and a 2.4% increase in NAR. Thus, the amount of leaf area a plant realizes

with a given total plant weight is an important factor determining the potential growth rate of a plant. Differences in the rate of dry weight gain per unit leaf area are of secondary importance in explaining interspecific variation in RGR.

These generalizations only apply when the same types of plants are compared, e.g. C₃ herbs or trees. Tree species, when compared with herbs, have both a low LAR and a low NAR. C₄ species tend to have a higher RGR due to a higher NAR, when compared with C₃ species. The relatively low RGR of shade-adapted species, grown at a high quantum flux density, is caused by a low NAR, rather than a low LAR (Poorter, 1989).

On average, a 10% increase in LAR is associated with a 4.3% decrease in NAR (Table 3). This is not as expected, because a high LAR decreases the respiratory burden per unit leaf area—see Eq. (4). In a few cases, this discrepancy may have been caused by the lower photosynthesis and NAR, resulting from self-shading in plants with a high LAR and a correspondingly large leaf area. However, in most cases it will be due to less well-defined interactions between the physiology, allocation, anatomy and chemical composition (Konings, 1989). Before discussing these interactions, we will first discuss inherent variation in each of these parameters (cf. Eq. (5)).

V. SPECIFIC LEAF AREA

As outlined in Section IV, variation in RGR is strongly correlated with that in LAR. Differences in LAR can be due to variation in LWR or in SLA. The specific leaf area is defined as the amount of leaf area per unit leaf weight. Its reciprocal, specific leaf weight or specific leaf mass, is also frequently used. Various aspects of inherent and environmentally induced variation in SLA have been reviewed by Dijkstra (1989). Large variations in SLA can be found between different types of plants and species from different habitats (Table 2). Evergreens mostly have a low SLA, whereas species with mesomorphic leaves show higher SLAs. Potter and Jones (1977), as well as Mooney *et al.* (1978) and Poorter and Remkes (1990; Figure 2A), found a positive relationship between RGR and SLA. A compilation of the data available from the literature led us to the conclusion that there is a close association between the potential growth rate of a species and its SLA (Table 3). SLA can therefore be considered as the prime factor determining interspecific variation in RGR.

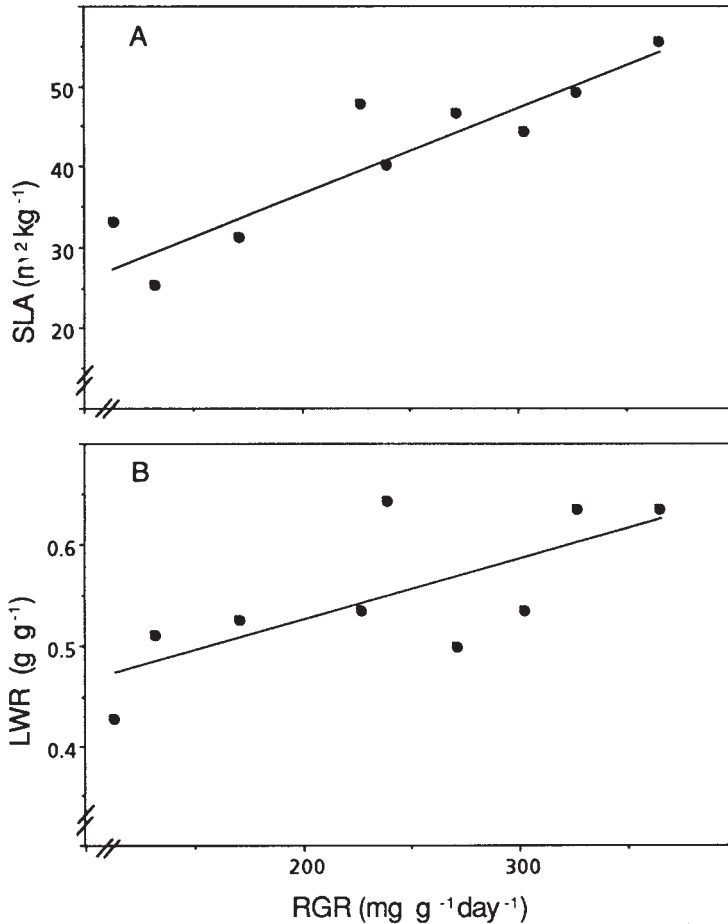


Figure 2 (A) The relationship between specific leaf area (SLA) and RGR and (B) the relationship between the leaf weight ratio (LWR) and RGR for the nine species described in Figure 1. (After Poorter and Remkes, 1990.)

A. Components of SLA

Which traits determine inherent variation in SLA? Starting from a simple leaf prototype, with chlorenchyma, vascular tissue and an epidermis, variation in SLA can be brought about by a change in several leaf characteristics. Firstly, a purely chemical difference between leaves may occur, due to accumulation of, for example, starch or secondary compounds. Starch may account for up to 30–40% of total leaf dry weight (McDonald *et al.*, 1986; Rufty *et al.*, 1988). Slower-growing species tend to

invest relatively more in compounds which reduce the plant's palatability, e.g. tannin and lignin (Coley, 1983, 1986; Coley *et al.*, 1985). Accumulation of secondary compounds may be considerable. In some Australian dryland plants, resins make up 10–30% of the total leaf biomass (Dell and McComb, 1978). Lignin and other phenolic compounds form 14–40% of the total leaf dry weight of Californian chaparral shrubs (Merino *et al.*, 1984).

Secondly, a lower SLA may be caused by anatomical differences, e.g. extra layers of palisade parenchyma in sun species as opposed to shade species (Pons, 1977; Björkman, 1981); more support tissue, such as additional sclerenchyma, with an eight-fold difference between two *Agrostis* species (Pammenter *et al.*, 1986; see also Baruch *et al.*, 1985); or smaller cell sizes. A reduction in cell size without altering the total leaf cell volume will drastically increase the cell-wall surface/cell volume ratio and thus decrease SLA. The size of the veinal transport system may also affect SLA. In *Triticum aestivum*, veins contain 10% of the leaf weight (Rawson *et al.*, 1987). Givnish (1986) found the large veins of *Podophyllum peltatum* to comprise 6–20% of the total leaf biomass, depending on leaf size.

Thirdly, variation in SLA can be caused by a difference in investment in leaf hairs, thorns, etc. In two *Espeletia* species, leaf hairs comprise 4 and 20%, respectively, of the total leaf biomass (Baruch and Smith, 1979). Exceptionally, as in *Encelia farinosa*, leaf pubescence may account for up to 60% of total leaf dry weight (Ehleringer and Cook, 1984). However, in most plants neither pubescence nor thorns account for large differences in SLA.

Thus, in general, inherent variation in SLA is not merely caused by a difference in the amount of leaf cells per unit area, but also by variation in leaf anatomy, morphology or chemical composition. These differences in anatomy or morphology will also affect the chemical composition, as each of the above-mentioned anatomical and morphological structures has a distinctive chemical composition (cf. Kimmerer and Potter, 1987). The consequences of such differences in chemical composition for plant growth are discussed in Section VIII.

B. Plasticity in SLA

Plants grown under a low quantum flux density generally have a higher SLA and thinner leaves (Young and Smith, 1980), which is associated with fewer mesophyll cell layers (Pons, 1977; Björkman, 1981) and less non-structural carbohydrate (Waring *et al.*, 1985). To a small extent the higher SLA is also associated with lower concentrations of phenolic

compounds, including lignin (Waring *et al.*, 1985; Mole and Waterman, 1988). There is hardly any evidence of differences in plasticity with respect to quantum flux density between species with different growth rates (Pons, 1977; Corré, 1983a,b; Grime *et al.*, 1989). However, the fast-growing *Holcus lanatus* increases SLA more at a low quantum flux density than the slow-growing *Deschampsia flexuosa* (Poorter, 1991). A similar difference was found in a comparison of *Veronica montana*, a (presumably slow-growing) woodland perennial, and *V. persica*, a (presumably fast-growing) annual weed. When grown under a leaf canopy as opposed to unshaded conditions, the SLA of *V. persica* changed considerably more than that of *V. montana* (Fitter and Ashmore, 1974).

Plants grown at low nutrient availability either show no change (Corré, 1983c; Sage and Percy, 1987; van der Werf *et al.*, 1992a) or a decrease in SLA (Sage and Percy, 1987; van der Werf *et al.*, 1992a). A decrease is at least partly due to accumulation of non-structural carbohydrates (Lambers *et al.*, 1981a; Waring *et al.*, 1985) or secondary compounds like lignin or other phenolics (Gershenzon, 1984; Waring *et al.*, 1985). No differences in plasticity have been found between fast- and slow-growing species (Corré, 1983c; van der Werf *et al.*, 1992a). However, data on the comparison of species grown under a range of conditions are scarce and differences in potential RGR between species sometimes small. A better-founded evaluation therefore awaits further experiments.

VI. BIOMASS ALLOCATION

Biomass allocation can be defined in terms of leaf, stem and root weight ratio, the fraction of total plant biomass allocated to leaves, stems and roots, respectively. A more frequently used parameter, the shoot: root ratio or its inverse, does not acknowledge the distinct functions of leaves and stems and is avoided here. Various aspects of inherent differences in biomass partitioning between leaves and roots have been discussed by Konings (1989). A low availability of nitrogen, phosphorus and water enhances allocation to roots, whereas a low quantum flux density promotes allocation to the leaves. The mechanism behind this "functional equilibrium" (Brouwer, 1963, 1983) is still poorly understood (Lambers, 1983). Genotypic differences in biomass partitioning between leaves, stem and roots have been correlated with differences in the level of gibberellins (*Zea mays*, Rood *et al.*, 1990a; *Brassica rapa*, Rood *et al.*, 1990b; *Lycopersicon esculentum*, Koornneef *et al.*, 1990; cf. Section XII.A) and abscisic acid (*Zea mays*, Saab *et al.*, 1990; *Lycopersicon esculentum*,

O.W. Nagel and H. Konings, personal communication) and with the plant's sensitivity to endogenous gibberellin (*Lycopersicon esculentum*, Jupe *et al.*, 1988).

A. Biomass Allocation at an Optimum Nutrient Supply

Some authors have found a negative correlation between LWR and RGR (Hunt *et al.*, 1987, plants grown at low quantum flux density; Shipley and Peters, 1990, at high quantum flux density), others a positive one (Ingestad, 1981; Poorter and Remkes, 1990, at intermediate quantum flux density, Figure 2B). Differences in growth conditions may have a decisive impact on the final result (Poorter and Lambers, 1991). Irrespective of the way the plants are grown, current information shows that LWR is less important than SLA in explaining inherent variation in RGR (Table 3).

Interestingly, monocotyledonous herbaceous species invest relatively more biomass in roots and less in leaves, compared to dicotyledonous ones with the same inherent RGR (Garnier, 1991). Moreover, the general trend of increasing RGR with increasing investment in leaf weight (Poorter and Remkes, 1990) only holds for dicotyledonous species and not for grasses (Garnier, 1991).

B. Plasticity in Biomass Allocation

In general, plants grown at a low quantum flux density show a shift in the allocation of biomass from roots and stem to leaves. This shift is generally more pronounced in faster-growing species (Pons, 1977; Werner *et al.*, 1982; Grime *et al.*, 1989; but see Corré, 1983b).

A decrease in nutrient availability often decreases LWR and increases RWR, particularly in fast-growing species (Christie and Moorby, 1975; Tilman and Cowan, 1989; Shipley and Peters, 1990). However, as noted previously, an interaction between nutrient supply and plant size may seriously affect the observed relationship between allocation and RGR, especially at a low nutrient supply (Ingestad, 1962, cited in Corré, 1983c). Taking into account only those references in which this artefact was most certainly avoided, a generally higher plasticity in allocation is still observed for fast-growing species (Christie and Moorby, 1975; Robinson and Rorison, 1988; Campbell and Grime, 1989; van der Werf *et al.*, 1992a; but see Bradshaw *et al.*, 1964; Crick and Grime, 1987).

VII. GROWTH, MORPHOLOGY AND NUTRIENT ACQUISITION OF ROOTS

The simple growth equation: $RGR = NAR \times LAR$, suggests that any investment in biomass other than leaf area reduces the plant's RGR. Such an approach tends to consider the roots merely as a carbohydrate-consuming organ and does not give credit to their role in the acquisition of nutrients and water or their function in transport, storage and anchorage. In this section we will concentrate on the root's role in the acquisition of ions. Growth can then best be approached from an alternative point of view, where RGR is defined in terms of the root weight ratio (RWR), the net rate of nitrogen acquisition (NIR) and the plant's nitrogen concentration (PNC)—Eq. (6). Equation (6) suggests that a high RGR can be achieved by a large investment in root biomass, by a high rate of nitrogen uptake per unit root weight (specific ion uptake rate), or by a combination of these. However, a large investment in root weight may in fact reduce RGR because investment in leaves is reduced.

A. Root Growth and Nutrient Acquisition at an Optimum Nutrient Supply

Root systems of fast- and slow-growing species differ in their architecture. Slow-growing *Festuca* species from nutrient-poor habitats tend to have "herringbone" morphologies, i.e. next to one main axis, the root systems have only primary laterals (Fitter *et al.*, 1988). Results of a simulation model indicate that a herringbone morphology allows the most effective exploration and exploitation of mobile resources (Fitter, 1987). On the other hand, such a morphology is less efficient for long-distance transport, because the total transport path is longer, and hence requires a greater investment in root biomass. Fast-growing grassland species have a more random or nearly dichotomous root morphology.

Slow-growing grass species from nutrient-poor habitats generally have a higher specific root length (SRL, the root length per unit root weight) and relatively more fine roots (Berendse and Elberse, 1989; Boot, 1989; Boot and Mensink, 1990). However, SRL tends to vary with age in an unpredictable manner (Fitter, 1985) and some studies show a higher SRL for fast-growing grasses (Robinson and Rorison, 1985). No correlation between SRL and RGR was found in a comparison of 24 monocotyledons and dicotyledons species, grown at an optimum nutrient supply (Poorter and Remkes, 1990). A higher SRL is likely to contribute to the acquisition of ions which diffuse slowly in the soil (Clarkson, 1985), but also of more mobile ones when plants have to compete for these. Similarly, root hairs contribute to the

acquisition of relatively immobile nutrients. There is a large variation between plant species with respect to root hair density and root hair length, but variation in these root characteristics does not seem to be related to the maximum growth rate of the species or its performance in nutrient-poor environments (Robinson and Rorison, 1987; Boot, 1989). The "proteoid" roots which are found in some dicotyledonous species are discussed in Section VII.C.

At an optimum nutrient supply, inherently fast-growing species have a somewhat lower RWR than slow-growing species from the same life form (Section VI). Since fast-growing species also have a higher nitrate and organic nitrogen concentration (Section VIII.A), it follows that the fast-growing species must have higher nitrogen absorption rates (cf. Eq. (6); Chapin, 1980).

Nassery (1970) compared the growth and phosphate uptake of the fast-growing *Urtica dioica* with that of the slow-growing *Deschampsia flexuosa*. At an optimum nutrient supply, the fast-growing species had the highest nutrient uptake rate per unit root weight. This conclusion was corroborated by Christie and Moorby (1975), Chapin and Bielecki (1982), Chapin *et al.* (1986a), Garnier *et al.* (1989) and Poorter *et al.* (1991); Figure 3A). This is not to say that fast-growing species grow faster because their rate of nitrate or phosphate uptake is higher. Rather, the rapid uptake may be a result of their higher growth rate. At an optimum supply, the rate of ion uptake is, at least partly, determined by "demand", which results in a strong negative feedback when the growth rate is low (Clarkson, 1986; Rodgers and Barneix, 1988). An increased demand diminishes the negative feedback, thus enhancing net uptake (Jackson *et al.*, 1976; Doddema and Otten, 1979; Lambers *et al.*, 1982). When pregrown at a low phosphate concentration, the rate of phosphate uptake at a saturating concentration was 35% higher for the fast-growing *Urtica dioica* than for the slow-growing *Deschampsia flexuosa*. Pregrown at an optimum phosphate supply, this difference is about 300% (Nassery, 1970). Similar results have been obtained for other species, both with phosphate (Harrison and Helliwell, 1979; Clarkson and Scattergood, 1982) and a range of other ions (Lee, 1982; Glass, 1983). It is therefore very likely that a low ability to incorporate large amounts of absorbed nutrients into organic matter, rather than their low absorption capacity, controls the growth rate of plants from nutrient-poor sites at optimum nutrient supply.

Is there evidence for an inherently higher affinity (lower K_m) of the uptake system of slow-growing species from nutrient-poor sites? The phosphate uptake system of slow-growing *Carex* species has a high affinity for phosphate, in comparison with that of crop species (Atwell *et al.*, 1980). Data of Muller and Garnier (1990) on growth at low nitrate

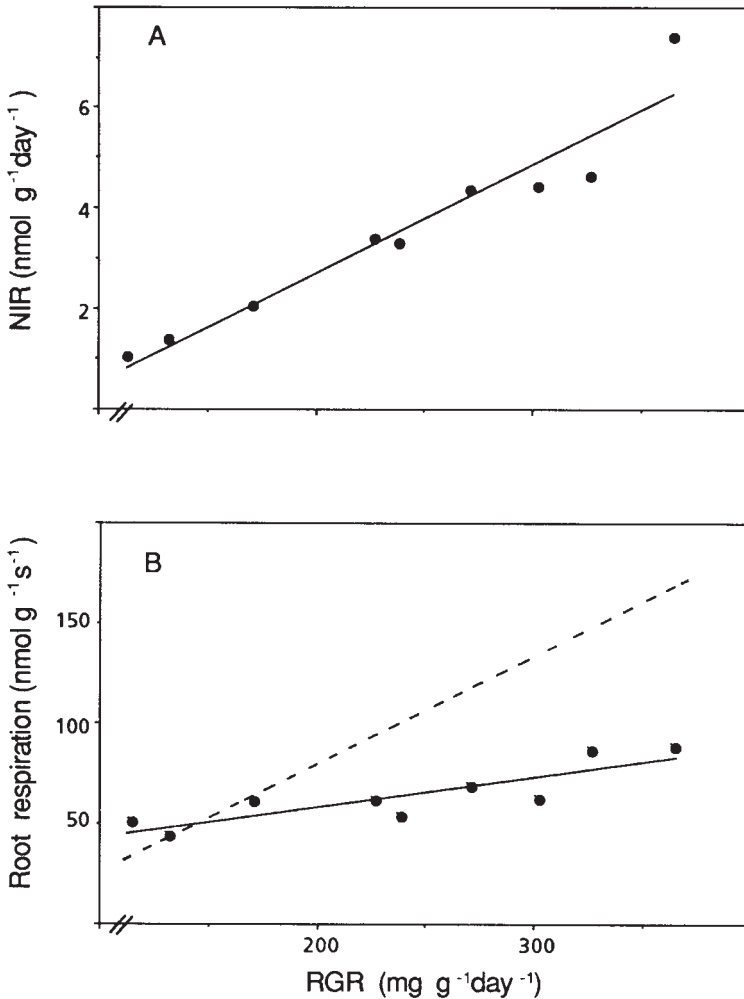


Figure 3 (A) The net influx of nitrate into roots (NIR) and (B) the rate of root respiration of fast-growing and slow-growing species, described in Figure 1. The dashed line in (B) gives the calculated rate of root respiration assuming specific costs for maintenance, growth and ion uptake to be the same as those for a slow-growing *Carex* species. (After Poorter *et al.*, 1990; Poorter *et al.*, 1991.)

concentrations, contrary to those of Freijesen and Otten (1984), suggest a lower K_m for nitrate of the uptake system in slower-growing species. However, in neither of these studies was the K_m determined. So far the experimental data do not support the hypothesis that the nitrate uptake

system of slow-growing species from nutrient-poor habitats has a higher affinity for nitrate (van de Dijk, 1980; Bloom, 1985; Oscarson *et al.*, 1989). However, not many systematic comparisons of kinetic parameters of nitrate uptake in contrasting species are available from the literature and experiments have been carried out under different experimental conditions, so that a final conclusion cannot yet be reached.

B. The Plasticity of Parameters Related to Root Growth and Nutrient Acquisition

As discussed in Section VI, fast-growing species tend to be more plastic with respect to biomass allocation. At a growth-limiting nitrogen supply, inherently fast-growing species have a higher RWR than slow-growing ones of the same life-form. Both a low phosphate supply (Powell, 1974; Christie and Moorby, 1975) and a low nitrogen supply (Robinson and Rorison, 1985; Boot, 1989) mostly increase SRL. Slow-growing and fast-growing species respond in a similar manner (Fitter, 1985).

Root hairs are of vital importance for the acquisition of ions which diffuse slowly in soil, e.g. phosphate (Clarkson, 1985), and stimulation of root hair formation at a low nutrient supply has been reported frequently (Föhse and Jungk, 1983). The inherently slow-growing species *Deschampsia flexuosa* has a remarkable plasticity with respect to root hair formation, in comparison with fast-growing grass species (Robinson and Rorison, 1987; Boot and Mensink, 1990). Both fast-growing and slow-growing grasses respond to nutrient shortage with increased root hair length, but the tendency appears to be greatest in slow-growing ones (Boot and Mensink, 1990; Liljeroth *et al.*, 1990). The greater plasticity in density and length of root hairs in response to nutrient supply in inherently slow-growing species is likely to contribute to their successful performance in phosphate-poor environments.

Roots of crop species (Drew *et al.*, 1973; de Jager, 1982), fast-growing herbaceous wild plants (de Jager and Posno, 1979), trees (Philipson and Coutts, 1977) and desert perennials (von Willert *et al.*, 1992) have an amazing capacity to proliferate growth in nutrient-rich or moist patches in the root environment. Crick and Grime (1987) compared morphological plasticity in the slow-growing *Scirpus sylvaticus* and the faster-growing *Agrostis stolonifera*. *A. stolonifera* had a greater capacity to proliferate its fine roots in nutrient-rich patches. Therefore, it can dynamically exploit a fertile root environment and successfully compete with neighbouring plants, whereas the relatively large, but unresponsive, root system of the slow-growing *S. sylvaticus* is more advantageous when

nutrients are strongly limiting and become available in temporally unpredictable pulses. A similar conclusion is drawn from data on two cold-desert bunchgrass species (Jackson and Caldwell, 1989) differing in RGR (Eissenstat and Caldwell, 1987). However, using a somewhat different technique from the one used by Crick and Grime (1987), Grime *et al.* (1991) concluded that the capacity to proliferate roots locally may be similar in slow- and fast-growing species. Our current information is insufficient to draw final conclusions on variation in the root's capacity to locally proliferate fine roots between fast-growing and slow-growing species.

Plants do not only respond to nutrient-rich patches with an increased root production, but also with an increased capacity for nutrient uptake (Drew and Saker, 1978; Lambers *et al.*, 1982). Jackson *et al.* (1990) compared the effect of a local increase in phosphate supply on two cold-desert *Agropyron* species, referred to above. Both species responded with an 80% increase in phosphate absorption capacity, and no differences between the two species were found with respect to the physiological plasticity of phosphate uptake.

Apart from spatial variation in nutrient availability, there may be variation in time. Campbell and Grime (1989) found that a potentially fast-growing species grows faster than an inherently slow-growing species when nutrient pulses are long, whereas the opposite is true under a regime of short pulses. In this case the frequency of pulses was constant, but the duration of the pulse varied, and thus the total amount of nutrients supplied. In an experiment with two *Plantago major* subspecies, where the frequency of pulses was increased, but total nutrient supply was constant, the faster-growing subspecies achieved an increasingly higher RGR than the slow-growing one (Poorter and Lambers, 1986).

It is concluded that fast-growing species are characterized by a high degree of plasticity in root morphology, such as the adjustment of their RWR and perhaps also the local proliferation of roots in nutrient-rich patches. Such a high degree of morphological plasticity is likely to be an integral part of the mechanism of resource acquisition in productive environments (Crick and Grime, 1987). Theoretical models predict that in infertile soils such a strategy leads to net losses of mineral nutrients from the plant (Sibly and Grime, 1986). Under poor conditions, alternative mechanisms requiring a lower investment of mineral nutrients but leading to greater losses of carbon from the roots, might have greater survival value. Here rapid proliferation of fine roots might incur net nutrient losses, as the nutrient costs of investing new roots in a generally poor soil might be higher than its returns. There is as yet no evidence for a difference in plasticity of nutrient acquisition between fast-growing and slow-growing species.

C. Other Root Characteristics Related to Nutrient Acquisition

Like leaves, roots are subject to a continuous turnover. Aerts (1989) reports a turnover rate of $0.6\text{--}1.7 \text{ g roots (g roots)}^{-1} \text{ year}^{-1}$. A high turnover rate of roots, like that of leaves, incurs a net loss of nutrients; as discussed in Section XV. We are not aware of systematic comparisons between fast-growing and slow-growing species with respect to root turnover.

Specialized root structures termed “proteoid” roots, are formed on members of the Proteaceae (Lamont, 1982), many of which are slow-growing species from very nutrient-poor soils (Barrow, 1977). Proteoid roots consist of sections of dense “bottle-brush-like” clusters of short (5–10 mm) rootlets, covered with a dense mat of root hairs. Such structures induce the release of various nutrients from sparingly soluble sources (Section XI.A). Proteoid roots, or functionally similar structures, are also known from fast-growing crop species (Gardner *et al.*, 1982a; Hoffland *et al.*, 1989a).

Another special structure, which allows plants to grow in phosphate-poor environments, is the mycorrhiza, an association between a fungus and roots. Both fast- and slow-growing species have the capacity to form such an association, predominantly under phosphate-poor conditions. Some species are inherently non-mycorrhizal, but this characteristic is also not associated with the inherent growth rate of the species (cf. Tester *et al.*, 1987).

D. Conclusions

Variation in RGR between species is certainly associated with variation in root attributes. Slow-growing species tend to have a “herring bone” architecture, rather than the more random structure of fast-growing species, and also a higher specific root length. Fast-growing species tend to invest relatively less biomass in roots when grown at an optimum supply of nutrients, but have a greater capacity to adjust their investment in root biomass as well as associated structures than slow-growing species. The nutrient uptake rate per unit root dry weight of fast-growing species is higher than that of slow-growing species, but this may well be an effect of rapid growth, rather than its cause.

VIII. CHEMICAL COMPOSITION

Plant dry matter is composed of a number of major compounds, which can be grouped into the following seven categories: lipids, lignin, organic

N-compounds, (hemi)cellulose, non-structural sugars, organic acids and minerals. Apart from “primary” compounds, there is a wealth of “secondary” compounds, defined by the absence of a clearly defined role in the metabolic processes of the plant (Baas, 1989; Waterman and McKey, 1989). Lignin is often included in the category of “secondary” compounds and this will also be done here.

A. Primary Compounds

When grown at an optimum nutrient supply, inherently fast-growing species have a higher total and organic nitrogen concentration per unit plant dry weight than slow-growing ones (Poorter *et al.*, 1990; Figure 4A). Their higher organic nitrogen concentration is due partly to a greater biomass investment in leaves, which tend to have a higher nitrogen concentration than other vegetative plant organs, and partly to a higher nitrogen concentration in all vegetative organs *per se* (Poorter *et al.*, 1990). Soluble protein constitutes a larger fraction of the total leaf nitrogen concentration in a fast-growing *Plantago major* subspecies than in a slower-growing one (Dijkstra and Lambers, 1989a).

Fast-growing (sub)species generally contain more minerals and organic acids per unit dry weight than slow-growing ones, when grown at an optimum nutrient supply (Chapin and Bielecki, 1982; Dijkstra and Lambers, 1989b; Poorter and Bergkotte, 1992). Some comparative studies show that phosphorus, particularly inorganic phosphate, accumulates to a greater extent in fast-growing (sub)species (Nassery, 1970; Chapin and Bielecki, 1982; Dijkstra and Lambers, 1989b). Others show the opposite (Christie and Moorby, 1975; Chapin *et al.*, 1982). Accumulation of nitrate appears to be characteristic of fast-growing, “nitrophilous” species (Dittrich, 1931; Smirnoff and Stewart, 1985; Poorter and Bergkotte, 1992). Such accumulation is most pronounced at a high nitrate supply (Stulen *et al.*, 1981) and at a relatively low quantum flux density, when nitrate replaces soluble carbohydrates and carboxylates as an osmotic solute (Stienstra, 1986; Veen and Kleinendorst, 1986; Blom-Zandstra and Lampe, 1985).

It is sometimes claimed (cf. Chapin, 1988) that slow-growing species show more “luxury consumption” than fast-growing ones. Apart from the fact that this is not compatible with most of the comparative data cited in this section, it still remains to be demonstrated whether luxury consumption exists at all. We propose to define “luxury consumption”, as the absorption beyond a rate which leads to more growth, rather than as “vacuolar storage during the period of active growth” (Chapin, 1988). Accumulation of nitrate does not imply “luxury consumption”, since nitrate

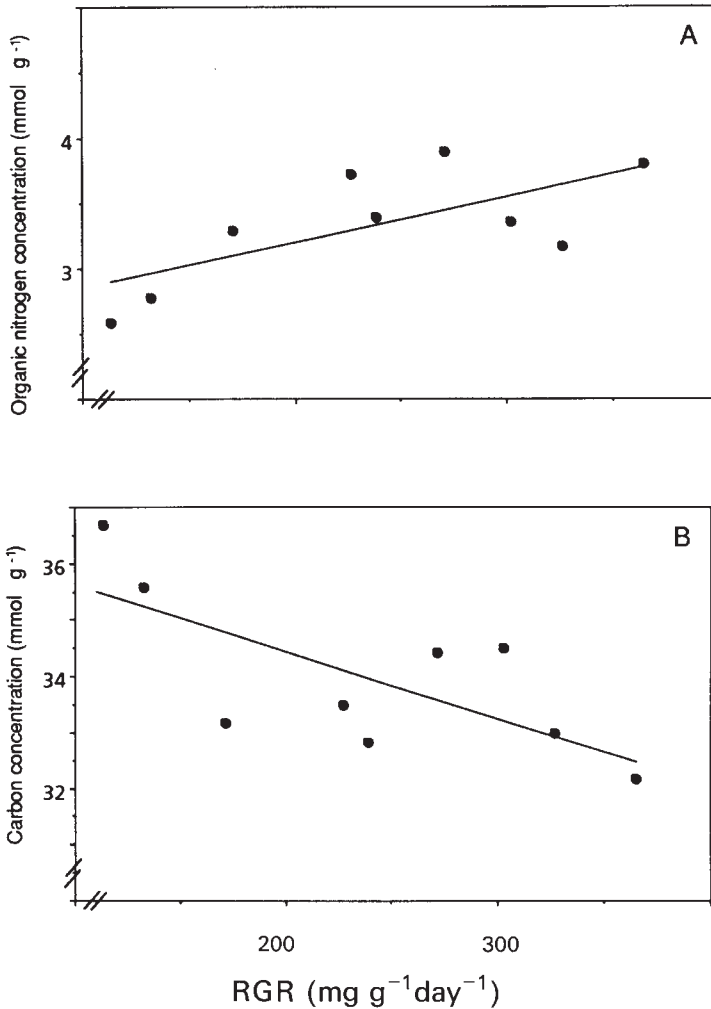


Figure 4 Aspects of the chemical composition of fast-growing and slow-growing species, described in Figure 1. (A) Organic nitrogen concentration of plant dry matter. (B) Carbon concentration of plant dry matter. (C) Dry matter content (dry weight \times 100/fresh weight) of plant biomass. (D) Construction costs of plant biomass, calculated as outlined in Penning de Vries *et al.* (1974) and Lambers and Rychter (1989). (After Poorter *et al.*, 1990; Poorter and Bergkotte, 1992.)

may replace organic solutes, which leads to more carbon being available for metabolic processes. For example, faster-growing genotypes of *Lactuca sativa* accumulate nitrate, rather than organic solutes (Blom-Zandstra *et al.*, 1988). For phosphate, the situation may be different, but

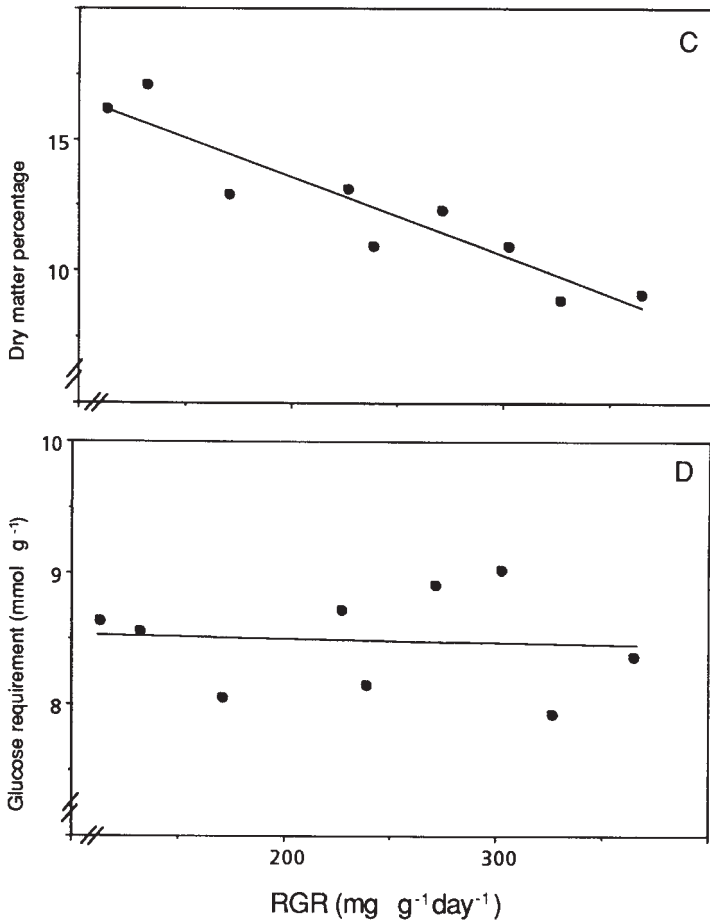


Figure 4 Continued.

data in the literature are conflicting (e.g. Chapin and Bielecki, 1982; Chapin *et al.*, 1982).

Slow-growing (sub)species contain more cell-wall components (lignin and (hemi)cellulose) than fast-growing ones, when grown at optimum nutrient supply (Dijkstra and Lambers, 1989a; Poorter and Bergkotte, 1992). Using pyrolysis-mass-spectrometry, Niemann *et al.* (1992) showed that fast-growing species contain relatively more compounds associated with the cytoplasm and slow-growing ones more of those associated with cell walls. At a relatively fixed cell size, accumulation of cell-wall components and solutes will also alter the water content ($\text{g H}_2\text{O g}^{-1}\text{ DW}$) of the different organs. Indeed, both leaves, stems and roots of slow-growing

(sub)species contain rather low amounts of water per unit dry weight (Dijkstra and Lambers, 1989b; Poorter and Bergkotte, 1992; Figure 4C). In the *Lactuca sativa* genotypes mentioned above, replacement of nitrate for organic acids partly explains genotype differences in leaf dry matter content (Reinink *et al.*, 1987; Blom-Zandstra *et al.*, 1988).

B. Secondary Compounds

Plants contain a suite of “secondary” compounds, which serve a range of distinct ecological functions, including allelopathy, the deterrence of herbivores, attraction of pollinators and attraction of organisms preying on herbivores (Harborne, 1982; Chou and Kuo, 1986; Baas, 1989; Dicke and Sabelis, 1989). Much attention has been paid to the role of secondary plant compounds in reducing herbivory. In this context they are often classified as “quantitative” vs. “qualitative” defence compounds (Harborne, 1982; Waterman and McKey, 1989). Typically, quantitative secondary compounds are composed of C, H and O only, have low turnover rates and act as digestibility reducers when present in large amounts. Qualitative secondary compounds tend to be specific toxins which occur in low concentrations and may be subject to rapid turnover. Some of these toxins contain nitrogen (cyanogenic glycosides, analogues of amino acids, alkaloids), but many do not (cardenolides, glucosinolates, saponins).

Slow-growing species or genotypes accumulate more quantitative secondary plant compounds than fast-growing ones (Coley, 1986; Waterman and McKey, 1989). The concentration of lignin (Coley, 1983), condensed tannin (Waterman and McKey, 1989), volatile terpenoids (Morrow and Fox, 1980) or diplacol (Merino *et al.*, 1984) may comprise 10–30% of a plant’s leaf dry weight.

There is no clear-cut correlation between a plant’s inherent growth rate and the concentration of qualitative secondary compounds in its tissues. Perhaps the only generalization that can be made is that fast-growing species, if they have any antiherbivore chemicals at all, accumulate only qualitative compounds. There is a vast array of qualitative secondary compounds, which generally account for less than 1% of the dry weight (Baas, 1989). However, their distribution has not been systematically investigated for a range of species grown under standard conditions.

Slow-growing species may also accumulate qualitative compounds, often in a manner which complements accumulation of quantitative secondary compounds. A special case is that of young leaves. Most herbivores preferentially feed on leaves with a high protein and

water content, a low leaf toughness and a low concentration of antiherbivore compounds (Coley, 1983; Kimmerer and Potter, 1987; Waterman and McKey, 1989). In young leaves of slow-growing plants, leaf toughness and the concentration of digestibility-reducing compounds is often low, whereas the nutrient and water content is relatively high compared to older leaves. Hence, young leaves appear to be attractive for herbivores, but they also accumulate toxic compounds, e.g. anthocyanins in tropical trees (Coley and Aide, 1989) or saponins in *Ilex opaca* (Potter and Kimmerer, 1989). Also mature leaves of *Ilex opaca* accumulate saponins, namely in their mesophyll cells, which are not protected by digestibility-reducing compounds like lignin, crystals and tannin. These quantitative secondary compounds accumulate instead in other cells of the same leaves (Kimmerer and Potter, 1987).

One obvious risk of the accumulation of specific toxins is that herbivorous organisms coevolve and become insensitive to the defence (Harborne, 1982). In the case of *Ilex opaca*, mentioned above, specialist leaf miners consume only the mesophyll tissue, apparently able to neutralize the toxic saponins in these cells. The chances for tolerance to evolve against quantitative antiherbivore compounds are considerably smaller. However, some degree of tolerance against palatability-reducing compounds has been demonstrated (Bernays *et al.*, 1989) and some herbivores even incorporate these quantitative compounds, thus possibly gaining protection (Taper and Case, 1987).

C. Defence under Suboptimal Conditions

Environmental conditions, such as nutrient supply and water stress, may restrict plant growth more than expected from their effect on photosynthesis. Under such conditions non-structural carbohydrates accumulate, leading to an excess of carbon in the plant. When plants have such an excess of carbon, accumulation of carbon-based defences is expected. Similarly, at a high availability of nutrients and a relatively low quantum flux density, accumulation of nitrogen-based secondary compounds is predicted. Confirmation of this carbon/nutrient balance theory (Bryant *et al.*, 1983) has been found in studies where plants, grown at a low nutrient availability, show an increase in the concentration of condensed tannins, total phenols and/or phenol glycosides (Waring *et al.*, 1985; Bryant *et al.*, 1987; Nicolai, 1988; Margna *et al.*, 1989; but see Denslow *et al.*, 1987). Similarly, Johnson *et al.* (1987) observed a positive correlation between N-supply and the concentration of alkaloids.

D. Effects of Chemical Defence on Growth Potential

What are the costs associated with the accumulation of antiherbivore compounds? The amount of glucose needed to produce 1 g of a toxic compound may be high (cf. Baas, 1989). However, as the concentration of toxins in plant tissues is rather low, their accumulation hardly affects the cost of synthesizing plant biomass.

The glucose needed to produce 1 g of digestibility-reducing compounds is generally lower than that of qualitative secondary compounds (Baas, 1989; Lambers and Rychter, 1989). In the case of tannin, approximately the same amount of glucose is required as to construct cellulose or starch. However, because these compounds may accumulate in large quantities in plant tissue, they may comprise a large part of the plant's carbon resources. This carbon cannot be used for the construction of the photosynthetic apparatus, so that the photosynthetic return per unit weight of a well-protected leaf is less than that of a leaf which allocates less carbon to quantitative defence compounds.

The costs of the accumulation of secondary compounds exceed the specific costs of synthesis. The enzyme apparatus to produce these compounds must also be maintained and there is a turnover of different compounds (e.g. monoterpenes: Burbott and Loomis, 1969; alkaloids: Waller and Nowacki, 1978; cyanogenic compounds: Adewusi, 1990). Moreover, toxic compounds must be stored in special compartments or structures in which they cannot harm the plant's metabolism. Examples include oil glands containing essential oils in *Eucalyptus* species (Welch, 1920), leaf hairs containing carvone in *Mentha spicata* (Gershenzon *et al.*, 1989) and the separation of cyanogenic glycosides from the enzymes releasing HCN in *Phaseolus lunatus* (Frehner and Conn, 1987).

An alternative approach to calculate the costs of accumulating secondary compounds relates their concentration to the growth of a plant. Coley (1986) found a negative correlation between the rate of leaf production and the leaf tannin concentration of *Cecropia peltata* (Figure 5). However, the negative correlation may be a reflection of correlating, but in themselves unrelated, plant characteristics. Accumulation of secondary compounds may even be the phenotypic result of slow growth, as discussed above.

E. The Construction Costs of Plant Material

At an optimum nutrient supply, fast-growing species have a lower carbon concentration in the various organs than slow-growing ones

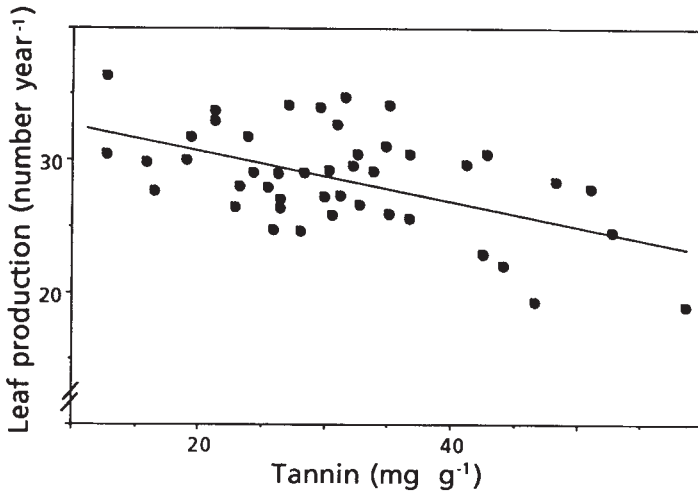


Figure 5 Leaf production and tannin concentration in *Cecropia peltata*. (After Coley, 1986.)

(Poorter and Bergkotte, 1992; Figure 4B). This is a consequence of a difference in chemical composition. The different components of the plant's biomass vary in carbon concentration ranging from high in lipids to zero for minerals (cf. Table 4). Therefore, a plant with a high proportion of biomass invested in compounds with a high proportion of carbon, like lipids and protein, has to fix more carbon to construct one unit of plant weight than a plant that consists mainly of (hemi)cellulose, organic acids and minerals (cf. Eq. (5), Section III). The difference in carbon concentration of fast- and slow-growing species is about 10%, whereas that in RGR is over 300% (Figure 4B). Thus, variation in carbon concentration has only a rather small effect on variation in RGR.

Construction of the different compounds not only requires glucose for C-skeletons, but also for the generation of ATP and NAD(P)H (Section X). Generally, compounds with a high carbon concentration are more reduced and require more glucose for their synthesis (Penning de Vries *et al.*, 1974; Table 4). Hence, glucose costs for the synthesis of biomass can be derived from the carbon concentration of biomass, provided a correction is made for the mineral concentration (Vertregt and Penning de Vries, 1987). Alternatively, these costs can be calculated from the concentration of the various primary and secondary compounds of plant biomass (Penning de Vries *et al.*, 1974; Lambers and Rychter, 1989). Although variation in glucose requirement exists, there is not much

Table 4 The carbon concentration (mmol/g) of a number of primary and secondary compounds present in plant biomass, as well as the requirement of glucose (mmol g⁻¹) and oxygen (mmol g⁻¹), and the carbon dioxide release (mmol g⁻¹) during synthesis of these compounds from glucose and nitrate. The values for oxygen requirement and carbon dioxide release are used to calculate the expected respiratory quotient (RQ) during synthesis of these compounds. (The principles of the calculations are outlined in Penning de Vries *et al.* (1983) and Lambers and Rychter (1989), but different values have been used, where appropriate.)

Component	Carbon concentration	Glucose costs	O ₂ - requirement	CO ₂ - release	RQ
Volatile terpenoids					
Limonene	61.3	18.8	29.6	59.2	2.0
Lipids	53.8	16.8	11.0	36.5	3.3
Protein	36.8	13.8	13.5	37.9	2.8
Phenolics					
Lignin	46.3	11.8	5.9	13.1	2.2
Ellagitannin	32.8	8.6	12.1	22.7	1.9
Structural carbohydrates					
Hemicellulose	32.0	7.1	3.6	3.6	1.0
Cellulose	30.8	6.5	2.1	2.1	1.0
Non-structural carbohydrates					
Starch	30.8	6.5	2.1	2.1	1.0
Sucrose	29.3	6.1	1.5	1.5	1.0
Organic acids					
Citric acid	26.1	4.3	5.2	0.0	< 1
Malic acid	24.8	3.7	0.0	-7.5	< 1
Minerals	0.0	—	—	—	—

difference between slow-growing evergreens, slow-growing deciduous plants and faster-growing species (Chapin, 1989; Lambers and Rychter, 1989). In a comparison of a range of herbaceous species, the costs for construction of plant biomass was very similar for fast-growing and slow-growing species (Poorter and Bergkotte, 1992; Figure 4D). There are two reasons for this relative constancy of construction costs. Firstly, the production of protein, which is present in larger amounts in fast-growing species, requires a similar amount of glucose to that of quantitative secondary compounds, characteristic of slow-growing species (Table 4; cf. Sections VIII.A and VIII.B). And, secondly, the higher concentration of costly proteins coincides with an increased concentration of cheap compounds, such as organic acids and minerals (cf. Section VIII.A).

F. Conclusions

Fast-growing species are characterized by a high organic nitrogen and mineral concentration, whereas slow-growing species accumulate relatively more quantitative secondary compounds, which play a role in reducing herbivory. The cost of constructing leaves with these contrasting chemical composition differs only marginally, but the photosynthetic return per unit weight of the leaves of fast-growing plants will be much higher.

IX. PHOTOSYNTHESIS

A. Species-specific Variation in the Rate of Photosynthesis

Fast-growing crop species (Evans, 1983; Makino *et al.*, 1988) and their accompanying weeds (Sage and Pearcy, 1987) tend to have higher maximum rates of photosynthesis (expressed per unit leaf area) than evergreen trees and shrubs (Field *et al.*, 1983; Langenheim *et al.*, 1984). Similarly, sun species have a higher rate of light-saturated photosynthesis per unit area than slower-growing shade species, when the plants are grown at an optimum quantum flux density (e.g. Pons, 1977; Björkman, 1981; Seemann *et al.*, 1987). Fast-growing tree and shrub species have higher rates of photosynthesis per unit leaf area than slower-growing ones (Mooney *et al.*, 1978, 1983; Field *et al.*, 1983; Oberbauer *et al.*, 1985). Some of these differences may be phenotypic, rather than inherent for a species, reflecting a poor nutrient or water supply in the natural habitat.

Generally, fast-growing species tend to have higher rates of photosynthesis than slow-growing ones, at least when photosynthesis is expressed per unit leaf weight (Gottlieb, 1978; Dijkstra and Lambers, 1989a; Poorter *et al.*, 1990). The difference may persist when expressed per unit leaf area (Schulze and Chapin, 1987; Evans, 1989a), as long as species of vastly different life forms are compared. In comparisons of species of similar life forms, e.g. herbaceous species (Dijkstra and Lambers, 1989a; Poorter *et al.*, 1990), fast-growing and slow-growing species have very similar rates of photosynthesis per unit leaf area. Hence, variation in the rate of photosynthesis per unit leaf area does not offer an explanation for differences in RGR between species of similar life form.

Very little research has been done to elucidate differences in photosynthesis between inherently slow-growing and fast-growing species. Information providing a framework for further analysis of inherent

differences in photosynthesis is discussed below and is confined in the main to C_3 species and not C_4 or CAM plants.

Variation in photosynthetic capacity may reflect differences in organic nitrogen concentration. This capacity is related to a leaf's nitrogen concentration, because the major part of all organic nitrogen in the mesophyll cells of a C_3 plant is found in the chloroplasts (Evans, 1989a). Indeed, leaves of fast-growing species have a higher nitrogen concentration (Section VIII). However, at the same nitrogen concentration in the leaf, there is still a wide variation in light-saturated rates of photosynthesis between species (Evans, 1989a).

B. Photosynthetic Nitrogen Use Efficiency

The rate of photosynthesis per unit leaf nitrogen, the photosynthetic nitrogen use efficiency (PNUE), is higher for fast-growing herbaceous species than for slow-growing ones with the same life form, at least when measured at the moderate quantum flux density at which the plants were grown (Poorter *et al.*, 1990). Therefore, we will discuss plant traits which may explain inherent variation in PNUE.

With increasing nitrogen concentration per unit leaf area, photosynthesis is saturated at an increasingly higher quantum flux density. If measured at a quantum flux density which saturates photosynthesis at a low, but not at a high nitrogen concentration in the leaf, a curvilinear photosynthesis–leaf–nitrogen relationship is inevitable (Evans, 1989a). Such a situation was found in a comparison of *Plantago major* subspecies (Dijkstra, 1989). The slow-growing subspecies, with a low PNUE when determined at the relatively low quantum flux density at which plants were grown, has a higher chlorophyll concentration per unit leaf area (Dijkstra and Lambers, 1989a). At the relatively low quantum flux density, this will cause shading of the chloroplasts near the lower leaf surface. However, measured at light- and CO_2 -saturation the PNUE was the same for both subspecies. These results agree with those on six fast- and slow-growing monocotyledonous species. When the quantum flux density during the measurements of photosynthesis was increased from that at which the plants were grown to light saturation, both the slope of the CO_2 -response curve and the CO_2 -saturated rate of photosynthesis increased significantly more for the slow-growing species than for the fast-growing ones (A. van der Werf, personal communication). Since many leaves often function at a quantum flux density well below the saturation level of photosynthesis, comparison of PNUE values determined at a low quantum flux density is valid, providing the quantum flux density is the same for all plants compared (Schulze, 1982; Karlsson, 1991).

Measuring photosynthesis at light saturation in field-grown plants, Field and Mooney (1986) found the highest PNUE values for annuals, intermediate values for drought-deciduous shrubs, and the lowest values for evergreen trees and shrubs. Though some of these differences may have been phenotypic, there is likely to be a strong inherent component as well (cf. Evans, 1989a). What could be the basis of the relatively low PNUE of slow-growing species?

1. Partitioning of Nitrogen between Chloroplasts and other Cell Components

Variation in PNUE might reflect a difference in investment of nitrogen in photosynthetic and non-photosynthetic leaf components. In C_3 species with a high PNUE, approximately 75% of the nitrogen in mesophyll cells is located in the chloroplasts (Evans, 1989a). It is likely that non-photosynthetic and photosynthetic cells require a similar amount of nitrogen not associated with photosynthesis. Part of this nitrogen is associated with primary cell walls, which are claimed to contain up to 20% structural proteins by weight (Jones and Robinson, 1989). These proteins ("extensin") are rich in hydroxyproline and appear to be associated with resistance to microbial attack and some forms of abiotic stress (Esquerré-Tugayé *et al.*, 1979; Lamport and Catt, 1981). Apart from "extensin", other (hydroxy)proline-rich proteins occur in plant cell walls and some of these are probably also associated with plant defence reactions (Lamport, 1980; Kleis-San Francisco and Tierney, 1990). Cell wall components such as (hemi)cellulose and lignin represent a considerably greater fraction of the leaf dry weight in slow-growing herbaceous species than of that in fast-growing ones, whereas the reverse is true for the organic nitrogen fraction (Poorter and Bergkotte, 1992). We do not know if the amount of protein per unit weight of cell walls of fast- and slow-growing species is the same. If so, then the fraction of organic nitrogen that is tied up in cell walls is certainly much greater in slow-growing species. This indicates that a low PNUE may be partly associated with greater investment in cell-wall components.

Leaves with a very thick or multiple epidermis (Esau, 1977), crystal cells (Kimmerer and Potter, 1987), collenchyma and sclerenchyma elements (Konings *et al.*, 1989), or cells with specific functions (e.g. water storage; Schmidt and Kaiser, 1987), must invest part of the nitrogen in their leaves in these structures. Thus, leaves which contain some of these additional elements are bound to have a lower PNUE.

Similarly, accumulation of relatively large quantities of nitrogen-containing molecules as compatible solutes (e.g. proline and glycinebetaine;

Wyn Jones and Gorham, 1983), storage proteins (Franceschi *et al.*, 1983; Staswick, 1988), peptides that sequester heavy metals (Lolkema *et al.*, 1984; Robinson and Jackson, 1986), protective compounds (e.g. polyamines; Galston and Sawhney, 1990; Kuehn *et al.*, 1990), antifungal polypeptides (e.g. thionins; Reimann-Philipp *et al.*, 1989; Apel *et al.*, 1990), or toxic antiherbivore compounds (e.g. cyanogenic glycosides: Kakes, 1987; cyanolipids: Poulton 1990; alkaloids: Hartmann *et al.*, 1989) also decreases PNUE.

We conclude that a low PNUE may be a consequence of a large investment of nitrogen in cell walls, specialized cells or compounds that are not associated with photosynthesis.

2. Suboptimal Partitioning of Nitrogen within the Chloroplast

When grown at optimum nitrogen supply, slow-growing herbaceous species have higher chlorophyll concentrations per unit leaf area and unit nitrogen (Poorter *et al.*, 1990). Slow-growing herbs have double the concentration of chlorophyll found in fast-growing species (0.6 vs. 0.3 mmol m⁻²). This requires the extra investment of at least 15 mmol of nitrogen per square metre of leaf area, which amounts to 12% or more of a leaf's total nitrogen concentration in the slow-growing herbs, but only increases the leaf's absorptance by 7% (Evans, 1989b). Although extra investment in chlorophyll increases photosynthetic performance under shade conditions (Evans, 1989b), there may well be some excess in capacity of the light-harvesting machinery. But this offers only a partial explanation for the low PNUE of slow-growing species.

3. Activation of Rubisco

Activation of Rubisco requires carbamylation of the enzyme (Salvucci, 1989). The degree of carbamylation depends on the quantum flux density. In some, but not all higher plant species, Rubisco is also regulated by a naturally occurring tight-binding inhibitor: 2-carboxyarabinitol 1-phosphate (Servaites, 1990). The difference in photosynthesis per unit Rubisco at high quantum flux density cannot be explained by variation in the degree of enzyme activation by either of the above mechanisms (Seemann, 1989). Intrinsic differences in the enzyme from different species, rather than regulation of its activity by activation, are the likely cause of variation in the specific activity of Rubisco.

4. *Variation in Rubisco Specific Activity*

Variation in PNUE has been further analysed in a comparison of *Alocasia macrorrhiza*, a tropical understorey plant, with two crop species (Seemann *et al.*, 1987; Seemann, 1989). *Alocasia* has a considerably lower photosynthetic capacity per unit leaf nitrogen or Rubisco protein. The relatively low PNUE of *Alocasia* is partly a consequence of a relatively low specific activity (carboxylating activity per unit enzyme) of its Rubisco. A low specific activity is not restricted to shade-tolerant or inherently slow-growing species, but has also been found in comparisons of fast-growing crop species (Seemann and Berry, 1982, cited in Evans, 1989a; Makino *et al.*, 1988). So far we do not know the biochemical basis of variation in specific activity of Rubisco or if there is any systematic link between specific activity and ecological traits.

5. *Feedback Inhibition of Photosynthesis*

Comparing the rate of photosynthesis at normal and high internal partial pressure (p_i) of CO_2 , provides insight into the extent of feedback control of photosynthesis (Sharkey *et al.*, 1986; Sage and Sharkey, 1987). Such control may play an important role when the products of photosynthesis, i.e. sucrose and its phosphorylated precursors, accumulate, due to for example a relatively low temperature (Sage and Sharkey, 1987) or a limited activity of the sink (Plaut *et al.*, 1987). Under these conditions the photosynthetic apparatus is only partly used, so that the PNUE is less than maximal. We do not know if such a situation of feedback inhibition is the norm in slow-growing species, but if so it could offer an explanation for their relatively low PNUE.

6. *Effects of the CO_2 Concentration inside the Leaf*

Photosynthesis increases with increasing internal partial pressure of CO_2 inside the leaf (p_i), up to a maximum. Differences in p_i between species or populations have been reported (Mooney and Chu, 1983) and might offer a partial explanation for a low PNUE in leaves with a low SLA and a high nitrogen concentration per unit leaf area, as found for slow-growing species (Poorter *et al.*, 1990). Parkhurst *et al.* (1988) found a significant CO_2 pressure gradient inside the leaf, more so for hypostomatous than for amphistomatous leaves (Parkhurst and Mott, 1990). Moreover, the CO_2 pressure at the site of carboxylation (p_c) might be significantly lower than p_i . Hence, a greater internal CO_2 diffusion limitation also partly

explains a low PNUE. If generally valid, species with a low PNUE should show less discrimination against $^{13}\text{CO}_2$ than those with a higher PNUE. The degree of discrimination reflects the ratio of the CO_2 concentration inside the leaf and that in the atmosphere (p_i) (cf. Farquhar *et al.*, 1982).

Our own data on a range of herbaceous species grown under the same conditions do not show a correlation between carbon isotope discrimination and RGR (Figure 6B). In a comparison of species from high altitudes with related species from low altitude, the high-altitude species show less discrimination, which correlates with their lower ratio of p_i/p_a (Körner and Diemer, 1987; Körner *et al.*, 1988). Leaf carbon isotope discrimination of annuals (Smedley *et al.*, 1991) and short-lived perennials (Ehleringer and Cooper, 1988) is less than that of longer-lived (and presumably slower-growing) perennials, also when grown under the same environmental field conditions. Our plants (Figure 6) were grown under well-watered conditions and at a relatively low vapour pressure deficit, which may have led to a relatively high p_i (cf. Schulze *et al.*, 1987; Brugnoli and Lauteri, 1991). We cannot fully exclude that variation in p_i between species occurs when plants are supplied with a limiting amount of water or at a higher vapour-pressure deficit and that this correlates with that in PNUE. However, the variation in PNUE in comparisons of widely different species (Evans, 1989a) is certainly too great to be fully accounted for by variation in p_i . Moreover, the variation in PNUE as found in a comparison of herbaceous species cannot be accounted for by variation in p_i (Figure 6A,B).

7. Conclusions

To summarize the above, slow-growing species with a relatively low PNUE may invest relatively large quantities of nitrogen in components not associated with photosynthesis. They may also have a suboptimal distribution of nitrogen between elements of the photosynthetic apparatus or a Rubisco enzyme with a low catalytic capacity. A larger degree of feedback inhibition or a relatively low CO_2 concentration at the site of carboxylation might also play a role. There is as yet no convincing evidence for any of these possible explanations.

C. Is There a Compromise between Photosynthetic Nitrogen Use Efficiency and Water Use Efficiency?

The leaf's stomatal conductance tends to be regulated in each a way that a compromise is reached between gain of CO_2 and loss of H_2O (Farquhar and

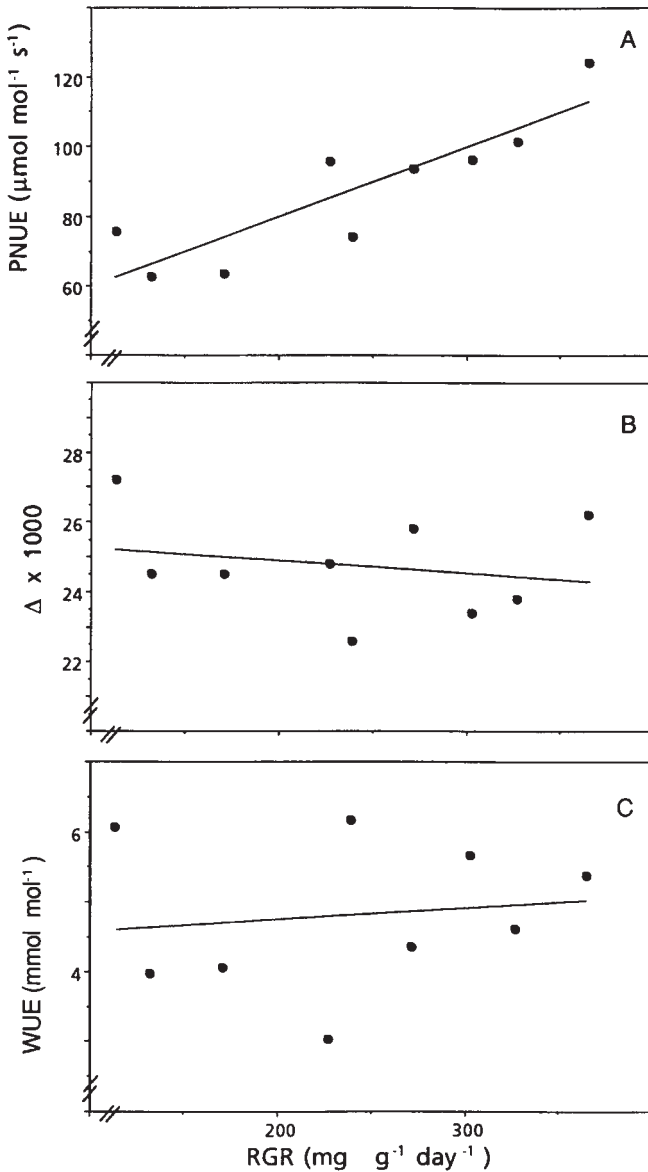


Figure 6 Gas exchange-related characteristics of fast-growing and slow-growing species, described in Figure 1. (A) The rate of photosynthesis expressed on a leaf nitrogen basis. (B) Carbon isotope discrimination. (C) The water use efficiency. Gas exchange characteristics were determined under conditions used for growing the plants. (After Poorter *et al.* (1990) and unpublished data of H. Poorter and G. D. Farquhar; further information, based on 24 species, is unpublished.)

Sharkey, 1982). Increased conductance would lead to roughly proportionally greater transpiration, but marginally greater photosynthesis. However, different environmental conditions may require a different compromise (Cowan, 1977). Species which naturally occur in environments where the water supply is low and/or the evaporative demand is high might have a lower stomatal conductance and a lower intercellular pressure of CO_2 (p_i). This tends to increase their water use efficiency of photosynthesis (WUE), but, all other parameters being equal, leads to a lower PNUE, as discussed above. Hence, a low PNUE might be a reflection of a high WUE. In a comparison of five Californian evergreen species, Field *et al.* (1983) indeed found that species with a lower PNUE tended to have a higher WUE. The water-efficient species typically occurred in the driest habitats. Pavlik (1983) did not find a different WUE for two dune grasses differing in their PNUE.

If there were a general trend in a wider comparison, for species with a low PNUE to have a high WUE, such species are expected to show less discrimination against $^{13}\text{CO}_2$ (Farquhar *et al.*, 1982; Hubick and Farquhar, 1989). However, five Californian evergreens with a low PNUE showed exactly the same discrimination as the average C_3 plant (Field and Mooney, 1986), which does not lend support to the contention that a low PNUE generally reflects a high WUE. Our own data on the PNUE and WUE of nine herbaceous species (Figures 6A,C) do not support the hypothesis either. Therefore, if such a compromise between PNUE and WUE exists, it can at best be relevant in comparisons of species with similar life form grown at a relatively high quantum flux density and with a high evaporative demand.

D. Photosynthesis under Suboptimal Conditions

The photosynthetic capacity decreases with decreasing nitrogen concentration in the leaf, in a (curvi)linear fashion (Evans, 1989a). In the slow-growing *Carex diandra*, p_i increases with decreasing steady state nitrogen supply (H. Lambers and R. Welschen, unpublished). Such an increase with decreasing leaf nitrogen has also been found for other species, including fast-growing ones (Morgan, 1986; Sage and Pearcy, 1987; Ghashghaie and Saugier, 1989; but see Sage and Pearcy, 1987). This increase in p_i may contribute to curvilinearity in the photosynthesis–leaf nitrogen relationship, at least when photosynthesis is measured at an ambient CO_2 concentration. An alternative explanation is that the CO_2 gradient between the intercellular spaces and the site of carboxylation and/or the gradient in p_i within the leaf increases with increasing leaf nitrogen concentration (Evans, 1989a). A relatively lower investment in

chlorophyll-complexing thylakoid proteins at a low nitrogen supply, as long as this does not significantly affect the leaf's absorptance, also tends to contribute to curvilinearity (Section IX.B). Curvilinearity of the photosynthesis–leaf nitrogen relationship does not appear to be due to inactivation of Rubisco at a high leaf nitrogen concentration (Evans and Terashima, 1988). Despite these reasons which tend to produce curvilinearity, such a relationship is not invariably found, due to the proportionally greater investment of nitrogen in Rubisco with increasing leaf nitrogen concentration (Evans, 1989a).

Curvilinearity of the photosynthetic capacity vs. leaf nitrogen relationship can be interpreted as a relatively inefficient use of nitrogen for photosynthesis at a high nitrogen concentration in the leaf and as such might be expected to occur particularly in slow-growing species adapted to nutrient-poor soils. Indeed, at high N-supply the PNUE of slow-growing species is lower than at low N-supply. A similar tendency, though not as strong, has also been observed for fast-growing species, so that the PNUE of plants grown at a low N-supply is rather similar for fast- and slow-growing species (Boot *et al.*, 1992; A. van der Werf, personal communication). Perhaps the low PNUE of slow-growing species at a high N-supply merely indicates that the rate of biomass accumulation and cell expansion of these species is saturated by the supply of N before that of N-uptake and N-assimilation.

When plants are grown at a low quantum flux density, their leaves have a lower photosynthetic capacity (e.g. Pons, 1977; Young and Smith, 1980). Allocation of nitrogen to the light-harvesting machinery is increased at the expense of that to Rubisco and other enzymes of the Calvin cycle (Björkman, 1981). This change in pattern of nitrogen distribution over the various components of the photosynthetic apparatus leads to optimization of the use of nitrogen for photosynthesis. There is some evidence that slow-growing, shade-tolerant species, have a greater capacity to adjust their nitrogen partitioning in this manner than fast-growing ones (Evans, 1989b).

E. Conclusions

From the above discussion it transpires that slow-growing species have a relatively low PNUE, when grown at optimum nitrogen supply. As yet, there is no satisfactory explanation for this difference. At the low N-supply which the slow-growing species encounter in their natural habitat, the PNUE of fast- and slow-growing species is rather similar. A further appreciation of the ecological advantage, if any, associated with a low PNUE, clearly awaits more information on the physiological, biochemical

or anatomical background of the variation in PNUE and possible negative correlations of PNUE with WUE.

X. RESPIRATION

Respiration provides the driving force for three major energy-requiring processes: maintenance, growth and ion uptake. Maintenance respiration is mainly associated with turnover of various cellular components and the conservation of solute gradients across membranes. Growth respiration is used to supply ATP and NADH, needed to convert glucose into the different chemical compounds. In roots, respiratory energy is also needed for the absorption of nutrients from the environment.

A. Species-specific Variation in the Rate of Respiration

Fast-growing species have a higher rate of nitrate uptake (Figure 3A) and a higher RGR. Therefore, it is not surprising that they have a higher rate of shoot and root respiration (Dijkstra and Lambers, 1989a; Poorter *et al.*, 1990, 1991; van der Werf *et al.*, 1992b; Figure 3B). However, the rate of root respiration of fast-growing species is not as high as would be expected from their higher RGR and NIR. Using data of van der Werf *et al.* (1988), who determined specific costs for root growth, maintenance and ion uptake for two slow-growing *Carex* species, the calculated rate of root respiration of fast-growing species is approximately four times higher than that of slow-growing ones (Poorter *et al.*, 1991; Figure 3B, broken line). This value is at variance with that determined experimentally, showing that the rate of root respiration of fast-growing species is only 50% higher than that of slow-growing ones (Figure 3B, regression line through data points). Why do the fast-growing species respire at a rate which is so much lower than expected from their RGR and NIR?

1. Variation in Respiratory Efficiency

The relatively low rate of respiration of fast-growing species might be due to a relatively more efficient respiration. Apart from the cytochrome pathway, which yields three molecules of ATP per oxygen atom reduced, plants have an alternative, non-phosphorylating respiratory pathway. Engagement of this path, rather than the cytochrome path, yields only one third as much ATP (Lambers, 1985). Do fast-growing species employ this alternative

pathway to a lesser extent than the slow-growing ones and therefore produce more ATP for the same amount of glucose respired and oxygen reduced? Despite a wide variation in the participation of the alternative, nonphosphorylating electron transport path in respiration, varying from 0 to 44% of total root respiration (van der Werf *et al.*, 1989) and from 4 to 58% for leaves (Collier and Cummins, 1989; Atkin and Day, 1990), there is no evidence that this respiratory path contributes less to respiration in fast-growing species or genotypes (Dijkstra and Lambers, 1989b; Atkin and Day, 1990; Poorter *et al.*, 1991; van der Werf *et al.*, 1992b). In fact, Collier and Cummins (1989) found that respiration rates of the leaves of ruderals collected in the field were higher and that their alternative path was engaged to a greater extent than that of understorey species. Next to a greater alternative path activity, the ruderals also had a greater capacity for respiration via this path. This might contribute to their functioning in fluctuating environments, in line with results on root respiration of other species (Lambers *et al.*, 1981b).

The rate of ATP production per oxygen consumed might also be higher in fast-growing species if their mitochondria operate under substrate limitation or further away from "state 4" conditions. (State 4 is the condition where the respiration is strongly restricted by the availability of ADP, as opposed to state 3, where ADP is available in saturating amounts.) If so, they do not produce ATP whilst still reducing oxygen (cf. Whitehouse *et al.*, 1989). In state 3 conditions, they operate more efficiently, producing maximally three ATP per oxygen atom. If the fast-growing species would respire closer to state 3, their ADP: O ratio *in vivo* might be higher. Straightforward methods exist to test this hypothesis (Day and Lambers, 1983), but so far no comparative data are available on fast- and slow-growing species.

2. Variation in Specific Costs of Energy-Requiring Processes

The current data provide no indication that fast-growing species produce ATP more efficiently than slow-growing ones. Therefore, it is very likely that the relatively low respiration rate of fast-growing species is caused by lower specific respiratory costs for energy-requiring processes, such as maintenance, growth or ion acquisition, at least under optimum growth conditions.

We have very little information on the biochemistry and physiology of "maintenance processes". Protein turnover and the maintenance of solute gradients are considered major components (Penning de Vries, 1975), but quantitative information on either of these processes in roots is scarce (van der Werf *et al.*, 1992c). Assuming the same turnover rate per unit

protein, we expect the maintenance respiration of fast-growing species, which have a higher protein concentration (Section VIII.A), to be higher than that of slow-growing species, but this is not borne out by experimental results. Other processes which require respiratory energy and which do not contribute to growth or ion uptake will also increase the maintenance costs. For example, the relatively large turnover of carbohydrate pools in slow-growing species as compared to fast-growing ones (Farrar, 1989), might partly explain the high respiratory costs of roots in slow-growing species. However, maintenance respiration is only a small portion of total respiration, at least in young plants grown at an optimum nutrient supply (van der Werf *et al.*, 1989; Poorter *et al.*, 1991). Thus variation in the specific costs for maintenance is unlikely to affect substantially the rate of root respiration.

In the case of growth respiration, the construction costs per unit biomass may vary with the chemical composition of the plant. Table 4 provides information on the gas exchange which could be expected to occur with the synthesis of a range of primary and secondary compounds. The calculated oxygen uptake and carbon dioxide release include gas exchange associated with ATP production, (de)carboxylating reactions, as well as the use of oxygen in reactions catalysed by such enzymes as mixed function oxygenases. We calculated that the oxygen requirement for the synthesis of roots of fast-growing species is higher than that for slow-growing ones (Poorter *et al.*, 1991). Hence, differences in chemical composition cannot explain why respiration rates of slow-growing species are only marginally lower than those of species growing three times as fast and absorbing ions at over four times the rate of the slow-growing ones.

If the specific costs for maintenance and growth cannot explain the relatively high respiration rates of slow-growing species, then the most likely explanation for the observed differences in root respiration between slow-growing and fast-growing species is variation in the specific cost for nutrient acquisition. Slow-growing species, which are often associated with unproductive environments (Section II), are likely to be geared towards nutrient uptake from a very dilute solution in comparison with the fast-growing species from relatively nutrient-rich habitats. This may require more energy, either because it involves extrusion and re-uptake of compounds which release ions from complexes in the soil (Section XI.A) or because the ratio of proton entry and ion absorption is higher, compared to the system of fast-growing species (cf. Clarkson, 1986; McClure *et al.*, 1990). For *Hordeum vulgare*, two transport systems for nitrate uptake have been described. One of these systems is an energy-requiring one, operating at very low external concentrations. The other one does not require metabolic energy and functions at an external nitrate concentration sufficiently high, compared to the cytoplasmic concentration, to allow

passive diffusion of nitrate across the plasma membrane (Glass *et al.*, 1990; Siddiqi *et al.*, 1990). Perhaps fast-growing species maintain a relatively low nitrate concentration in the cytoplasm of their roots cells, due to rapid reduction of nitrate in the cytosol, transport into their, presumably relatively large, vacuoles (cf. Section XII.A), or efficient export to the shoot, made possible by the relatively high rate of transpiration per unit root weight (Poorter *et al.*, 1990). If so, the system which does not require metabolic energy may predominate in the roots of fast-growing species, whereas the energetically more expensive one is more important in the roots of slow-growing ones. This is not to say that fast-growing species lack a similar system. Rather, it may be constitutive in slow-growing species and inducible under nutrient-deficient conditions in fast-growing ones, when the electrochemical gradient across the plasma membrane does not allow passive uptake of nitrate (van der Werf *et al.*, 1992b, cf. Section VII.A). An alternative and more attractive explanation for presumably higher costs for nitrate uptake is that the ratio between ion influx and efflux is lower in slow-growing species (cf. Pearson *et al.*, 1981; Deane-Drummond and Glass, 1983; Oscarson *et al.*, 1987).

B. Respiration at Suboptimal Nitrogen Supply or Quantum Flux Density

With a decreasing nitrogen supply, there is a decline in the nitrogen concentration and the rate of respiration per unit mass, both in roots (Lambers *et al.*, 1981a; Duarte *et al.*, 1988; Granato *et al.*, 1989; van der Werf *et al.*, 1992b) and in leaves (Waring *et al.*, 1985; Boot *et al.*, 1992). The respiration rate is less, because of reduced energy requirements for biosynthetic processes, ion transport and loading of sucrose in the phloem. Upon a decrease of the nitrogen supply, both the nitrogen concentration and the rate of leaf respiration of the faster-growing *Agrostis vinealis* decline to a greater extent than that of the slow-growing *Corynephorus canescens* (Boot *et al.*, 1992). Similar results have been obtained in a comparison of the fast-growing *Holcus lanatus* and the slow-growing *Deschampsia flexuosa* (C.A.D.M. van de Vijver, R.G.A. Boot and H. Poorter, unpublished). At optimum nitrogen supply, *Agrostis* has a higher leaf nitrogen concentration (cf. Section VIII.A), whereas it is reduced to the same level as in *Corynephorus* when the nitrogen supply is reduced. There is some evidence that specific costs for ion transport and/or maintenance increase at a limiting nitrogen supply, particularly in fast-growing species (A. van der Werf *et al.*, 1992b).

When plants are transferred to a low quantum flux density, the rate of root respiration declines (Kuiper and Smid, 1985; H.H. Prins, R. Hetem and H. Poorter, unpublished), as expected from the lower rate of root growth

under such conditions. Upon prolonged exposure to a low quantum flux density, there is only a small, or no difference in root respiration between plants grown at high vs. low quantum flux density (Lambers and Posthumus, 1980; A. van der Werf and P. Poot, unpublished). This is attributed to the increase in LWR upon prolonged exposure to a low quantum flux density, which increases the root's energy requirement for uptake of ions destined for the shoot. Also, the rate of leaf respiration is less for plants grown at a low quantum flux density (Pons, 1977; Waring *et al.*, 1985). Presumably the lower rates of respiration reflect the lower energy requirement for biosynthetic and transport processes. We do not know of any comparative data on fast-growing and slow-growing species.

C. Conclusions

At an optimum nutrient supply, the specific rate of root respiration of fast-growing species is lower than expected from their high RGR and high NIR. A satisfactory explanation for this relatively low respiration rate cannot be provided yet, but it may well be due to a relatively low energy requirement for ion acquisition. At a nutrient supply or quantum flux density which is suboptimal for growth, the rate of respiration in both leaves and roots is less than for plants growing under optimum conditions. This is at least partly explained by reduced rates of energy-requiring processes. Upon a change in nitrogen supply, fast-growing species adjust their respiration rate to a greater extent than slow-growing ones, possibly with concomitant changes in specific costs for energy-requiring processes.

XI. EXUDATION AND VOLATILE LOSSES

Plants lose photosynthates through exudation and volatilization as well as during respiration. Exudation may occur both above- and below-ground, whereas volatilization predominantly occurs above-ground.

A. The Quantitative and Qualitative Importance of Exudation

It is well established that roots exude a range of organic compounds, including sugars (McCully and Canny, 1985), organic acids (Gardner *et al.*, 1983) and amino acids (McDougall, 1970), especially when phosphate is

in short supply (Graham *et al.*, 1981; Lipton *et al.*, 1987). Estimates of the loss of exudates from roots vary widely, largely depending on the methods used to quantify this process and perhaps on the species under investigation (Cheshire and Mundie, 1990). Soluble exudates constitute less than 0.5% of the carbon present in the plant (Cheshire and Mundie, 1990). Their production ranges from 10 to 100 mg per gram root dry weight produced; root cap plus mucigel may provide a further 20–50 mg (Newman, 1985; Gregory and Atwell, 1991). At the very most 5% of the photosynthates are lost through “rhizodeposition”, i.e. the loss of organic matter via both processes (Lambers, 1987), with the exception of plants with proteoid roots in which very high values are found (see below). If losses due to continual cell death are also included, losses due to rhizodeposition (*sensu lato*) may amount to 10% of all photosynthates produced (Helal and Sauerbeck, 1986; Lynch and Whipps, 1990).

Exudates are of distinct importance for the acquisition of sparingly available nutrients and for interactions with symbionts. Highly efficient chelators (phytosiderophores) are excreted by roots of Gramineae and these allow the roots to absorb Fe, Zn, Mn and Cu from poorly soluble sources in calcareous soils (Römheld and Marschner, 1986; Marschner *et al.*, 1989; Zhang *et al.*, 1989). At least part of the excreted phytosiderophores are absorbed again by the roots as a metal–siderophore complex (Römheld and Marschner, 1990). Non-gramineous species also release chelating compounds, generally of a phenolic nature, but these are less efficient than the true phytosiderophores (Römheld, 1987). Many species, particularly those with proteoid roots, release citric acid (Gardner *et al.*, 1983; Hoffland *et al.*, 1989a; Hoffland *et al.*, 1989b) which may amount to as much as 23% of the biomass at plant harvest (Dinkelaker *et al.*, 1989). The excretion of citric acid greatly enhances the root's capacity to use insoluble phosphate (Hoffland *et al.*, 1990). Proteoid roots also have an increased capacity for reduction of iron and manganese in the rhizosphere and, consequently, to mobilize sparingly soluble Fe or Al phosphates (Gardner *et al.*, 1982a, b). Excretion of citric acid may also be significant in releasing cations from humic substances (Albuzzio and Ferrari, 1989). We conclude that the release of chelating substances, such as citric acid and possibly other organic acids is important in acquiring nutrients from both calcareous substrates and acidic soils where cations are bound to a humic complex. Many slow-growing species are associated with such calcareous or acidic soils (Grime and Hunt, 1975). Hence the release of root exudates is likely to confer an advantage in such soils and should not merely be considered as a loss of carbon.

Some micro-organisms exude organic compounds that precipitate heavy metals outside the cells. There is no evidence that this mechanism is

important in ecotypes of higher plants that tolerate high concentrations of heavy metals in the root environment (Verkleij and Schat, 1990).

Release of organic substances from roots can also play a pivotal role in symbiotic associations. For example, flavonoids, released from the roots of Leguminosae induce the nodulation genes of *Rhizobium*, the primary step in the nodulation process (Richardson *et al.*, 1988; Hartwig *et al.*, 1990). Plants capable of a mycorrhizal symbiosis release organic compounds to the rhizosphere when they contain very little phosphate in the roots, presumably due to the fact that their membranes contain less than an optimum amount of phospholipids (Ratnayaka *et al.*, 1978).

Some root exudates, predominantly of a phenolic nature, play a role in allelopathic interactions between plants. Although the exact nature of the compounds released, their biochemical effect on neighbouring plants and their ecological significance are often not known, the existence of allelopathic interactions, including those based on exuded compounds, is beyond doubt (Putnam and Tang, 1986; Kuiters, 1990). Root exudation can also affect, both negatively and positively, the rates of a number of soil biological processes, such as denitrification (Woldendorp, 1963), nitrification (Haider *et al.*, 1987; Vitousek *et al.*, 1989) and mineralization (Sparling *et al.*, 1982). Different plant species affect these soil biological processes to varying degrees (Janzen and Radder, 1989; Berendse *et al.*, 1989; van Veen *et al.*, 1989), but the exact nature of the effects is generally not fully known. There is some evidence that losses through exudation are quantitatively more important in a slower-growing *Hordeum vulgare* variety than in a faster-growing one (Liljeroth *et al.*, 1990).

Losses of carbon through exudation also occur above-ground. We have very little information on their quantitative importance and inherent variation of this process (Tukey, 1970).

B. The Quantitative and Qualitative Importance of Volatile Losses

Although it is probably fair to state that volatile losses are generally not of great quantitative significance, they are of fairly wide importance, e.g. in allelopathic interactions and herbivory (Harborne, 1982; Rhoades, 1985; Dicke and Sabelis, 1989).

Emissions of isoprene in three fern species accounted for 0.02 to 2.6% of the carbon fixed during photosynthesis, increasing with photon flux density and temperature and varying between species (Tingey *et al.*, 1987). These values are in the same range as those found for tree leaves

(Sanadze, 1969; Tingey *et al.*, 1981). They are up to 2.5 times lower than those based on field measurements for a number of tree species, which may reflect species differences in emission or effects of high quantum flux density (Flyckt *et al.*, 1980, cited in Tingey *et al.*, 1981). In extreme cases, such as in *Ledum groenlandicum* during part of the year (Prudhomme, 1983) and *Populus tremuloides* at high temperatures (35–45°C) (Monson and Fall, 1989), up to 8% of recently fixed carbon may be lost as volatiles.

Losses of specific volatiles, though quantitatively minor (less than 0.001% of the photosynthates produced daily), are responsible for attraction of predators upon attack of leaves by herbivores, e.g. spider mites, and thus reduce herbivore damage (Dicke and Sabelis, 1989).

C. Conclusions

Losses through exudation *sensu lato* can significantly reduce a plant's growth rate. Carbon loss through exudation and volatilization is most certainly of ecological importance in a nutrient-poor environment and in interactions of a plant species with other organisms. Although not supported by hard evidence, we hypothesize that exudation is more important in slow-growing species from nutrient-poor sites. Exudation might allow such species to acquire nutrients which are otherwise unavailable.

XII. OTHER DIFFERENCES BETWEEN FAST- AND SLOW-GROWING SPECIES

Apart from the above-mentioned traits, which directly affect the growth of a plant, some other aspects of fast-growing and slow-growing species and mutants thereof have been investigated. In recent years fascinating information has become available on the role of a specific class of phytohormones in the control of a plant's growth rate—the gibberellins.

A. Hormonal Aspects

Fast-growing genotypes contain more gibberellin than slower-growing ones (Rood *et al.*, 1983; Rood *et al.*, 1990a; Rood *et al.*, 1990b; Rood *et al.*, 1990c; Dijkstra *et al.*, 1990; H. Konings and M. Berrevoets, personal communication). Rapid growth of hybrids ("heterosis") has been

associated with higher levels of gibberellin in both herbaceous species and trees (Rood and Pharis, 1987; Bate *et al.*, 1988). Interestingly, in a *Zea mays* hybrid, both the superior growth and the higher level of gibberellin, compared to those of its parents, are restricted to favourable conditions and not displayed during growth at low temperature (Rood and Pharis, 1987). Gibberellins control leaf size (*Brassica rapa*, Zanewich *et al.*, 1990; *Thlaspi arvense*, Metzger and Hassebrock, 1990; *Lycopersicon esculentum*, H. Konings and M. Berrevoets, personal communication) and it seems likely that the variation in leaf size between fast- and slow-growing species is at least partly associated with differences in the concentration of endogenous gibberellins.

Mutants of *Lycopersicon esculentum* with reduced levels of gibberellin, have a range of characteristics similar to slow-growing species, e.g. a higher RWR, but lower LAR and SLA, relatively more dry matter per unit fresh weight, and a low rate of photosynthesis per unit leaf dry weight (H. Konings and M. Berrevoets, personal communication). Treatment with gibberellin reduces genotypic differences in RGR, indicating that this hormone plays a role in intraspecific variation in growth potential, probably via its effect on leaf area development and biomass partitioning (Dijkstra and Kuiper, 1989; Dijkstra *et al.*, 1990; Rood *et al.*, 1990a, b, c; Zanewich *et al.*, 1990; H. Konings and M. Berrevoets, personal communication).

The detailed mechanism of the gibberellin effects on growth is largely unknown. However, it is well documented that this phytohormone affects stem growth via both cell elongation and cell division (Métraux, 1987; Jupe *et al.*, 1988; Rood *et al.*, 1990b). Effects of gibberellin on cell enlargement could account for a number of the chemical differences between fast- and slow-growing species (cf. Section VIII.A). The larger surface-to-volume ratio of plants with smaller cells is expected to be associated with a relatively large investment in cell-wall components and hence a high dry matter percentage. Smaller cells are bound to have relatively small vacuoles, which would explain the relatively low capacity of slow-growing species to accumulate organic acids, nitrate and other minerals. The effects of gibberellin on cell division could account for differences in biomass partitioning (cf. Section VI.A). A low level of gibberellins prevents rapid incorporation of photosynthates into leaf and stem biomass, so that a relatively large proportion is translocated to and incorporated into the roots.

Clearly, further work is needed on the mechanism of gibberellin action on cell growth and on the level of this phytohormone in different species. This may well lead to physiological explanations for inherent variation in RGR and provide insight into evolutionary mechanisms causing such variation.

B. Miscellaneous Traits

Fast-growing grass species tend to have wider leaves than slow-growing ones; leaves of dicotyledonous fast-growing species also tend to be larger than those of slow-growing ones (Christie and Moorby, 1975; Ceulemans, 1989; Körner and Pelaez Menendez-Riedl, 1989; H. Poorter, unpublished). Leaves of fast-growing poplar hybrids are larger than those of either of their parents, *Populus trichocarpa* and *P. deltoides*. Leaf cells of *P. trichocarpa* are larger than those of *P. deltoides*, whereas *P. deltoides* has more cells per leaf. The greater leaf size of the hybrids can be explained by inheritance of a larger cell number from *P. deltoides* and larger cells from *P. trichocarpa* (Ceulemans, 1989). In general, variation in leaf size appears to be due predominantly to fewer cells per leaf, rather than to cell size (Körner and Pelaez Menendez-Riedl, 1989).

The diurnal pattern of leaf growth may vary between species and hybrids thereof. Leaves of *Populus trichocarpa* mainly grow in the light, with little growth in the dark, those of *P. deltoides* grow during the dark period, with little stimulation in the light, whereas their fast-growing interspecific hybrids grow during both night and dark (Ceulemans, 1989).

For a wide range of species and for families of *Poa annua*, a slightly negative correlation between nuclear DNA content and RGR has been reported (Grime *et al.*, 1988). A negative correlation between RGR and seed size has been suggested (Fenner, 1978; Gross, 1984). However, no such relationship has been detected in a much larger data set (Thompson, 1987). Seeds of fast-growing species germinate more rapidly than those of slow-growing ones (Grime *et al.*, 1988).

XIII. AN INTEGRATION OF VARIOUS PHYSIOLOGICAL AND MORPHOLOGICAL ASPECTS

In the previous sections several aspects of the physiology, morphology, allocation and biochemical composition have been discussed in relation to the potential growth rate of plant species. We now address the question of what proportion each parameter contributes to the observed differences in growth rate, using (Eq. (5)) as a framework.

A. Carbon Budget

For the nine species presented in Figures 1–4 and 6, RGR varies more than three-fold. The carbon concentration (Section VIII) is lower for

fast-growing species, which is partly due to their higher mineral concentration. The lower carbon concentration contributes to a higher RGR, but is only of minor importance in explaining the observed variation in RGR. Quantifications of exudation and volatile losses are scarce but these processes are unlikely to determine a large part of the variation in RGR either (Section IX). Hence, the major differences are due to variation in photosynthetic gain and respiratory losses of carbon. Indeed, carbon gain of the fastest-growing of these 9 species is about 3.1 times that of the slowest-growing one (Figure 7). This is caused by a much higher SLA (Section V) and a slightly higher LWR (Section VI), rather than by a higher rate of photosynthesis per unit leaf area (Section VIII). Species also differ in the way they utilize the fixed carbon. Although fast-growing species have higher shoot and root respiration rates, the proportion of fixed carbon used in respiration is less. This is due largely to a higher rate of photosynthesis per unit plant weight and, as far as root respiration is concerned, also to the lower RWR of fast-growing species. It is to be expected that the lower RWR contributes to the higher RGR, provided the smaller root size is compensated for by a higher specific activity. Indeed, fast-growing species do have a much higher rate of net ion uptake (Section VII) and water absorption (Poorter *et al.*, 1990) than slow-growing ones. Compared to slow-growing species, their rate of root respiration is not as high as would be expected from their four times higher rate of nitrate uptake and their three times higher relative growth rate. This relatively low respiration rate contributes to the rapid growth of fast-growing species.

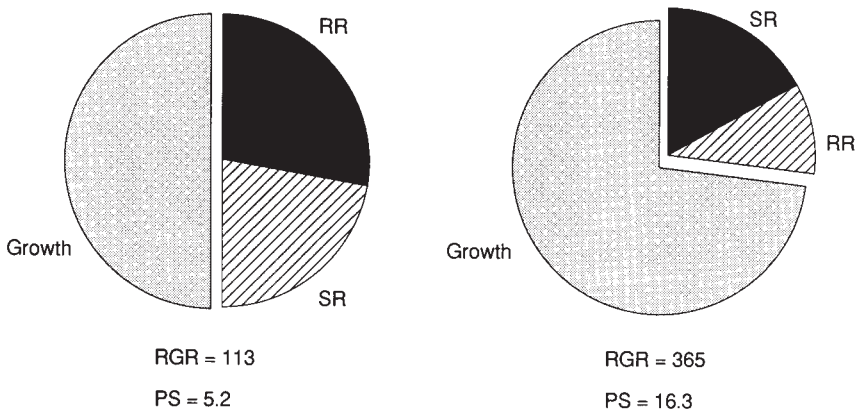


Figure 7 The carbon budget of a slow-growing species (*Corynephorus canescens*, left) and a fast-growing species (*Galinsoga parviflora*, right). In the upper line the RGR of these species is given (expressed in mg g⁻¹ day⁻¹). The second line gives the daily gross CO₂ fixation (mmol (g plant)⁻¹). (After Poorter *et al.*, 1990.)

B. Interrelations

Up till now we have treated the different physiological and morphological aspects as being independent of each other. This is a simplified view, as there are numerous interrelations. For example, a shift in biomass allocation from leaves to roots implies a decrease in the photosynthetically active area and an increase in the respiratory burden. Consequently, a decrease in the rate of carbon fixation and growth of such a plant is expected. At the same time, a high allocation to roots may ensure better access to nutrients and water, which may result in an increased plant nitrogen concentration, a higher photosynthetic capacity per unit leaf area and also a higher stomatal conductance. Moreover, there may be a decrease in self-shading. Consequently, the rate of photosynthesis per unit leaf area will increase. Also, root biomass is generally energetically cheaper to construct (Poorter and Bergkotte, 1992), so that growth rate will not decrease to the same extent as LWR decreases.

Another simplification we have made so far is to compare different types of plants over a limited time course. Investment of biomass in compounds that reduce herbivory or increase a plant's stress tolerance then inevitably leads to a decrease in the rate of photosynthesis per unit plant weight (Section IX.D). However, due to these investments, the life expectancy of a leaf increases, the net result being a possibly similar or even higher rate of photosynthesis integrated over the entire life span of a leaf (Schulze, 1982).

Strong correlations between different plant traits do not necessarily imply causal relations. For example, the correlation of RGR with SLA is probably partly fortuitous. Based on the conventional growth analysis (Eqs. (1)–(5)), we conclude that variation in SLA is the main cause for inherent variation in RGR. Simplified, it means that an increase in leaf area relative to leaf weight increases the growth rate. From a mechanistic point of view this statement is not entirely correct. Although photosynthesis indeed is an area-related process, the actual quantum capture and CO₂-fixation require, light-harvesting complexes, the coupling factor, Rubisco and other photosynthetically active components (Section IX). As this photosynthetic machinery incorporates the major part of a leaf's organic nitrogen, PNUE and leaf organic nitrogen may be used as a good approximation of the efficiency and size of the photosynthetic machinery (Section IX). Fast-growing species have both a higher PNUE and a higher organic nitrogen concentration. These two parameters appear to be closely correlated with SLA and, combined, show the same 2.2-fold variation for the nine species presented here, as found for SLA. This correlation partly reflects a causal relation, in so far as a high SLA coincides with a low concentration of chlorophyll per unit leaf area (Poorter *et al.*, 1990), which

reduces internal shading and therefore increases PNUE (Section IX.B). However, it seems likely that the strong positive correlation between RGR and SLA is also partly fortuitous, in that SLA correlates merely in a non-causal manner with a number of other factors which really determine RGR. Clearly, the parameters of Eq. (5) cannot provide the full answer to the causes of inherent variation in RGR.

XIV. SPECIES-SPECIFIC PERFORMANCE UNDER SUBOPTIMAL CONDITIONS

Up till now we have paid most attention to plants grown under conditions favourable for plant growth. But how do fast- and slow-growing species perform under suboptimal conditions?

When grown at a low nutrient concentration in the environment, the RGR of potentially fast-growing species is reduced more than that of slow-growing ones (e.g. Christie and Moorby, 1975; Robinson and Rorison, 1987; Boot and Mensink, 1991). However, the inherently fast-growing species are still growing faster than slow-growing ones. This seems to be the general trend (Mahmoud and Grime, 1976; Chapin, 1983; Chapin *et al.*, 1983; Berendse and Elberse, 1989; C.A.D.M. van de Vijver, R.G.A. Boot and H. Poorter, unpublished; but see Hommels *et al.*, 1990; Muller and Garnier, 1990). This raises the question whether similar results would have been obtained in a situation where a fast-growing species competes with a slow-growing one under nutrient stress. This question will be addressed in Section XV.A.

The higher RGR of the inherently fast-growing *Holcus lanatus*, in comparison with the slow-growing *Deschampsia flexuosa*, at a low nutrient supply is explained by differences in LAR (C.A.D.M. van de Vijver, R.G.A. Boot and H. Poorter, unpublished). This is probably true for most comparisons (Christie and Moorby, 1975; van Andel and Biere, 1989). However, there are very few comparative data showing the cause of the higher RGR of fast-growing species at low nutrient supply.

When grown at a low quantum flux density, fast-growing sun species have a similar RGR to slow-growing shade species (Pons, 1977). In extreme cases, such as that of the fast-growing tropical pioneer tree *Cecropia obtusifolia*, the RGR declines to a very low rate when plants are grown in the understorey, rather than large gaps. This is due to the decrease in NAR (Popma and Bongers, 1988). The successful performance of most shade species in shaded habitats is likely to be due to a different response of germination, stem elongation and other processes, to light quality,

rather than to quantum flux density (cf. [Fitter and Ashmore, 1974](#); [Pons, 1977](#)).

XV. THE ECOLOGICAL CONSEQUENCES OF VARIATION IN POTENTIAL GROWTH RATE

A. What Ecological Advantage can be Conferred by a Plant's Growth Potential?

The ecological advantage of a high RGR seems straightforward: fast growth results in the rapid occupation of a large space, which is advantageous in a situation of competition for limiting resources. A high RGR may also facilitate rapid completion of the life cycle of a plant, which is essential for ruderals. But what is the survival value of slow growth? [Grime and Hunt \(1975\)](#) and [Chapin \(1980, 1988\)](#) mention several possibilities:

- (i) Slow-growing species make modest demands and will therefore less likely exhaust the available resources, e.g. nutrients. However, this does not seem to be an evolutionary stable strategy, as a neighbouring individual with a faster nutrient uptake could absorb most nutrients (cf. [Schulze and Chapin, 1987](#)). Moreover, these modest demands cannot explain slow growth under, e.g. alpine or saline conditions.
- (ii) Slow-growing species function closer to their optimum than fast-growing species in an adverse environment. However, the "ecological" optimum of a plant species often differs from its "physiological" optimum. As the physiological optimum of slow-growing species more or less equals that of fast-growing species ([Grime and Hunt, 1975](#)), and all plants, especially fast-growing species, have a great ability to adapt to different environmental conditions ([Bradshaw, 1965](#); [Grime *et al.*, 1986](#); [van der Werf, 1992a](#)), we do not expect fast-growing species to be at a disadvantage in such cases. In fact, both in growth analyses ([Section XIV](#)) and in short-term competition experiments ([Mahmoud and Grime, 1976](#); [Berendse and Elberse, 1989](#)) carried out at a limiting nutrient supply, potentially fast-growing species grow faster and have a greater competitive ability than slow-growing ones.
- (iii) Slow-growing species incorporate less photosynthates and nutrients into structural biomass and may thus form reserves for later growth, enabling them to maintain physiological integrity during periods which severely restrict growth, e.g. low nutrient

availability. However, under adverse conditions growth is restricted before photosynthesis, causing sugars to accumulate (Chapin *et al.*, 1986b; McDonald *et al.*, 1986). Hence, it is unlikely that survival during periods of nutrient shortage depends on storage of photosynthates. The presence of stored nutrients may indeed buffer fluctuations in nutrient supply in the field. However, perhaps with the exception of phosphate, there is no convincing evidence that slow-growing species accumulate nutrients to a greater extent (Section VIII.A). None the less, slow-growing species may deplete their smaller resources less rapidly, due to their lower RGR. So far, data on the occurrence of fluctuations in nutrient supply and the plant's response to them are too scarce and conflicting (Grime *et al.*, 1986; Poorter and Lambers, 1986; Campbell and Grime, 1989) to allow the conclusion that an inherently low RGR has survival value in this context.

- (iv) In a low-resource environment a high growth rate cannot be realized, so a high potential RGR is a selectively neutral trait. However, as noted before, potentially fast-growing species are still growing faster than potentially slow-growing species. Fast-growing species will then attain a larger size (van Andel and Biere, 1989), which has been shown to be advantageous in terms of competition and fitness (Black, 1958; Stanton, 1984). So, although a very high RGR is not attainable, a slightly higher RGR may still be of advantage.

We conclude that a low potential growth rate *per se* does not confer ecological advantage. Why then do slow-growing species occur more frequently in unfavourable habitats than fast-growing ones? An alternative explanation for the observed differences in potential growth rate is that not RGR itself, but rather one of the components linked with RGR, has been the target of selection (Lambers and Dijkstra, 1987; cf. Grime, 1979).

B. Selection for Traits Associated with a Low SLA

The most likely trait selected for is SLA, as variation in this trait is closely correlated with that in RGR (Section V; cf. Poorter, 1989; Poorter and Remkes, 1990).

In a situation where, water or nutrients are limiting, conservation of the scarce resource is at least as important as its capture. Hence, plants under water stress should decrease their transpiration (von Willert *et al.*, 1992). But also for nutrients it has been shown that unproductive species

are more successful due to less leaf turnover, so that nutrient losses are restricted (Monk, 1966; Berendse *et al.*, 1987; Karlsson and Nordell, 1987; Aerts and Berendse, 1989). How can turnover be decreased? This depends on the environmental factor which affects leaf longevity.

Herbivory can be reduced by increasing leaf toughness (Coley, 1983; Grubb, 1986), accumulating palatability-reducing compounds (Coley, 1987; Waterman and McKey, 1989) and investment in leaf hairs (Woodman and Fernandes, 1991) or thorns. The abrasive effects of high wind speeds can be reduced by investment in fibre (Woodward, 1983; Pammenter *et al.*, 1986). Trampling resistance may be the result of a large amount of cell wall material per cell (Dijkstra, 1989). Transpiration can be decreased and water use efficiency can be increased by the construction of leaf hairs or epicuticular waxes (Ehleringer, 1983; Richards *et al.*, 1986; Ehleringer and Cook, 1990). Epicuticular waxes may also serve a function by decreasing damage by ultraviolet light, preventing contact between rain water and the interior of a leaf and so restricting leaching of nutrients out of a leaf (Mulroy, 1979). Furthermore, waxes may confer disease resistance (Carver *et al.*, 1991) and diminish deleterious effects of salt spray (McNeilly *et al.*, 1987). Each of these additional investments increases the leaf's longevity, but decreases SLA with a concomitant decrease in the rate of photosynthesis per unit leaf weight. Consequently, all of these inherent adaptations to adverse conditions diminish the plant's growth potential, but positively influence its fitness.

Is there any indication that plants without these types of adjustment could survive in unfavourable habitats? This would require introduction of plants that only differ in one specific trait in different environments. However, such isogenic genotypes are not available, and variation in one trait could be expected to affect related traits (Section VIII.B). The best ecological information available is that from introduction of foreign species, e.g. the introduction into Venezuela of two African C₄ species. The introduced species with a high SLA have outcompeted a native C₄ species, which possesses a low SLA, in relatively fertile places, but not in more infertile habitats (Baruch *et al.*, 1985). On subantarctic islands the introduced grass *Agrostis stolonifera*, with a high SLA, is able to survive in the wind-sheltered places but is not found outside these shelters, whereas *Agrostis magellanica*, characterized by a lower SLA due to more sclerenchyma, occurs in the wind-swept parts of these islands (Pammenter *et al.*, 1986). Similarly, *Stephanomeria malheurensis*, a species with a relatively low SLA which occurs in the same environment as its progenitor *S. exigua* ssp. *coronaria* with a higher SLA, is restricted to sites where it may encounter greater stress. The number of individuals of *S. exigua* ssp. *coronaria* by far exceeds, that of *S. malheurensis*, though their RGR is very similar (Gottlieb, 1978).

Here again, a high SLA appears associated with competitive ability and a low SLA with persistence.

C. Selection for Other Traits Underlying RGR

It is likely that other traits underlying RGR have also been the target of natural selection. For example, the relatively high RWR of slow-growing species is a cause of their low RGR (Section VII.A). However, RWR is a rather plastic trait, especially in fast-growing species, so that correlations between plant performance and RWR may reflect phenotypic, rather than inherent variation.

In so far as a high RWR reflects a greater ability to compete for soil-derived resources (Baan Hofman and Ennik, 1980, 1982; Aerts *et al.*, 1991), it may be of advantage in specific environments. Also, if indeed slow-growing species exude specific compounds which effectively release nutrients from a nutrient-poor soil (Section XI.A), this trait which reduces RGR may be selected for at nutrient-poor sites. Exudates, lute volatiles, may also have allelopathic effects and aid a plant to thrive in an environment amongst competitors.

A low nitrogen concentration in the leaf, though reducing the photosynthetic capacity, may add to the leaf's longevity by decreasing herbivory (Section VIII.B), and thus the photosynthetic yield during the leaf's entire life span may be higher when the leaf nitrogen concentration is relatively low.

These patterns of investment, which inexorably reduce the plant's growth potential, tend to add to a species' success in nutrient-poor or and environments where losses due to herbivory severely reduce the plant's fitness. Thus, they imply a trade-off between growth potential and adaptation to specific habitat features that limit growth.

D. Consequences of a High Growth Potential for Plant Performance in Specific Environments

Fast-growing species often grow in competitive situations in a vegetation which develops a high leaf area index during the season. Optimization of the use of nitrogen for photosynthesis and maximization of production then requires the discharge of the oldest, shaded leaves and retranslocation of a part of the N to the youngest, more exposed leaves (Hirose and Werger, 1987; Hirose *et al.*, 1988; Pons *et al.*, 1989). Under such circumstances, where leaves function only a relatively short period, protection against adverse conditions, requiring a large investment in quantitative secondary compounds, does not lead to an increased photosynthetic return.

Consequently, in fairly dense vegetations where light capture is essential and leaf turnover is high, there is a selection pressure for leaves with a high SLA (Schulze, 1982; Poorter, 1989).

Also when grown at a limiting nitrogen supply, when the leaf area index is relatively low, fast-growing species tend to have higher rates of leaf turnover (Williamson, 1976). Here it inevitably leads to greater losses (Berendse and Elberse, 1989) and possibly ultimately to the disappearance of the fast-growing species from such environments. The rapid leaf turnover of fast-growing species in a dense canopy might depend on the same, as yet poorly understood, mechanism of N-translocation operating at a limiting nitrogen supply (cf. Horgan and Wareing, 1980; Simpson *et al.*, 1982; Kuiper *et al.*, 1988). If correct, then the poor performance of fast-growing plants in a nutrient-poor environment is the consequence of their adaptation to nutrient-rich situations.

E. A Low Growth Potential and Plant Performance in Adverse Environments, Other than Nutrient-poor Habitats

So far, we have concentrated on nutrient-poor habitats, when referring to adverse soil conditions. Although there is quite convincing information that traits associated with a low RGR confer selective advantage in some unproductive environments, it is by no means certain that this is invariably so.

Sites that are rich in heavy metals tend to be inhabited by slow-growing ecotypes (Wilson, 1988; Verkleij and Prast, 1989). However, considering the mechanisms involved in heavy-metal tolerance (Verkleij and Schat, 1990), it appears unlikely that such stress tolerance inexorably reduces an ecotype's RGR. Moreover, some cadmium-tolerant ecotypes of *Silene vulgaris* (synonymous for *S. cucubalus*) have very similar RGRs to a sensitive ecotype (Verkleij and Prast, 1989; Verkleij *et al.*, 1990). Possibly, some heavy-metal tolerant ecotypes have evolved in habitats which are not only rich in heavy metals, but nutrient poor as well, so that their inherently low RGR is not causally related to their stress tolerance. Similarly, there is some evidence that salt-tolerant ecotypes of *Beta vulgaris* do not necessarily have a lower RGR than sensitive ones (J. Rozema, personal communication), again suggesting that stress-tolerance and a low RGR are not correlated all that tightly.

F. Conclusions

We conclude that there are trade-offs between investment in structures that lead to a high growth potential and in structures associated with

conservation of nutrients and biomass, when accumulation of large amounts of secondary plant compounds are involved. In so far as nutrient losses are associated with rapid leaf turnover there may well be consequences of efficient functioning in one environment for the performance in another. A final conclusion awaits further information on the regulation of the nitrogen concentration in leaves of fast- and slow-growing species, both as dependent on the nitrogen supply and on the light climate in the canopy.

It is likely that there are trade-offs between tolerance of adverse conditions, other than nutrient-poor conditions, and growth potential, but there is no convincing evidence that stress-tolerance and a low RGR are invariably causally related. More information on the mechanisms underlying RGR and stress-tolerance is required before further generalizations can be made.

XVI. CONCLUDING REMARKS AND PERSPECTIVES

Generalizing the above leads to suites of traits of a "typical fast-growing" and a "typical slow-growing" plant species (Table 5). Most of these traits refer to slow-growing species from nutrient-poor sites. Species from other adverse habitats may also have a lower RGR (Section II and XVE), but much less comparative data are available. The difference with species from more favourable conditions is probably less pronounced and information on special traits of such slow-growing species is scanty.

A typically fast-growing species occurs in productive habitats and, under optimum growth conditions, invests heavily in leaf area (high SLA, high LAR), possibly as a result of higher gibberellin production. Although their rate of photosynthesis per unit leaf area is not necessarily higher, fast-growing species have higher rates of photosynthesis per unit leaf weight: The higher photosynthesis is partly caused by a higher leaf organic nitrogen concentration, partly by variation in the efficiency with which nitrogen is used for photosynthesis (PNUE). One of the likely causes of the low PNUE of slow-growing species is the investment of nitrogen in compounds and structures associated with the protection of their leaves against both biotic and abiotic adverse conditions, but this is unlikely to offer the full explanation.

Fast-growing species have higher rates of shoot and root respiration, expressed per unit shoot and root weight, respectively. But their root

Table 5 Typical characteristics of fast-growing and slow-growing C₃ species, summarizing information presented in the text. Unless stated otherwise, the differences refer to plants grown at optimum nutrient supply. A ? indicates that there are indications but no hard data available in the literature

Characteristic	Fast-growing species	Slow-growing species
<i>Habitat</i>		
Nutrient supply	high	low
Productivity	high	low
<i>Morphology and allocation</i>		
Leaf area ratio	high	low
Specific leaf area	high	low
Leaf weight ratio	higher	lower
Root weight ratio	lower	higher
Investment of nitrogen in leaves (% of total plant N)	high	low
<i>Physiology</i>		
Photosynthesis/leaf area (when species of similar life form are compared)	equal	equal
Photosynthesis leaf weight	high	low
Shoot respiration/shoot weight	higher	lower
Root respiration/root weight	higher	lower
Photosynthetic nitrogen use efficiency	higher	lower
Respiratory losses (% of total C fixed)	low	high
Exudation rate/root weight	low?	high?
Ion uptake rate	high	low
Gibberellin content	high?	low?
<i>Chemical composition</i>		
Nitrogen concentration	high	low
Concentration of minerals	high	low
Water content	high	low
Carbon concentration	low	high
Concentration of quantitative secondary compounds	low	high
Concentration of qualitative secondary compounds	variable	variable
<i>Plasticity with respect to nutrient supply</i>		
of SLA	equal	equal
of allocation	high	low
of photosynthesis	high	somewhat lower
<i>Other aspects</i>		
Leaf turnover	high	low
Root turnover	?	?

respiration is not as much higher as to be expected from their much higher rate of growth and nutrient uptake. We hypothesize that slow-growing species constitutively have a rather costly uptake system which is more effective under nutrient-poor conditions.

Fast-growing species have a greater ability to adjust their biomass allocation when exposed to nutrient-poor conditions. There is no evidence that the greater plasticity of allocation of biomass and nitrogen of fast-growing species *per se* confers any disadvantage under nutrient-limited conditions. However, the leaf longevity of fast-growing species is also shorter and further reduced under nutrient-poor conditions, leading to relatively large losses of nutrients. This inefficient use of nutrients is considered one of the main reasons for the lack of success of inherently fast-growing species in nutrient-poor environments. Trade-offs between investment in photosynthetic machinery and the degree to which a plant is defended against herbivory, leaf damage due to strong winds, trampling, drought, salt and/or diseases are likely to have occurred, mainly by adaptations which decrease SLA.

A number of topics relating to characteristic differences between fast-growing and slow-growing species still need continued attention. These include the physiological mechanisms determining inherent variation in specific leaf area, biomass allocation, photosynthetic nitrogen use efficiency, root respiration, the importance of gibberellins and the life-span of the different plant organs. There is also a lack of information on the quantitative importance of losses through exudates and volatiles and their association with nutrient acquisition and interactions between a plant and other organisms. A cost-benefit analysis for symbiotic associations, as dependent on environmental conditions, is needed to evaluate their significance in the acquisition of nutrients. Further evidence is also required to substantiate our belief that biomass allocation of fast-growing species is more plastic with respect to factors other than nutrient supply. If proven correct, information on the regulation of such plasticity and on the ecological significance thereof is needed. Finally, the physiological and ecological costs and benefits of the various inherent adaptations to adverse environments warrant further research.

We have attempted to provide a general background on inherent variation in growth rate and to identify major research areas which need further investigation. Such investigations require a combined approach from ecologists, physiologists, biochemists, phytochemists and theoretical biologists. They are bound to yield information which is of great importance for our understanding of the functioning of plants, both in their natural environment and in a crop situation.

ACKNOWLEDGEMENTS

We would like to thank all colleagues who generously allowed us to use some of their unpublished data, and the following colleagues for their constructive criticism on (parts of) earlier drafts of this manuscript: Frank Berendse, Arjen Biere, René Boot, Marion Cambridge, Heinjo During, Eric Garnier, Henk Konings, Dick Pegtel, Thijs Pons, Jacques Roy, Adrie van der Werf, Marinus Werger and Chin Wong. We thank Marion Cambridge for her linguistic advice.

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