7
Growth and Allocation

1. Introduction: What Is Growth?

Plant growth results from interactions among all the processes discussed in previous chapters: 2 (photosynthesis, respiration, and long-distance transport), 3 (plant water relations), and 6 (mineral nutrition). By the same token, growth rate may control these physiological processes through its effect on plant demands for carbon, water, and nutrients, as discussed in the preceding chapters. What exactly do we mean by plant growth? **Growth** is the increment in dry mass, volume, length, or area that results from the **division**, **expansion**, and **differentiation** of cells. Increment in dry mass may not, however, coincide with changes in each of these components of growth. For example, leaves often expand and roots elongate at night, when the entire plant is decreasing in dry mass because of carbon use in respiration. On the other hand, a tuber may gain dry mass without concomitant change in volume, as starch accumulates. Discussion of "growth" therefore requires careful attention to context and the role of different processes at different times. For example, although cell divisions often initiate growth, this process by itself is insufficient to cause growth. In addition, growth requires cell elongation and the deposition of mass in the cytoplasm and cell walls which determine the increment in volume or mass. To appreciate ecophysiological aspects of plant growth, we must understand its cellular basis. Although this is a fascinating and rapidly moving field, many questions remain unanswered, as will be revealed in this chapter.

This chapter also deals with the question of why some plants grow more rapidly than others. A plant's growth rate is the result of both its genetic background and the environment in which it grows. Plants are the product of natural selection, resulting in genotypes with different **suites of traits** that allow them to perform in specific habitats. Such a suite of traits constitutes a "strategy". The term is used here, as well as elsewhere in this text, to indicate the capacity of a plant to perform effectively in a specific ecological and evolutionary context (Box 9E.1). In this chapter we discuss how genetic and environmental factors affect the growth of plants.

2. Growth of Whole Plants and Individual Organs

Plant growth can be analyzed in terms of an increase in total plant dry mass and its distribution (**allocation**) among organs involved in acquisition of above-ground or below-ground resources. In such an approach, the pattern of biomass allocation plays a pivotal role in determining a plant's access to resources and therefore its growth rate. Plant growth can also be studied at the level of individual organs or cells. Using this approach we can ask why the leaves of one plant grow faster or bigger than

H. Lambers et al., *Plant Physiological Ecology*, Second edition, DOI: 10.1007/978-0-387-78341-3_7,

those of another. The two approaches are complementary and should be integrated to highlight traits that determine a plant's growth potential.

2.1 Growth of Whole Plants

Growth analysis provides considerable insight into the functioning of a plant as dependent on genotype or environment. Different growth analyses can be carried out, depending on what is considered a key factor for growth (Lambers et al. 1989). Leaf area and net assimilation rate are most commonly treated as the "driving variables". As discussed in Sect. 4.2 of Chapter 6 on mineral nutrition, however, we can also consider the plant's nutrient concentration and nutrient productivity as driving variables. In either case, "driving variables" represent aspects of a plant's suite of traits (Sect. 3.7), rather than offering a mechanistic explanation for differences in growth rate.

2.1.1 A High Leaf Area Ratio Enables Plants to Grow Fast

We first concentrate on the plant's leaf area as the driving variable for the **relative growth rate** (**RGR**, the rate of increase in plant mass per unit of plant mass already present) (Evans 1972). According to this approach, RGR is factored into two components: the **leaf area ratio** (**LAR**), which is the amount of leaf area per unit total plant mass, and the **net assimilation rate** (**NAR**), which is the rate of increase in plant mass per unit leaf area (see Table 1 for a list of abbreviations and the units in which they are expressed):

$$\mathrm{RGR} = \mathrm{LAR} \cdot \mathrm{NAR} \tag{1}$$

LAR and NAR, in turn, can each be subdivided into additional components. The LAR is the product of the **specific leaf area** (**SLA**), which is the amount of leaf area per unit leaf mass, and the **leaf mass ratio** (**LMR**), which is the fraction of the total plant biomass allocated to leaves:

$$\mathrm{LAR} = \mathrm{SLA} \cdot \mathrm{LMR} \tag{2}$$

The NAR, which is the rate of dry mass gain per unit leaf area, is largely the net result of the rate of carbon gain in **photosynthesis** per unit leaf area (A) and that of carbon use in **respiration** of leaves, stems, and roots (LR, SR, and RR) which, in this case, is also expressed 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 the carbon concentration of the newly formed material, [C], to obtain the increase in dry mass. The balance can be completed by subtracting losses due to volatilization and exudation per unit time, again expressed on a leaf area basis. For simplicity's sake, volatilization and exudation will be ignored here, although these processes can be ecologically important to the plant's carbon budget under some circumstances. We already discussed volatile losses (Sect. 3.3 of Chapter 4B on effects of radiation and temperature) and discuss this further in Sect. 5.2; the process of exudation has been treated in Sects. 2.2.5, 2.2.6, 3.1.3, and 3.2 of Chapter 6 on mineral nutrition. The simplified equation for the net assimilation rate is

$$\mathrm{NAR} = \frac{\{A_\mathrm{a} - \mathrm{LR_a} - (\mathrm{SR} \cdot \mathrm{SMR})/(\mathrm{LAR}) - (\mathrm{RR} \cdot \mathrm{RMR})/(\mathrm{LAR})\}}{[\mathrm{C}]} \tag{3}$$

The subscript a indicates that the rates are expressed on a leaf area basis. This is a common way to express rates of CO_2 assimilation (Chapter 2A on photosynthesis). Of course, stem and root respirations are not directly related to leaf area, but rather to the biomass of the different organs. This has been resolved by multiplying the rate of stem respiration (SR) and root respiration (RR) by SMR/LAR and RMR/LAR, respectively; SMR and RMR are the stem mass ratio and the root mass ratio, i.e., the fraction of plant biomass allocated to stems and roots, respectively (Table 1). Although the net assimilation rate is relatively easy to estimate from harvest data, it is not really an appropriate parameter to gain insight into the relation between physiology and growth. Rather, we should concentrate on the underlying processes: **photosynthesis**, **respiration**, and **allocation**.

For the relative growth rate, we can now derive the following equation:

$$\mathrm{RGR} = \frac{A_\mathrm{a} \cdot \mathrm{SLA} \cdot \mathrm{LMR} - \mathrm{LR_m} - \mathrm{SR} \cdot \mathrm{SMR} - \mathrm{RR} \cdot \mathrm{RMR}}{[\mathrm{C}]} \tag{4}$$

This equation has been widely used to identify traits that are associated with genetic variation in a plant's RGR at an optimum nutrient supply as well as variation caused by environmental factors, such as light intensity, temperature, or nutrient supply.

2.1.2 Plants with High Nutrient Concentrations Can Grow Faster

In an alternative approach, the plant's nutrient concentration (mostly **plant N concentration**, **PNC**) is assumed to be a driving variable, as discussed in Sect. 4 of Chapter 6 on mineral nutrition. PNC, in combination with the nutrient productivity (mostly

Table 1. Abbreviations related to plant growth analysis and the units in which they are expressed.

Abbreviation	Meaning	Preferred units
A_a	Rate of CO_2 assimilation per unit leaf area	μmol CO_2 m^{-2} s^{-1}
[C]	Carbon concentration	mmol C g^{-1}
LAR	Leaf area ratio	m^2 kg^{-1}
LMA	Leaf mass per unit leaf area	kg m^{-2}
LMR	Leaf mass ratio	g g^{-1}
LR_a (LR_m)	Rate of leaf respiration per unit leaf area or mass	μmol CO_2 m^{-2} (leaf area) s^{-1} [nmol CO_2 g^{-1} (leaf mass) s^{-1}]
NAR	Net assimilation rate	g m^{-2} day^{-1}
NP	Nutrient productivity	g (plant mass) mol^{-1} (plant nutrient) day^{-1}
PNC	Plant nutrient concentration	mol (nutrient) g^{-1} (plant mass)
RGR	Relative growth rate	mg g^{-1} day^{-1}
RMR	Root mass ratio	g g^{-1}
RR	Rate of root respiration	nmol CO_2 g^{-1} (root mass) s^{-1}
SLA	Specific leaf area	m^2 kg^{-1}
SR	Rate of stem respiration	nmol CO_2 g^{-1} (stem mass) s^{-1}
SRL	Specific root length	m g^{-1}
SMR	Stem mass ratio	g g^{-1}

N productivity, **NP**), determines plant growth. Thus, we arrive at

$$\mathrm{RGR} = \mathrm{NP} \cdot \mathrm{PNC} \qquad (5)$$

As pointed out in Sect. 4.2 of Chapter 6 on mineral nutrition, plants differ widely in their N productivity, when grown with free access to nutrients. A high N productivity is associated with a relatively large investment of N in photosynthesizing tissue, an efficient use of the N invested in the leaves for the process of photosynthesis, and a relatively low carbon use in respiration (Poorter et al. 1990, Garnier et al. 1995).

2.2 Growth of Cells

Insights into the cellular basis of growth analysis come from studying the actual processes of growth (cell division, cell expansion, mass deposition) in greater detail.

2.2.1 Cell Division and Cell Expansion: The Lockhart Equation

Growth of leaves and roots, like that of other organs, is determined by **cell division**, **cell expansion,** and **deposition** of cell material. Cell division cannot cause an increase in volume, however, and therefore does not drive growth by itself. Rather, it provides the structural framework for subsequent cell expansion (Green 1976).

The processes of cell division and cell expansion are not mutually independent. Cells probably divide when they reach a certain size (i.e., they elongate after division and then divide again, before they have elongated substantially). This limits the developmental phase at which cell division can occur and implies that any process that slows down cell expansion inevitably leads to fewer cells per leaf or root and hence smaller leaves or roots. For example, consider a newly formed meristematic leaf cell that differentiates to produce epidermal leaf cells. Suppose this cell divides only after it doubles in cell volume, and that it has 240 hours left to undergo repeated mitoses at the point of determination. If the cell doubled in volume every 10 hours, then cell divisions will occur 24 times, which produce 2^{24} cells. If an environmental factor slows the rate of cell expansion such that the cells now take 12 hours to double in volume, however, then only 20 division cycles will occur which give rise to 2^{20} cells. Such a reduction in cell number could substantially reduce leaf surface area (Van Volkenburgh 1994).

Once a cell has divided, it can elongate and expand, provided the turgor pressure (Ψ_P, MPa) exceeds a certain **yield threshold** (Y, MPa). In cells capable of expansion, this threshold value is around 15–50% of the turgor pressure under normal conditions (no stress) (Pritchard 1994). The proportional growth rate (r, s^{-1}) is measured as the rate of increase in volume (dV, m^3) per unit volume (V, m^3); r is proportional to the difference between **turgor** and **yield threshold**. The proportional rate of

expansion ($dV/V \cdot dt$, s^{-1}) is described by the simplified **Lockhart equation**:

$$R = dV/(V \cdot dt) = \phi(\Psi_p - Y) \quad (6)$$

where ϕ is the cell-wall **yield coefficient** (MPa^{-1} s^{-1}), which is a proportionality constant that depends on biochemical and biophysical properties of the cell wall. Plant cell expansion is, therefore, a **turgor-driven** process believed to be controlled, both in extent and in direction, by the physical properties of the primary (growing) cell wall. If cells expand more in one direction than in another, the cell walls are more **extensible** (looser) in the direction in which they expand most. This simple analysis using the Lockhart equation assumes that neither water flow nor solute influx is limiting. This assumption appears to be met when plants are growing under favorable conditions. In later sections of this chapter we will discuss whether this assumption still applies under conditions of environmental stress.

Because cell expansion and cell division are closely linked, the increase in length or volume of entire leaves and other organs can be analyzed with a similar equation (Passioura & Fry 1992). Both the cell-wall yield coefficient, ϕ, and the yield threshold, Y, reflect the **extensibility** of the cell walls, as determined by their biochemical and biophysical properties. The turgor pressure, Ψ_p, or, more precisely, the difference between Ψ_p and Y, allows cell expansion. Uptake of ions into the cell maintains the turgor pressure, which tends to drop as the cell volume increases.

Turgor tends to be **tightly regulated**, particularly in growing cells (Pritchard 1994). This tight regulation of cell turgor is most likely due to modification of the activity ("gating") of **aquaporins** in the plasma membrane and tonoplast which are highly expressed in zones of rapid division and expansion (Tyerman et al. 2002, Siefritz et al. 2004). There are several examples, however, where a step-change in turgor does *not* lead to (full) readjustment to the original turgor pressure (Zhu & Boyer 1992, Passioura 1994). This probably reflects differences in original water status (Hsiao et al. 1998) or between-species and/or tissue-specific behavior. These results also point out that growth is not really controlled by turgor in the simple manner suggested by the Lockhart equation. Above the turgor threshold, the rate of cell enlargement is controlled by metabolic reactions, which cause synthesis and/or extension of wall polymers. Inside the cell, sufficient solutes must be generated to maintain turgor above the threshold.

2.2.2 Cell-Wall Acidification and Removal of Calcium Reduce Cell-Wall Rigidity

The fundamental structure of the primary (growing) cell wall is very similar in all land plants: Cellulose microfibrils are embedded in a hydrated matrix composed mostly of neutral and acidic polysaccharides and a small amount of structural proteins (Cosgrove 1999). The polysaccharides include the negatively charged cation-binding **polygalacturonic acids**. **Cellulose microfibrils**, which consist of bundles of around 50 cellulose molecules, provide the tensile strength of the cell wall. In expanding cells, the microfibrils tend to be arranged transversely, which favors expansion in a longitudinal, rather than in a radial direction. **Glycoproteins** add further strength to the cell walls. **Hemicelluloses** (i.e., polysaccharides with a glucan or similar backbone) probably bind to cellulose microfibrils and to each other by means of hydrogen bonds. Because there are many hemicellulose molecules per cellulose microfibril, the microfibrils are completely coated, making a three-dimensional net. Finally, there are several enzymes that can cleave covalent bonds that link the sugar residues of the noncellulosic polymers in the walls, and other enzymes that can join loose ends of similar polymers (Carpita & Gibeaut 1993). The growing wall possesses a remarkable combination of strength and pliancy, enabling it to withstand the large mechanical forces that arise from cell turgor pressure, while at the same time permitting a controlled polymer "creep" that distends the wall and creates space for the enlarging protoplast. Cellulose microfibrils themselves are effectively inextensible; wall expansion occurs by slippage or rearrangement of the matrix polymers that coat the microfibrils and hold them in place. Until recently this was thought to occur primarily by hydrolysis of matrix polysaccharides, but the discovery of **expansins** (enzymes involved in loosening of cell walls) has uncovered another mechanism of wall enlargement (Cosgrove 1999, 2000).

Hormonal and environmental stimuli promote growth of plant cells by inducing polymer rearrangement and loosening of the primary (growing) cell wall. Expansin's unique physical effects on plant cell walls include rapid induction of wall extension and stimulation of stress relaxation. Expansins do not progressively weaken the cell wall, nor do they cause a lasting change in wall structure, except that the wall is longer and thinner after it extends. No ligands or cofactors are necessary for expansin action. Normally, expansin is a very minor component of the cell wall; binding and activity both saturate at an expansin-protein-to-wall ratio of about 1:1000. From an architectural perspective, one might expect

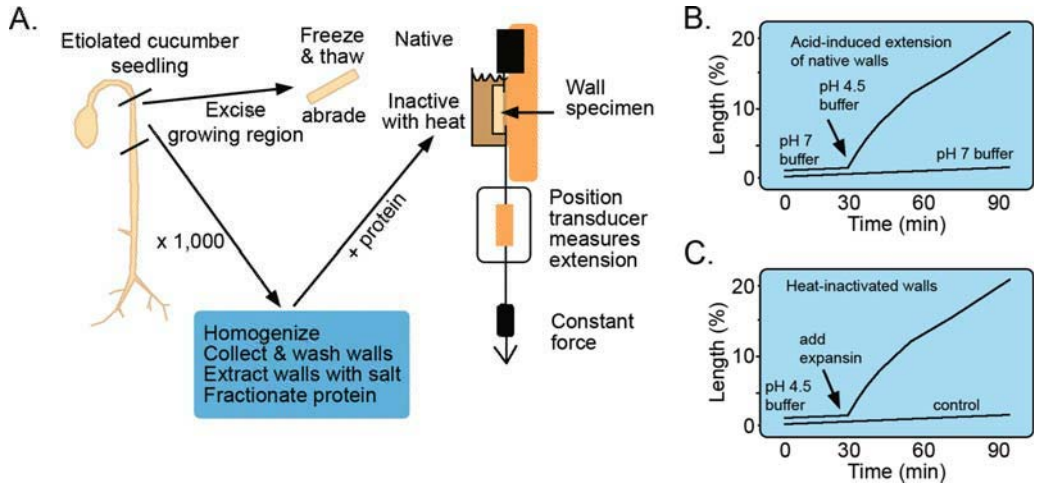


FIGURE 1. Diagram of extensometer assays. (A) The growing hypocotyl of a seedling is cut and frozen to kill the cells. The wall specimen is either directly clamped in a constant-force extensometer ("native walls") or first inactivated with a brief heat treatment before being clamped in the extensometer ("heat-inactivated walls"). Expansin protein is prepared by extraction from native walls, followed by fractionation and addition to the wall. (B) Native walls extend very little at neutral pH, but rapidly extend in acidic pH. (C) Heat-inactivated walls lack acid-induced extension, which can be restored by addition of expansin to the walls (modified after Cosgrove 2000). Reprinted with permission from *Nature* copyright 1996 Macmillan Magazines Ltd.

expansin's loosening action to result from hydrolysis of the matrix polymers that hold the cellulose microfibrils in place, but none of the available evidence supports this. The current thinking is that expansins weaken the noncovalent binding (hydrogen bonding) between wall polysaccharides, thereby allowing turgor-driven polymer creep (Cosgrove 2000).

Expansins are encoded by a gene family; expression of individual genes may be differentially regulated at various developmental stages and by diverse environmental stimuli (Sects. 5.3 and 5.6.1). Loosening of primary and secondary walls can be modulated in various ways (e.g., by changes in wall pH, secretion of molecules that affect the activity of wall enzymes, and secretion of substrates). Additionally, the wall can be modified by other enzymes that change the structure in such a way that they can no longer be affected by the wall-loosening agents: **wall stiffening** (Cosgrove 1999).

Calcium enhances cell-wall stiffening by binding to pectin components, forming **Ca-pectate complexes** (Pritchard 1994). For example, shade enhances stem elongation as a result of the removal of Ca from the cell walls. Protons also play an important role in the breaking of cross-linkages. For example, the light-induced growth of leaves (phototropism) is preceded by extrusion of protons from the cytosol into the cell wall. A low pH in the cell wall, through activation of **expansins**, induces disruption of hydrogen bonding between cellulose microfibrils and matrix polymers (Fig. 1). Hydrolytic enzymes, especially **xyloglucan endotransglycosylases**, catalyze breakage of some of the hemicellulose cross-links between cellulose molecules (Fry 2004).

The **light-induced enhancement of leaf growth**, which is preceded by the perception of light by both a red-light receptor (phytochrome) and a blue-light receptor, is due to **cell-wall acidification**, which enhances expansin activity (Fig. 1) and increases the extensibility of the cell walls (Sect. 5.1.1). Cells of stems may also respond to light, which is perceived by phytochrome, i.e., red light suppresses stem elongation and far-red light enhances it. Gibberellins enhance cell elongation, but through a different mechanism. In *Lactuca sativa* (lettuce) hypocotyls this effect of gibberellin is associated with the removal of **Ca** from the cell walls rather than with cell-wall acidification. **Cytokinins** promote and **abscisic acid** reduces the rate of **leaf expansion**, but, as with gibberellins, this is unlikely to be due to cell-wall acidification. Cytokinins and abscisic acid have either no effect or the opposite effect on **root elongation** (i.e., cytokinins tend to inhibit and ABA tends to promote root growth); in the case of ABA that may depend on the level of water stress (Sect. 5.3.2).

Phototropic reactions, which allow coleoptiles to grow toward the light, are based on greater **acidification** of the walls of cells furthest away from the light source as compared with the more proximal cells.

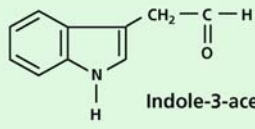
Box 7.1
Phytohormones

Many aspects of plant growth and development are controlled by internal messengers: phytohormones (Davies 2004). In the animal literature, the term hormone refers to a molecule that is produced in cells of a specific organ (gland) and that has specific effects on other cells (target cells). Phytohormones are not produced in specific glands, but in organs and tissues that serve other functions as well. The effect of phytohormones is also less specific than that of their animal counterparts. They may mediate among several environmental factors and lead to several plant responses.

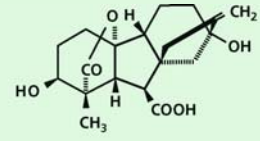
Phytohormones are characterized as

1. organic molecules produced by the plant itself
2. compounds that affect growth and development (either positively or negatively) at very low concentrations
3. compounds that act primarily in a part of the plant that differs from the site they are produced
4. compounds whose action depends on their chemical structure, rather than on the elements they contain

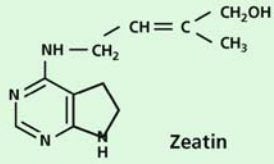
There are six groups of phytohormones (Fig. 1). The first phytohormone was discovered in the 1920s by F.W. Went (1926), who was doing a PhD with his father, F.A.F.C. Went, at Utrecht University, where the structure of **auxin** was identified. It is indoleacetic acid (IAA), termed auxin, because of its involvement in the growth of *Avena sativa* (oat) coleoptiles toward the light (auxin comes from the Greek verb to grow). It is involved in the promotion of cell growth, differentiation in the root and shoot meristem, and apical dominance. Auxin is produced in leaves and transported to the site of action through specific carrier proteins located in the plasma membrane. Localized effects, such as tropisms and tissue polarity, depend on this highly regulated transport.



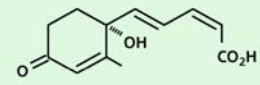
Indole-3-acetaldehyde



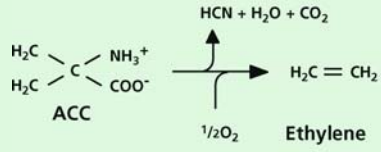
Gibberellin A_1 or GA_1



Zeatin



Abscisic acid



Ethylene

Brassinolide

FIGURE 7.1.1. The chemical structure of a representative of the six groups of phytohormones: indole-3-acetyaldehyde (IAA, an auxin), gibberellin A_1 (GA_1, one of many gibberellins, of which only a small number is physiologically active; GA_1 is the gibberellin that usually induces stem elongation), zeatin [a common bioactive cytokinin first identified in *Zea mays* (corn)], abscisic acid (ABA), ethylene (the only gaseous phytohormone) and its water-soluble precursor: 1-amino-cyclopropane-1-carboxylic acid (ACC), and brassinolide, which is the most biologically active brassinosteroid.

continued

Box 7.1 *Continued*

The **gibberellins** or gibberellic acids (GAs) derived their name from the fungus *Gibberella fujikori*, which turns dwarf rice cultivars into tall ones. It is a complex class of phytohormones of which the active compounds strongly stimulate elongation growth through an effect on both cell division and cell elongation. GA has also a key role in the first steps leading to germination of seeds.

Cytokinins were discovered in a search for a medium suitable for tissue culture, where they stimulate cell division. The bioactive members of this family of phytohormones are also involved in chloroplast maturation, the delay of senescence, leaf expansion, and several other morphogenetic processes. Root tips are a major site of cytokinin production, and the primary transport path to the site of action is in the transpiration stream.

Abscisic acid (ABA) derives its name from its stimulation of leaf abscission. This phytohormone is, however, involved in a wide range of regulatory process. ABA plays a key role in stress responses (e.g., desiccation, salinity). ABA causes stomatal closure, inhibits extension growth, and induces senescence. ABA also induces dormancy of buds and seeds.

Ethylene is the only gaseous hormone. It is produced from the water-soluble precursor 1-amino-cyclopropane-1-carboxylic acid (ACC) in an oxygen-requiring step, catalyzed by ACC oxidase. It induces senescence and inhibits cell growth at higher concentrations in most plants, but it stimulates growth in flooding-resistant plants (Sect. 7.5.7).

The hormonal status of **brassinosteroids** has been established more recently (Yokota 1997). They were first isolated in 1974 from *Brassica napus* (oilseed rape) pollen and have since been found in many species. This group of hormones stimulates growth, as evidenced by mutants with defects in brassinosteroid biosynthesis or sensitivity which are all dwarfs. They stimulate senescence, stress tolerance, and germination of seeds.

Hormonal status is also claimed for other compounds such as jasmonate, salicylic acid, and several small peptides, but this is not generally accepted (Reski 2006). These compounds play, among others, a role in plant defense against pathogens and herbivores (Chapter 9B on ecological biochemistry).

Phytohormones are important both to internally coordinate the growth and development of different organs and as chemical messengers whose synthesis may be affected when plants are exposed to certain environmental factors. Many, if not all, developmental processes in plants depend on a coordinated action of several hormones. External or internal factors need to be sensed first, which is the first step in a signal-transduction pathway, ultimately leading to the plant's response. The plant's response is not necessarily due to an effect on the rate of production of the phytohormone, but it may involve its rate of breakdown or the sensitivity of the target cells to the hormone. At a molecular level, a plant's response may involve up-regulation or down-regulation of genes coding for enzymes involved in synthesis or breakdown of the phytohormone, or genes encoding a receptor of the phytohormone. Most of these receptor proteins have recently been identified in *Arabidopsis thaliana* (thale cress).

Such a difference in acidification is based on a difference in **auxin activity** in the distal and proximal cells (Box 7.1). These examples show that cells respond to light and hormones, sometimes in interaction, by changes in cell-wall properties that, in turn, affect growth of leaf, stem, or root cells. Genetic or environmental factors that affect the cell-wall cross-linkages, and hence φ or Y, affect the rate of cell expansion and the extent to which an organ will grow. Environmental factors such as hypoxia, water stress, and light affect leaf or stem growth exactly in this manner (Sect. 5).

Cell-wall extensibility declines with age of the cells, so that the walls of older cells no longer respond to cell-wall acidification. This is associated with changes in chemical composition (e.g., incorporation of more galactose). Formation of **phenolic cross-links** between wall components might also play a role, as do **extensins**, which are rigid cell-wall glycoproteins that are particularly abundant in secondary cell walls. A wide range of environmental factors, including water stress, flooding, and soil compaction, affect leaf growth through their effect on cell-wall extensibility, as discussed later in this chapter (Pritchard 1994).

2.2.3 Cell Expansion in Meristems Is Controlled by Cell-Wall Extensibility and Not by Turgor

The growth rate of individual cells along a growing root tip varies considerably. A pressure probe that

measures the **turgor pressure** in individual growing root cells shows that the turgor varies little along the growing root. Changes in **cell-wall mechanical properties**, rather than in turgor, must therefore be responsible for the immediate control of the expansion rate of roots (Pritchard 1994).

Removal of minute quantities of sap from expanding cells shows that the **osmotic component of the water potential** becomes less negative by approximately 15% during cell expansion. This change is small, compared with that in cell volume during expansion, and it results from the drop in concentration of K^+ by about 50%. The concentration of other solutes is constant, showing that solute uptake into the expanding cells occurs at just about the same rate as that of water. There is little information to indicate which processes affect the cell-wall properties of roots. It may be similar to the situation in leaves, where cell-wall acidification plays a major role. On the other hand, Ca might play a role, as it does in hypocotyls.

As the cells expand, more cell-wall material is deposited, so that the cell-wall thickness remains approximately the same during the expansion phase. Further **deposition of cell-wall material** may occur after the cells have reached their final size which causes the cell walls to become thicker.

2.2.4 The Physical and Biochemical Basis of Yield Threshold and Cell-Wall Yield Coefficient

From a physical point of view, the parameters ϕ, the cell-wall yield coefficient, and Y, the yield threshold, in the Lockhart equation make intuitive sense. They can also be demonstrated experimentally, by using a pressure probe to determine turgor in the growing zone. The Lockhart "parameters" often behave as "variables", however (i.e., the relationship between r and P is often nonlinear) (Passioura 1994). What exactly do these "parameters" mean?

In hypocotyl segments of *Vigna unguiculata* (cowpea) the cell-wall mechanical properties are affected by the phytohormones auxin and gibberellin (Box 7.2). In segments that are deficient in endogenous gibberellin, **auxin** only affects the **yield threshold**, but not the yield coefficient. As a result the effect of auxin is only half that in segments with normal gibberellin levels. After pretreatment with **gibberellin**, auxin does affect the **yield coefficient**. These results suggest that auxin decreases the yield threshold independently of gibberellin, but that it increases the yield coefficient only in the presence of gibberellin (Okamoto et al. 1995). In the same tissue, both the yield coefficient and the yield threshold are affected by the **pH** in the cell wall. Both parameters are also affected by exposure to high temperature and proteinase, but not in the same manner. That is, a brief exposure to 80°C affects the yield threshold, but not the yield coefficient. Exposure to proteinase affects the yield coefficient, but not the yield threshold. These results suggest that the two cell-wall mechanical properties are controlled by two different proteins, both of which are activated by low pH (Okamoto & Okamoto 1995).

2.2.5 The Importance of Meristem Size

As discussed in previous sections, cell elongation depends on an increase in cell-wall extensibility. A more rapid rate of cell elongation may lead to a higher rate of leaf expansion or root elongation. A higher rate of leaf expansion or root elongation, however, is not invariably due to greater cell-wall extensibility. If more cells in the meristem divide and elongate at the same rate, this also results in higher rates of expansion. Indeed, variation in growth can be associated with variation in **meristem size** (i.e., the number of cells that divide and elongate at the same time). In a comparison of the growth of *Festuca arundinacea* (tall fescue) at high and low N supply, the major factor contributing to variation in leaf elongation is the size of the meristem (Fig. 2A). Along these lines, two genotypes of *Festuca arundinacea* that differ in their rate of leaf elongation by 50% when grown at high nutrient supply differ in the number of cells that elongate at the same time, whereas the rate of elongation of the expanding cells is fairly similar (Fig. 2B). Similarly, the number of meristems can be an important determinant of whole-plant growth rate.

3. The Physiological Basis of Variation in RGR–Plants Grown with Free Access to Nutrients

Plant species characteristic of **favorable environments** often have inherently higher maximum relative growth rates ($\mathbf{RGR_{max}}$) than do species from less favorable environments (Parsons 1968, Grime & Hunt 1975). For example, inherently slow growth has been observed in species characteristic of nutrient-poor (Grime & Hunt 1975), saline (Ball & Pidsley 1995), and alpine (Atkin et al. 1996) environments. It is clear from Equations (1) and (2) that a high RGR could be associated with a high NAR (reflecting high photosynthesis and/or

Box 7.2
Phytochrome

Plants monitor various aspects of the light climate, and they use this information to adjust their growth and reproduction to environmental conditions. Phytochrome is one of the systems in plants that allow them to gain information about their light environment. It was discovered by Butler et al. (1959) as the photoreceptor involved in red to far-red reversible reactions. Other photoreceptors have been identified more recently (cryptochromes and phototropins; Jiao et al. 2007). In vivo the phytochrome chromophore exists in two different photoconvertible forms (Fig. 1): the red-light (R) absorbing form (P_r) and the active far-red (FR) light-absorbing form (P_{fr}). Other transformation processes are the synthesis of phytochrome as P_r and its breakdown as P_{fr}. Conversion of P_{fr} to P_r can also take place independent of light, as the process of dark reversion (Fig. 1). The main function of phytochrome is the detection of the presence of competing neighbors and mediation of a response known as shade avoidance (Sect. 5.1.1). This is achieved by the perception of the presence of light per se, its spectral composition, its irradiance level, and its direction (Ballaré 1999). Phytochrome is also involved in the perception of daylength. It plays a key role throughout the life cycle of plants, from seed maturation, dormancy, and germination, seedling development, during vegetative growth, and on to the control of flowering and senescence.

In *Arabidopsis thaliana* (thale cress) five genes encoding different apoproteins of phytochrome have been identified: *PHYA–PHYE*. They have

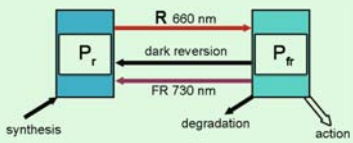


FIGURE 1. Conversion of phytochrome between the red (R) and far-red (FR) absorbing forms of phytochrome (P_r and P_{fr}, respectively). Phytochromes are synthesized in the P_r form and broken down in the P_{fr} form. Absorption of R (peak sensitivity 660 nm) and FR (peak sensitivity 730 nm) generates photoconversions of the chromophore. P_{fr} is the biologically active form that migrates to the nucleus where it promotes transcription.

different and partly overlapping functions during the various developmental stages. PhyA is easily degraded in the P_{fr} form, but phyB is more stable and can be subject to repeated photoconversions. The use of mutants lacking one or more phytochromes has been a powerful tool in unraveling their functions. *Arabidopsis thaliana* has an extreme shade-avoiding phenotype when all phytochrome is absent due to a mutation in the synthesis of the chromophore, even to the extent that the plant no longer has a rosette habit. The presence of phytochromes in the P_{fr} form is apparently necessary for attaining a normal light-grown phenotype (Smith 2000).

The more abundant phyB is the principal regulator of the classical R–FR reversibility of seed germination in the so-called low fluence response (LFR; Sect. 2.5 of Chapter 8 on life cycles). A similar role has been identified for phyE. Buried seeds can detect extremely low quantities of light in the so-called very low fluence response (VLFR) where phyA is the actor. Exposures to a light dose of 0.1 μmol photons m^{-2} are effective in these sensitized seeds, whereas the LFR operates in the 100–1000 μmol m^{-2} range (Sect. 2.5 of Chapter 8 on life cycles). Phytochrome A is also important for the high-irradiance response (HIR) that inhibits germination under prolonged exposure to light of high irradiance (Fig. 2A; Franklin & Whitelam 2004).

After germination, the etiolated seedling is highly sensitive to light due to the accumulation of phyA. De-etiolation starts after exposure to light, even before the seedling breaks through the soil surface. Subsequent hypocotyl extension is under control of the R:FR ratio (and thus canopy density), where phyB is the principal actor in inhibition of hypocotyl extension in normal daylight together with phyD, and possibly phyC, whereas phyA has a unique role, because it reduces the extension at low R:FR (Fig. 2B) (Quail et al. 1995).

A vegetative non-shade-tolerant herbaceous plant, such as *Arabidopsis thaliana* (thale cress), exposed to canopy shade develops a shade-avoiding phenotype characterized by erect growth and

continued

Box 7.2 *Continued*

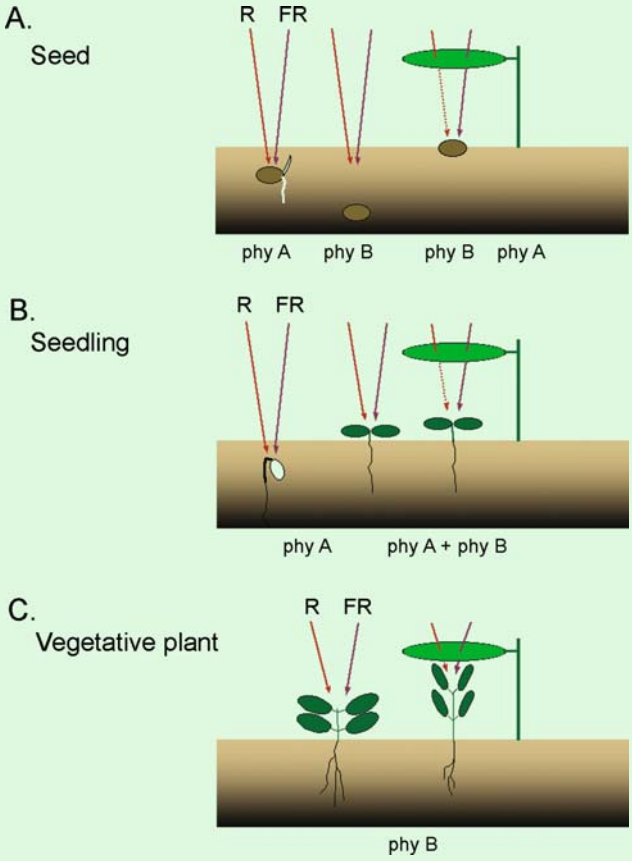


FIGURE 2. Simplified scheme to show the role of phytochromes in three developmental stages. Only phyA and phyB are depicted; for the roles of the other phytochromes see text. (A) Seed. Darkness keeps seeds in a dormant state. Daylight that is not modified by canopy filtration may break dormancy via the low (LFR; phyB) or the very low fluence response (VLFR; phyA), but canopy-filtered light with a low R:FR ratio maintains dormancy via the high-irradiance response (HIR; phyA) and the LFR (phyB). (B) Seedling. De-etiolation is initiated when the emerging seedling perceives light via the VLFR and the LFR (phyA and phyB, respectively), irrespective of canopy shade. Once emerged, hypocotyl extension is regulated via the HIR, where phyA and phyB have antagonistic effects under the low R:FR of canopy shade. (C) Vegetative plant. Shade avoidance, i.e., vertical orientation of leaves and petioles, and extension of leaves, petioles, and internodes are regulated mainly by phyB with respect to the degree of canopy shade.

an elongated shoot (Sect. 5.1.1). Mutants lacking phyB have a constitutive shade-avoiding phenotype, indicating that this phytochrome plays a major role in that response (Fig. 2C). However, the fact that these mutants still show a further shade-avoidance response in low R:FR indicates that other phytochromes are also involved. These appear to be phyD and phyE. The remaining phyA and phyC modulate the effects of the other photoreceptors (Franklin & Whitelam 2004).

low whole-plant respiration), a high SLA (i.e., high leaf area per unit leaf mass), and/or a high LMR (high allocation to leaf mass). Which of these traits is most strongly correlated with a high RGR?

3.1 SLA Is a Major Factor Associated with Variation in RGR

Several extensive surveys have shown that the main trait associated with inherently **slow growth** in temperate lowland species from nutrient-poor habitats is their **low SLA**, both in monocotyledonous and in dicotyledonous species (Poorter & Remkes 1990, Garnier 1992, Marañón & Grub 1993). The same conclusion holds for a wide range of both deciduous and evergreen tree species (Antúnez et al. 2001). Low SLA values decrease the amount of leaf area available for light interception and hence photosynthetic carbon gain, therefore reducing RGR. Although this conclusion follows logically from Equation (4), it may not provide insight into the exact **mechanisms** that account for slow growth. A further understanding of these mechanisms requires a thorough analysis of the processes discussed in Sect. 2.2.

Numerous surveys of herbaceous C_3 species show significant positive correlations of RGR with

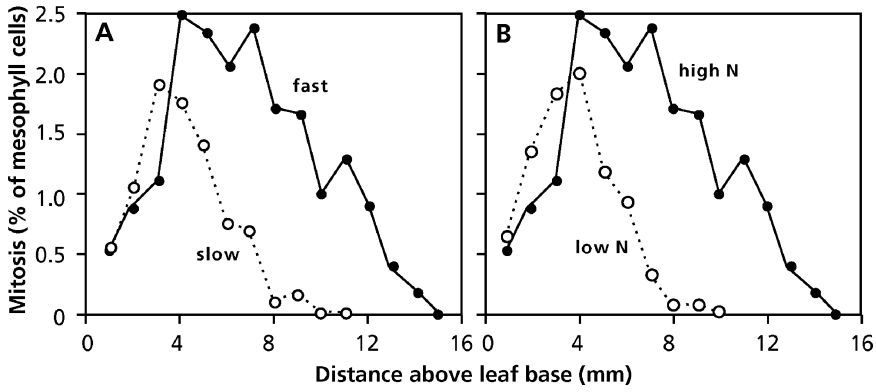


FIGURE 2. Percentage of mesophyll cells that are in mitosis as observed in longitudinal sections from the basal 40 mm of elongating leaf blades of *Festuca arundinacea* (tall fescue). A greater area under the curves indicates a larger meristem. (A) A comparison of meristem size of a fast-elongating and slow-elongating genotype. (B) Effects of N supply on leaf meristem size in the fast-elongating genotype (after MacAdam et al. 1989). Copyright American Society of Plant Biologists.

LAR, LMR, and SLA, but not with NAR (Fig. 3). For example, in a broad comparison using 80 woody species from the British Isles and Northern Spain, ranging widely in leaf habit and life form, RGR is also tightly correlated with LAR (Cornelissen et al. 1996). When comparing more productive cultivars of tree species with less productive ones, SLA, rather than photosynthesis, is the main factor that accounts for variation in RGR (Ceulemans 1989). In addition, leaf and twig architecture of the more productive trees is such that more of the light is harvested throughout the entire day (Leverenz 1992).

LMR does not correlate with RGR in monocotyledons, but it may account for some of the variation in RGR among dicotyledonous species. This reflects the phylogenetic constraints on a plant: a change in LMR appears to require a greater genetic change than that allowed by the genetic variation within a species, genus, or perhaps even family (Marañón & Grub 1993).

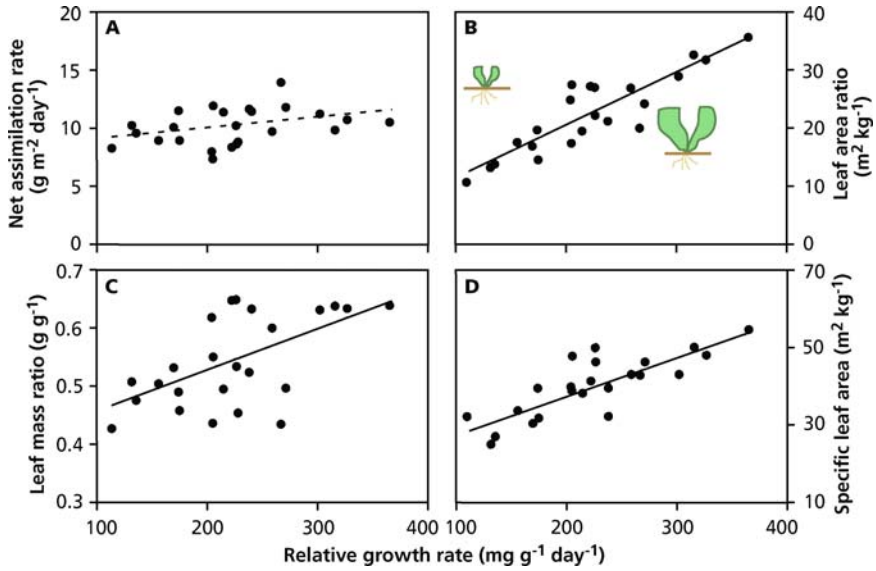


FIGURE 3. A comparison of the NAR, LAR, LMR, and SLA of 24 herbaceous C_3 species that differ in their RGR as determined on plants grown with free access to nutrients. The *broken line* indicates a nonsignificant regression; *solid lines* indicate significant regressions (Poorter & Remkes 1990).

Fast-growing species allocate relatively less to their stems, both in terms of biomass and N, when compared with slower-growing ones. Similarly, high-yielding crop varieties generally have a low allocation to stems (Evans 1980). A high allocation to stem growth reflects a diversion of resources from growth to storage in slower-growing species (Sect. 4).

In broad comparison, **NAR** is often not correlated with RGR in dicots, whereas it is in monocots. The effect of variation in SLA on the RGR of monocots is invariably stronger than that in NAR. When pairs of annual and perennial grass species that belong to the same genus are compared, the highest RGR is invariably associated with the **annual life form**. Because annuals are thought to have descended from perennial ancestors, it has been suggested that the same morphological changes that enhance a genotype's RGR have occurred repeatedly in different genera (**convergent evolution**) and that a high RGR is the more recent development (Garnier 1992, Garnier & Vancaeyzeele 1994).

3.2 Leaf Thickness and Leaf Mass Density

Variation in **SLA**, or its inverse [leaf mass per unit leaf area (**LMA**, kg m^{-2})] must be due to variation in **leaf thickness** (m) or in **leaf mass density** (kg m^{-3}) (Witkowski & Lamont 1991):

$$\mathrm{LMA} = (\mathrm{leafthickness}) \cdot (\mathrm{leaf\ mass\ density}) \quad (7)$$

When **shade leaves** and **sun leaves** are compared, leaf thickness is a major parameter in determining variation in LMA, and it reflects increased **thickness of palisade parenchyma** in sun leaves (Sect. 3.2.2 of Chapter 2A on photosynthesis). In addition, comparing alpine species, which are characteristically exposed to high light, and congeneric lowland species, variation in LMA is associated with that in leaf thickness. In comparisons of closely related species from nutrient-poor and nutrient-rich sites, however, variation in LMA is due to differences in leaf mass density (Garnier & Laurent 1994, Van Arendonk & Poorter 1994). In addition, leaf mass density also accounts for a part of the variation in LMA between shade leaves and sun leaves, between widely contrasting woody species (Cornelissen et al. 1996), and especially when comparing congeneric lowland and alpine species (Atkin et al. 1996). Comparing 53 European woody species yields a strong, positive correlation of LMA with leaf mass density, but no correlation with leaf thickness; in fact leaf mass density and leaf thickness are negatively correlated (Fig. 4). In summary,

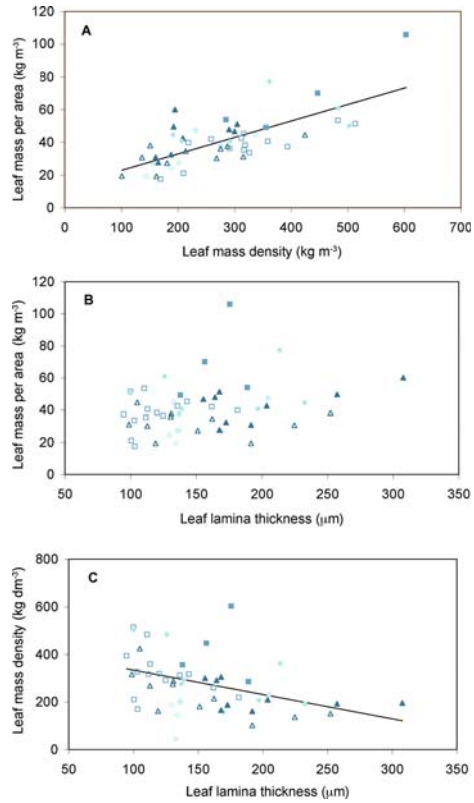


FIGURE 4. Regressions between leaf mass per area (LMA), lamina thickness, and leaf mass density. Graphs represent natural values of the variables, but regression coefficients were calculated using natural-logarithm transformations of leaf lamina thickness and leaf mass density; *open symbols* deciduous species, *closed symbols* evergreens, *squares* trees, *triangles* shrubs, *circles* subshrubs, *diamonds* climbers+scramblers (Castro-Díez et al. 2000).

differences in leaf mass density are generally the primary factor explaining differences in LMA (and its inverse: SLA), except in sun-shade comparisons, where number of cell layers (leaf thickness) is also important.

Fast-growing herbaceous species tend to have a lower tissue density in their roots as well as in their leaves (Wahl & Ryser 2000), but this pattern does not appear in woody species (Comas & Eissenstat 2004).

3.3 Anatomical and Chemical Differences Associated with Leaf Mass Density

The inherent variation in LMA and **leaf mass density** (Fig. 4) is associated with differences in both leaf

anatomy and **chemical composition** (Cunningham et al. 1999). Fast-growing species with a low LMA have relatively **large epidermal leaf cells**. Because these cells lack chloroplasts, which are a major component of the mass in the cytoplasm of mesophyll cells, they have a low density which contributes to the low leaf mass density of the fast-growing species. Slow-growing plants with a high LMA have **thicker cell walls** and contain more **sclerenchymatic cells**. These cells are small and characterized by very thick cell walls; therefore, they have a high mass density. Associated with these and other anatomical differences, the leaves of slow-growing species have more **lignin** and **cell-wall components** per unit leaf mass or area (Van Arendonk & Poorter 1994).

3.4 Net Assimilation Rate, Photosynthesis, and Respiration

As explained in Sect. 2.1.1, the **net assimilation rate** (NAR) is related to the balance of carbon gain in **photosynthesis** and carbon use in whole-plant **respiration**. Variation in NAR may, therefore, be due to variation in photosynthesis, respiration, or a combination of the two. In a broad comparison of herbaceous species (Fig. 3), there is no clear trend of NAR with RGR. Rate of photosynthesis per unit leaf area also shows no correlation with RGR (Fig. 5). **Slow-growing species**, however, use relatively more of their carbon for **respiration**, especially in their roots (Fig. 5), whereas **fast-growing** species invest a relatively greater proportion of assimilated carbon in **new growth**, especially **leaf growth**. Next to the variation in LAR (SLA and LMR), this difference in the amount of carbon required for respiration is the second-most important factor that is associated with inherent variation in RGR.

If widely different **tree species** are compared, rates of **photosynthesis** per unit leaf area are higher in **fast-growing pioneer species** than in **slower-growing climax species** (Evans 1989). SLA and allocation, however, also differ strikingly among these taxa. The lack of a correlation between photosynthesis and RGR among closely related taxa or among morphologically similar taxa (Fig. 3) indicates that these broad differences in photosynthetic rate are not a major cause of differences in RGR.

3.5 RGR and the Rate of Leaf Elongation and Leaf Appearance

The higher RGR and SLA of fast-growing grass species is associated with a more **rapid leaf elongation** (Fig. 6). The extent to which this difference in leaf expansion is associated with variation in cell-wall properties of the elongating cells is not known. Does cell-wall acidification or the removal of Ca from the cell walls play a role? Are the cells of rapidly elongating leaves more responsive to changes in pH or Ca? Does it reflect a difference in meristem size, as shown in Fig. 2? Answers to these basic questions provide rich opportunities for research to improve our basic understanding of plant growth. It is also apparent that in the fast-growing grass [*Holcus lanatus* (common velvet

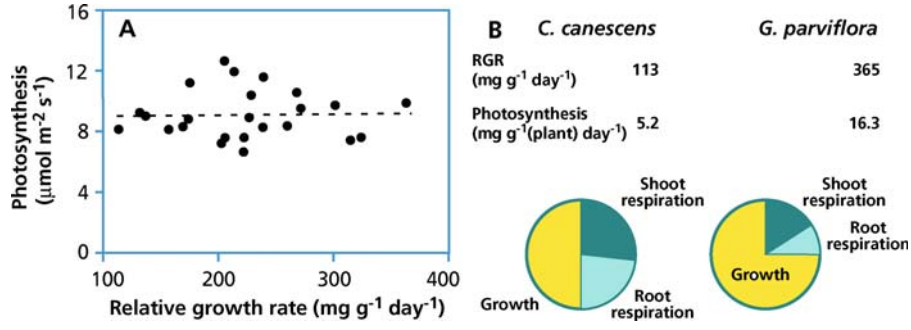


FIGURE 5. (A) The rate of photosynthesis per unit leaf area in fast- and slow-growing herbaceous species (after Poorter et al. 1990; copyright American Society of Plant Biologists). (B) The carbon budget of a slow-growing species [*Corynephorus canescens* (grey hair-grass)] and a fast-growing species [*Galinsoga parviflora* (gallant soldier)]. RGR and daily gross CO_2 fixation of these species are also shown (Lambers & Poorter 2004; Copyright Elsevier Science Ltd.)

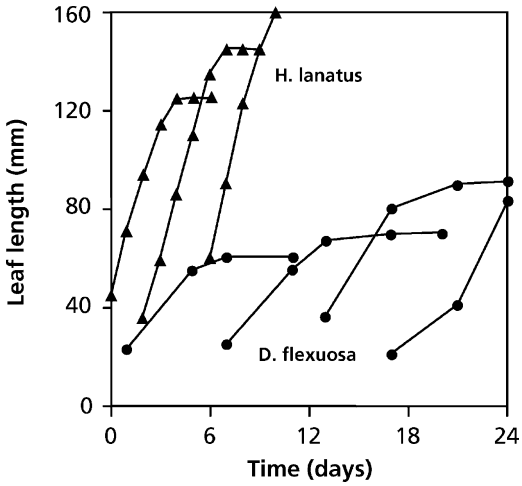


FIGURE 6. The rate of leaf elongation of a slow-growing grass species [*Deschampsia flexuosa* (tufted hair-grass), *circles*] and a fast-growing grass [*Holcus lanatus* (common velvet grass), *triangles*] (after Groeneveld & Bergkotte 1996). Copyright Blackwell Science Ltd.

grass)] the next leaf starts to grow just before the previous one has reached its final size. This typically contrasts with the pattern in slow-growing grasses [e.g., *Deschampsia flexuosa* (tufted hair-grass)], where the next leaf does not start elongating until well after the previous one has stopped (Fig. 6).

3.6 RGR and Activities per Unit Mass

The growth analysis discussed in Sect. 3.2 shows that SLA "explains" much more of the variation in RGR than do area-based measures of NAR and photosynthesis. This area-based measure is the most logical way to describe the environmental controls over capture of light and CO_2. **Economic analyses of plant growth** (the return on a given biomass investment in leaves or roots), however, more logically express resource capture (photosynthesis or nutrient uptake) per unit plant mass. This is achieved by multiplying the area-based measures of carbon gain by SLA, for example:

$$NAR_m = NAR_a \cdot SLA \quad (8)$$

Because of the strong correlation between SLA and RGR, RGR also has a strong positive correlation with NAR_m (Fig. 7A). The low NAR_m of slow-growing species in part reflects their high carbon requirement for root respiration (Fig. 5; Sect. 5.2.3 of Chapter 2B on plant respiration). Both the V_{max} for NO_3^- uptake and the net rate of NO_3^- inflow show a strong correlation with RGR_{max} (Fig. 7B,C). This correlation is probably a result, rather than the cause of variation in growth rates (Sect. 2.2.3.2 of Chapter 6 on mineral nutrition; Touraine et al. 1994). The positive correlations between RGR_{max} and mass-based activity of both roots and leaves hold for monocots and dicots (Fig. 7A–C). By contrast, there is no correlation of RGR_{max} with biomass allocation to roots and leaves for monocotyledonous species (Fig. 7D), whereas RGR_{max} decreases with increasing biomass allocation to roots in dicotyledonous species (Fig. 7E).

These correlations result from **rapidly growing plants** producing leaves and roots with relatively large allocation to metabolically active components, rather than to cell walls and storage (Fig. 4). As a result, they have leaves with a high mass-based photosynthetic capacity and roots with a high mass-based capacity for N inflow. It is the balance of net mass-based carbon gain (leaf photosynthesis minus total plant respiration, NAR_m) and mass-based maximum rate of NO_3^- inflow (NIR_m) in combination with the pattern of root:leaf allocation (Fig. 7E,F) that accounts for differences in RGR_{max}. The limited data available suggest that NIR_m has a stronger correlation with RGR_{max} than does NAR_m. This is evident from the positive correlation between RGR_{max} and the ratio of mass-based specific ion uptake rate and mass-based net assimilation rate (Fig. 7D).

3.7 RGR and Suites of Plant Traits

Our analysis of the correlations of RGR_{max} with plant traits suggests that SLA is the key trait because it enables the plant to expose a large leaf area to light and CO_2 per given biomass invested in leaves. Certain other traits, however, also correlate positively with RGR_{max} (e.g., mass-based measures of photosynthesis and nutrient uptake), whereas some traits are negatively associated with RGR_{max} (e.g., leaf mass density due to support tissues and root respiration). These observations suggest that there is a **suite of plant traits** associated with rapid growth (high SLA, high mass-based rates of photosynthesis, and nutrient uptake), whereas other traits are typically associated with slow growth (greater investment in cell walls and fiber) (Lambers & Poorter 2004). These dichotomies suggest a **trade-off** between traits that promote rapid growth and those that promote persistence.

Due to their greater investment in carbon-rich compounds, such as lignin, and less accumulation of minerals, the carbon concentration of the slow-

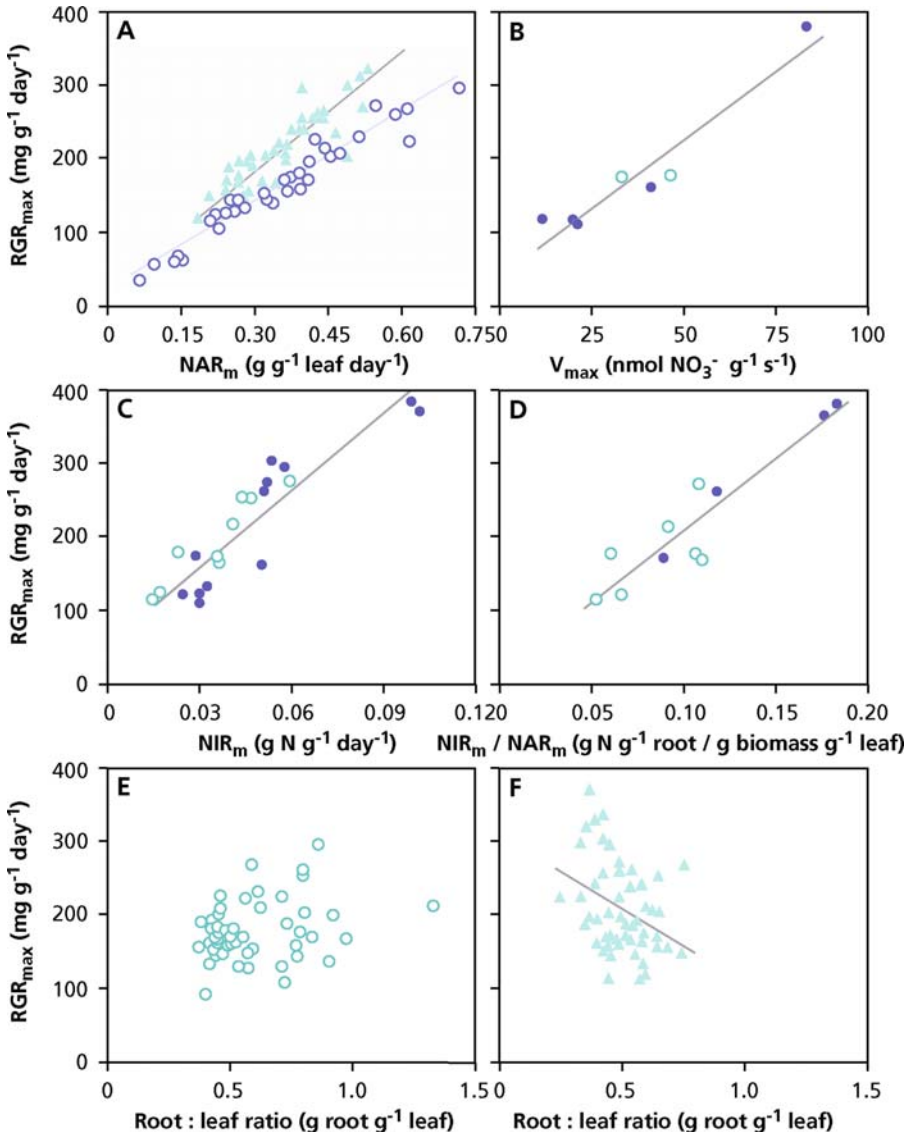


FIGURE 7. Correlation between maximum relative growth rate (RGR_{max}) and (A) mass-based net assimilation rate (NAR_m), (B) mass-based maximum rate of NO_3^- uptake (V_{max}), (C) mass-based specific NO_3^- inflow rate (NIR_m), (D) the ratio of NIR_m/NAR_m, and (E, F) the ratio of biomass allocation to roots and leaves for 51 monocotyledonous (E) and 53 dicotyledonous (F) species. Each *point* represents a separate species of monocot (*open symbols*) or dicot (*closed symbols*) grown with free access to nutrients (redrawn after data synthesized by Garnier 1991).

growing species is higher than that of fast-growing ones. This is an additional, albeit minor, factor that contributes to their low growth potential. There may well be differences in exudation and volatilization, but their quantitative significance in explaining variation in RGR is generally small, except for species with cluster roots (Sect. 2.2.5.2 of Chapter 6 on mineral nutrition).

4. Allocation to Storage

Up to now in this chapter, we have only dealt with allocation of resources to structural components of the plant, during vegetative growth. Plants, however, also channel some of their resources to storage compartments, where the stored

resources are available for future growth. Plants store both carbon and nutrients, but there is a wide variation in the amount and kind of resources that are stored and in the organ where the storage predominantly takes place: leaves, stems, roots, or specialized storage organs. We will first discuss the concept of storage and its chemical nature and then describe differences in the role of storage in annuals, biennials, and perennials.

4.1 The Concept of Storage

We define **storage** as resources that build up in the plant and can be mobilized in the future to support biosynthesis (Chapin et al. 1990). There are three general categories of storage:

1. **Accumulation** is the increase in compounds that do not directly promote growth. Accumulation occurs when **resource acquisition** exceeds **demands** for growth and maintenance (Millard 1988).
2. **Reserve formation** involves the metabolically regulated synthesis of storage compounds that might otherwise directly promote growth. Reserve formation may compete for resources with growth and defense (Rappoport & Loomis 1985).
3. **Recycling** is the reutilization of compounds whose immediate physiological function contributes to growth or defense, but which can subsequently be broken down to support future growth (Chapin et al. 1990).

Accumulation, also termed "interim deposition" (Heilmeier & Monson 1994), accounts for much of the short-term fluctuations in chemical composition of plants [e.g., the daily fluctuation of starch in chloroplasts (Sect. 2.1.4 of Chapter 2A on photosynthesis) or of NO_3^- in vacuoles (Sect. 2.2 of Chapter 6 on mineral nutrition)]. Accumulation allows a relatively constant export rate of carbohydrates from source leaves throughout the 24-hour cycle, despite the obvious diurnal pattern of photosynthetic carbon gain (Fondy & Geiger 1985). Carbohydrate accumulation also occurs when conditions favor photosynthesis more than nutrient acquisition (Heilmeier & Monson 1994). This accounts for accumulation of starch during sunny weather and its depletion under cloudy conditions. On the other hand, N accumulation, also termed "luxury consumption", occurs after pulses of N availability or when N supply exceeds the capacity of the plant to utilize N in growth. In a Mediterranean climate, nutrient uptake predominantly occurs in the wet season, whereas growth occurs later in the year (Mooney & Rundel 1979); this obviously requires nutrients to be stored. Although accumulation may explain many of the short-term changes in storage, it is less important over time scales of weeks to years. Over these longer time scales, capacities for photosynthesis and nutrient uptake adjust to plant demand, thus minimizing large long-term imbalance between carbon and nutrient stores.

Reserve formation diverts newly acquired carbon and nutrients from growth or respiration into storage. This can occur when rates of acquisition are high and vegetative growth is slow and during periods of rapid vegetative growth, often in competition with it. Grafting experiments clearly demonstrate this competition between storage and growth. For example, roots of sugar beet (*Beta vulgaris*), which allocate strongly to storage in a taproot, decrease shoot growth when grafted to shoots of a leafy variety of the same species (chard). On the other hand, chard roots, which have a small capacity for storage, cause grafted sugar beet shoots to grow larger than normal (Rappoport & Loomis 1985). Stored reserves make a plant less dependent on current photosynthesis or nutrient uptake from the soil and provide resources at times when growth demands are large, but when there are few leaves or roots present to acquire these resources, such as in early spring in cold climates. Stored reserves also enable plants to recover following catastrophic loss of leaves or roots to fire, herbivores, or other disturbances. Finally, stored reserves enable plants to shift rapidly from a vegetative to a reproductive mode, even at times of year when conditions are not favorable for resource acquisition.

Recycling of nutrients following **leaf senescence** allows reutilization of about half of the N and P originally contained in the leaf (Sect. 4 of Chapter 6 on mineral nutrition), but it is a relatively unimportant source of carbon for growth (Chapin et al. 1990). These stored nutrients are then a nutrient source for developing leaves. For example, in arctic and alpine plants 30–60% of the N and P requirement for new growth comes from retranslocated nutrients. Reserve formation and recycling allow plants to achieve rapid growth following snowmelt, despite low soil temperatures that may limit nutrient uptake from the soil (Chapin et al. 1986, Atkin 1996).

4.2 Chemical Forms of Stores

In Sect. 4.1 we demonstrated that there are several types of controls over carbon and nutrient stores (accumulation, reserve formation, and recycling). The chemistry and location of stored reserves, however, may be similar for each of these processes.

Carbohydrates are stored as **soluble sugars** (predominantly sucrose), **starch**, or **fructans**, depending on the species; fructans (polyfructosylsucrose) are only found in some taxa: Asterales, Poales, and Liliales. Storage of carbohydrates as sucrose [e.g., in the taproot of *Beta vulgaris* (sugar beet)] coincides with the accumulation of KCl in the apoplast, so that cell turgor is maintained, despite the accumulation of vast amounts of osmotic solutes inside the storage cells (Leigh & Tomos 1983). Stored carbohydrates in (tap)roots, e.g., of *Medicago sativa* (alfalfa) and *Lolium perenne* (perennial ryegrass), are predominantly used to support root respiration, rather than export to the shoot (Avice et al. 1996b, Schnyder & De Visser 1999). The capacity for storage depends on the presence of a specific organ, such as a stem, rhizome, tuber, bulb, or taproot. Thus, an important cost of storage is production of the storage structure, in addition to the stores themselves. In a comparison of 92 species (15 genera) of Ericaceae in a fire-dominated Australian habitat, species that regenerate from seeds ("**seeder species**") have low starch levels in their roots (2 mg g^{-1} dry mass) when compared with "**resprouter species**" (14 mg g^{-1} dry mass), whereas no differences occur in their shoots (Bell et al. 1996). The rate of root respiration decreases greatly when the capacity to store carbohydrates in the taproot increases with increasing plant age (Steingröver 1981). This indicates that storage of carbohydrates does not invariably occur at the expense of vegetative growth, but may involve a decline in carbon expenditure in respiration.

N is stored as $\mathbf{NO_3^-}$ (especially in petioles and shoot axes of fast-growing species), when plants are supplied with rather high levels of NO_3^- from soil. At a moderate or low N availability, N is stored as **amino acids** (often of a kind not found in proteins), **amides** (asparagine and glutamine), or **protein** (enzymes such as **Rubisco**, often special **vegetative storage proteins**) (Chapin et al. 1986, Heilmeier & Monson 1994, Meuriot et al. 2004). Storage as protein involves the additional costs of protein synthesis, but has no effects on the cell's osmotic potential. In addition, proteins may serve a catalytic or structural function as well as being a store of N. Leaves contain vast amounts of Rubisco, of which some may be inactivated and not contribute to photosynthesis (Sect. 4.2 of Chapter 6 on mineral nutrition). Rubisco is not a storage protein in a strict sense, but it is nonetheless available as a source of amino acids that are exported to other parts of the plant (Chapin et al. 1990). Storage of nitrogenous compounds is sometimes considered an indication of "luxury consumption". This is misleading, however, because N-deficient plants also store some N, which they later use to support reproductive growth (Millard 1988).

P is stored as **inorganic phosphate** (orthophosphate or polyphosphate) as well as in **organic phosphate-containing compounds** (e.g., inositol phosphate) (Sect. 2.2.5.1 of Chapter 6 on mineral nutrition; Chapin et al. 1982, Hübel & Beck 1996). In vivo NMR (Sects. 2.5.2 and 4.1.3 of Chapter 2B on respiration) has been used to determine the P_i concentration in the cytoplasm and vacuoles of the root tips of *Pinus serotina* (pond pine). In P-starved plants, the P_i concentration is 0.75 mM, as compared with 1.5 mM in plants that are grown with abundant P. In the vacuoles of the root tips, on the other hand, the concentration drops from 3.4 mM to a level that is too low to determine (Ayling & Topa 1998). This shows that the vacuoles are the major storage site for P_i, and that the concentration of P_i in the cytoplasm is relatively constant over a wide range of P_i concentrations in the root environment (Lee et al. 1990).

4.3 Storage and Remobilization in Annuals

Annuals allocate relatively little of their acquired resources (carbon and nutrients) to storage which contributes to their high growth rate (Schulze & Chapin 1987). Annuals are generally short-lived, and the rapid formation of a large seed biomass ensures survival of the population and avoids periods of low resource supply.

During seed filling, carbohydrate reserves in stems are depleted, and the N invested in the photosynthetic apparatus is exported, after hydrolysis of the proteins to amino acids, which are exported via the phloem. The gradual breakdown and export of resources invested in leaves occurs during leaf **senescence**. This is a **controlled process** in plants, and it is rather different from the uncontrolled collapse with increase in age of animal cells. It ensures remobilization of resources previously invested in vegetative structures to developing reproductive

Table 2. Net export of N (mainly as amino acids and amides after protein hydrolysis) from senescing glumes, leaves, stem, and roots, and accumulation of the same amount in the grains of *Triticum aestivum* (wheat), between 9 and 15 days after flowering.

Plant part	Change in nitrogen content [μg (plant part)$^{-1}$ day^{-1}]
Glumes	−192
Leaves	−335
Stem	−193
Roots	−132
Total	−852
Grains	+850

***Source*: Simpson et al. (1983).**

structures. Roots and some parts of the reproductive structures also show a net loss of N and a decrease in nutrient uptake during some stages of seed filling (Table 2).

In addition to the use of proteins that first function in the plant's primary metabolism during vegetative growth, *Glycine max* (soybean) also has specific **vegetative storage proteins**. These vacuolar glycoproteins accumulate abundantly in bundle sheath and associated mesophyll cells and in the upper epidermis of leaves (Staswick 1990). In hypocotyls, the storage proteins accumulate in epidermal and vascular tissues. As these organs mature, the storage proteins are hydrolyzed, and the amino acids are exported (Staswick 1988, 1990). In soybean, the amount of vegetative storage proteins and the level of mRNA encoding these depend on the N supply to the plants. Wounding, water deficit, blockage of export via the phloem, and exposure to jasmonic acid (a molecule signaling stress in plants; Sect. 4.3 of Chapter 9B on ecological biochemistry) all enhance the accumulation of the proteins in leaves of soybean (Staswick et al. 1991) and *Arabidopsis thaliana* (thale cress) (Berger et al. 1995).

4.4 The Storage Strategy of Biennials

Biennials represent a specialized life history that enables them to exploit habitats where resources are available intermittently and where a small change in these environmental conditions may tip the balance toward either annuals or perennials (Hart 1977). In their first year, biennials develop a storage organ, as do perennials. In their second year, they invest all available resources into reproduction, in a manner similar to annuals.

The storage organ contains both **carbohydrates** and **N**. Do the stored reserves of C or N add significantly to seed yield? In the biannual thistle, *Arctium tomentosum* (woolly burdock), the carbohydrates stored in the taproot are important to sustaining **root respiration**, but they contribute less than 0.5% to the formation of new leaves. Carbohydrate storage only primes the growth of the first leaves, after which the next leaves grow independently of stored carbon. Of all the N invested into growth of new leaves, however, about half originates from the N that is remobilized from the storage root. The N stored in roots contributes 20% to the total N requirement during the second season. Under shaded conditions, this fraction is as high as 30%. Seed yield is most significantly correlated with total plant N content early in the second year. In shaded plants, the amount of N in the seeds is very similar to the amount stored after the first year, whereas in plants grown at normal levels of irradiance the amount of N in the seeds is about twice that which was stored (Fig. 8).

4.5 Storage in Perennials

Perennials have a large capacity for storage of both nutrients and carbohydrates which reduces their growth potential in the early vegetative stage (Rosnitschek-Schimmel 1983). Once storage of resources has been achieved, however, it enables these plants to start growth early in a seasonal climate and to survive conditions that are unfavorable for CO_2 assimilation or nutrient absorption. The stored products allow rapid leaf development when annuals depend on recently acquired carbon and nutrients (Bausenwein et al. 2001).

In the tundra sedge, *Eriophorum vaginatum* (cotton grass), amino-acid N and organic P reserves vary nearly fourfold during the growing season and provide all the nutrients required to support leaf growth in early summer, when the arctic soil is largely frozen (Chapin et al. 1986). Plants whose roots are experimentally isolated from the soil are able to grow just as rapidly as plants rooted in soil for an entire growing season, based on stored nutrient reserves (Jonasson & Chapin 1985).

As in the annual *Glycine max* (soybean) (Sect. 4.1), some perennial herbaceous species also accumulate specific **storage proteins** [e.g., in the taproots of *Taraxacum officinale* (dandelion) and *Cichorium intybus* (chicory) (Cyr & Bewley 1990)]. Accumulation of vegetative storage proteins in

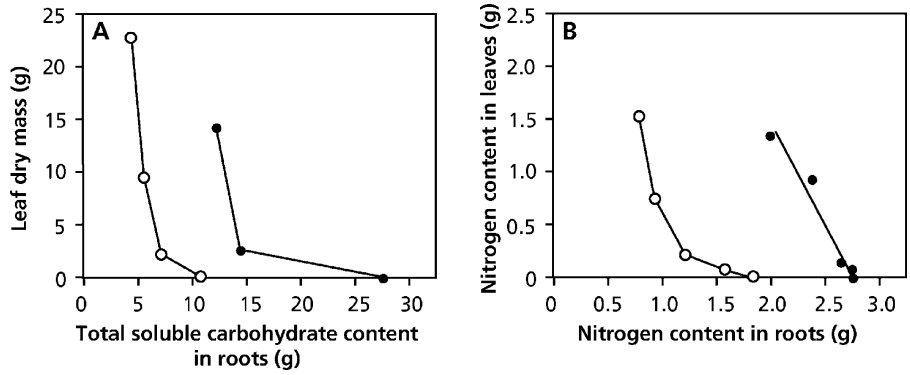


FIGURE 8. The relation between (A) the decrease with time of the content of total soluble carbohydrates in the taproot and the increase with time of leaf dry mass and (B) the decrease with time of the N content of the taproot and the increase with time of the N content of the leaves, at the beginning of the second season in the biennial herbaceous thistle, *Arctium tomentosum* (woolly burdock). *Filled circles* refer to control plants, grown under natural light in the field, and *open circles* to plants growing in shade, 20% of the irradiance of control plants (Heilmeier et al. 1986).

stolons of *Trifolium repens* (white clover) during autumn and winter is encoded by a cold-induced gene (Goulas et al. 2007). Storage proteins have the advantage over amino acids and amides as storage products in that they allow storage at a lower cellular water content and thereby reduce the danger of freezing damage. Upon defoliation, the storage proteins are remobilized during regrowth of the foliage [e.g., in the taproot of *Medicago sativa* (alfalfa)] where they constitute approximately 28% of the soluble protein pool. Several weeks after defoliation, the storage proteins may again comprise more than 30% of the soluble protein pool (Avice et al. 1996a).

Storage proteins also occur in woody plants, especially in structural roots, bark, and wood tissue of trees, where they may constitute 25–30% of the total extractable proteins. In *Populus canadensis* (Canada poplar), **storage glycoproteins** accumulate in protein bodies in ray parenchyma cells of the wood in autumn and disappear again in spring (Sauter & Cleve 1990). In *Populus trichocarpa* (black cottonwood) the synthesis of storage proteins is induced by exposure to short-day conditions (Fig. 9), most likely under the control of **phytochrome** (Coleman et al. 1992).

The persistence of grassland species such as *Lolium perenne* (perennial ryegrass) greatly depends on their capacity to grow after cutting or grazing. After defoliation, the carbohydrate reserves in the stubble (mainly fructans) are rapidly depleted during regrowth. The carbohydrate content of the roots also declines after defoliation, but the roots remain a net sink for carbon, even immediately after defoliation. Morvan-Bertrand et al. (1999) showed that after a regrowth period of 28 days, 45% of all carbon fixed before defoliation is still present in the root and leaf tissue, and only 1% is incorporated in entirely new tissue, demonstrating the importance of recently fixed carbon for regrowth.

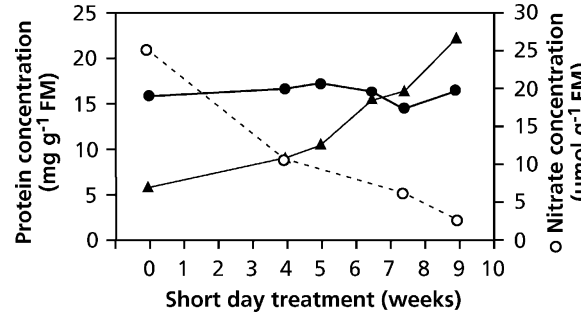


FIGURE 9. The effect of exposure to short days (8-hour light) following growth under long-day conditions (16-hour light) on the protein concentration in bark (*triangles*) and leaves (*filled circles*) and on the NO_3^- concentration (*open circles*) in leaves of *Populus trichocarpa* (black cottonwood). The plants were grown in a full nutrient solution in a growth chamber under a temperature regime of 22°C during the day and 18°C at night, both before and after exposure to short days (after Langheinrich & Tischner 1991). Copyright American Society of Plant Biologists.

4.6 Costs of Growth and Storage: Optimization

Costs of storage include **direct costs** for **translocation** of storage compounds to and from storage sites, **chemical conversions** to specific storage compounds, and **construction of special cells**, **tissues**, or **organs** for storage as well as their protection. There are also **opportunity costs** (i.e., diminished growth as a result of diverting metabolites from resources that might have been used for structural growth) (Bloom et al. 1985). The construction of storage cells and tissue does not necessarily occur at the same time as the accumulation of the stored products which makes it difficult to assess whether vegetative growth and storage are competing processes. If the storage compounds are derived from recycling of leaf proteins (e.g., Rubisco), which functioned in metabolism during the growing season, then storage does not compete with vegetative growth. Use of accumulated stores similarly does not compete with growth and has negligible opportunity cost. If carbohydrates accumulate during the period of most vigorous vegetative growth, particularly when plants are light-limited, then there is no competition between storage and vegetative growth (Heilmeier & Monson 1994).

5. Environmental Influences

In earlier sections we discussed the causes of inherent differences among species in growth rate under favorable conditions. Natural conditions, however, are seldom optimal for plant growth, so it is critical to understand the patterns and mechanisms by which growth responds to variation in environmental factors, including water and nutrient supply, irradiance, oxygen availability, and temperature. Plants may acclimate to different environmental conditions, or they may differ genetically in their programmed response to the environment. Aspects of both acclimation and adaptation are discussed in this section.

Plants generally respond to suboptimal conditions through reductions in growth rate and changes in allocation to minimize the limitation of growth by any single factor. Arguments based on economic analogies suggest that plants can minimize the cost of growth (and therefore maximize growth rate) if allocation is adjusted such that all resources are equally limiting to growth (Bloom et al. 1985). Thus, we might expect greater allocation to leaves when light strongly limits growth and greater allocation to roots in response to water or nutrient limitation (Brouwer 1963). The net result of these adjustments, through both adaptation and acclimation, should be a functional balance between the activity of roots and shoots in which below-ground resources are acquired in approximate balance with above-ground resources (Garnier 1991):

$$\text{root mass} \cdot \text{NIR}_m = k \cdot \text{leaf mass} \cdot \text{NAR}_m \quad (9)$$

where NIR_m is the net inflow of N per unit root mass; NAR_m is the net assimilation rate, which is now expressed per unit leaf mass rather than leaf area; and k is the concentration of N; instead of N, the net inflow and concentration of other nutrients can be used in this equation. The accumulation of nutrients under conditions of carbon limitation and of carbohydrates under conditions of nutrient or water limitation (Sect. 4) shows that plants never achieve perfect functional balance.

Growth is arguably the most important process to understand in predicting plant **responses to environment**, and we therefore need to understand the **basic mechanisms** by which growth responds to environment. Does growth decline in direct response to reductions in resource supply and acquisition or does the plant anticipate and respond to specific signals before any single resource becomes overwhelmingly limiting to all physiological processes? In other words, is growth **source-controlled** or do specific signals modulate sink activity (growth), which then governs rates of resource acquisition (**feedforward control**)? For example, if growth responds directly to reduced source strength, low availability of light or CO_2 would act primarily on photosynthesis which would reduce the carbon supply for growth; similarly, water or N shortage would restrict acquisition of these resources such that water potential or N supply would directly determine growth rate. On the other hand, if unfavorable environmental conditions are sensed and trigger signals that reduce growth rate directly, this would lead to a feedforward response that would reduce rates of acquisition of nonlimiting resources before the plant experiences severe resource imbalance.

Unfavorable environmental conditions tend to reduce growth. For example, unfavorable conditions below ground often trigger changes in the balance among abscisic acid, cytokinins, and gibberellins which lead to changes in growth rate that precede any direct detrimental effects of these changes in environment. This **feedforward response** minimizes the physiological impact of the unfavorable environment on plant growth. In

the following sections, we describe the evidence for the relative importance of direct environmental effects on resource acquisition (source control) vs. those mediated by feedforward responses. Current computer simulation models of plant growth in agriculture and ecology assume that source control is the major mechanism of plant response to environment. If this is incorrect, it is important to know whether the feedforward responses of plants lead to qualitatively different predictions of how plants respond to their environment.

5.1 Growth as Affected by Irradiance

Light is one of the most important environmental factors, providing plants with both a source of energy and **informational signals** that control their growth and development. Plants contain an array of **photoreceptors** that track almost all parameters of incoming light signals, including presence, absence, colors, intensity, direction, and duration. These effects of light are the topics of this section, whereas effects of UV radiation are discussed in Sect. 2.2 of Chapter 4B on effects of radiation and temperature. Effects of daylength (photoperiod) on flowering are treated in Sect. 3.3.1 of Chapter 7 on life cycles. N allocation to different leaves as dependent on incident irradiance is discussed in Sect. 5.4.6, after discussing the involvement of cytokinins in N allocation (Sect. 5.4.4).

5.1.1 Growth in Shade

Shade caused by a leaf canopy reduces the irradiance predominantly in the photosynthetically active region of the spectrum (400–700 nm), causing a shift in both the quantity and the spectral composition of light (Box 7.2).

5.1.1.1 Effects on Growth Rate, Net Assimilation Rate, and Specific Leaf Area

Plants that grow in a shady environment invest relatively more of the products of photosynthesis and other resources in leaf area: they have a **high LAR**. Their leaves are relatively thin: they have a **high SLA** (Sect. 3.2.2 of Chapter 2A on photosynthesis) and **low leaf mass density**. This is associated with relatively few, small **palisade mesophyll** cells per unit area. The leaves have a high **chlorophyll concentration** per unit fresh mass which results in a rather similar chlorophyll concentration per unit leaf area as that in sun leaves, but relatively **less protein** per unit chlorophyll (Sect. 3.2.3 of Chapter 2A on photosynthesis).

Trees, e.g., ecotypes of *Fagus crenata* (Japanese beech), produce sun leaves with thick palisade tissue comprising two cell layers. The number of cell layers in the palisade tissue is determined in the **winter buds**, by early winter of the year prior to leaf unfolding. When sun-exposed branches with young expanding leaves are shaded, the resultant leaves show intermediate characteristics: they have palisade tissue with two cell layers but the height of the palisade tissue is lower than that in the fully exposed sun leaves (Terashima et al. 2006). This suggests that several different signals are used for the determination of characteristics of sun leaves. When plants of the annual herb *Chenopodium album* (lambsquarters) are shaded in various ways, the developing leaves, irrespective of their own light environments, form palisade tissue with two cell layers if mature leaves are exposed to high light. On the other hand, when mature leaves are shaded, palisade tissue with one cell layer is formed. These results show that the light environment of mature leaves determines the number of cell layers in the palisade tissue of new leaves and suggest a signal-transduction system that conveys a signal from the mature leaves to the developing leaves (Yano & Terashima 2001). The signal from the mature leaves regulates the direction of cell division. In the future sun leaves, the signal probably induces periclinal division in addition to anticlinal division, while the signal from the shaded mature leaves only allows the cells to divide anticlinally (Yano & Terashima 2004). This signal might be the abundance of photosynthates (Terashima et al. 2006).

Table 3 summarizes the results of morphological acclimation and adaptation to a low irradiance. The RGR of the **shade-tolerant** *Dactylis glomerata* (cocksfoot) is reduced less by growth in shade as compared with full sun, when compared with *Dactylis polygama* (slender cocksfoot), which is a **shade-avoiding** species. This is due to a stronger increase of the LAR in the shade in *Dactylis polygama*, which is due to a large increase in SLA and a small increase in LMR (the various abbreviations used in growth analysis are explained in Table 1 and Sect. 2.1). The regulation of the increase in LAR may involve signaling as discussed in this section for *Chenopodium album*; it serves to capture more of the growth-limiting resource in the shade. Table 3 also shows trade-offs between resource allocation to leaves and roots. The overall patterns indicate that changes in allocation and leaf morphology in response to shade maximize capture of the growth-limiting resource (light), and

Table 3. Effects of the irradiance level on growth parameters of a sun-adapted species, *Dactylis glomerata* (cocksfoot), and a shade-adapted species, *Dactylis polygama* (slender cocksfoot). Daily irradiances (100% values) were full sunlight for both species

	Relative irradiance level			
Growth parameter	**100**	**30**	**20**	**5.5**
Relative growth rate (mg g^{-1} day^{-1})				
Dactylis glomerata	**98**	**88**	**88**	**56**
Dactylis polygama	**98**	**88**	**100**	**29**
Net assimilation rate (g m^{-2} day^{-1})				
Dactylis glomerata	**13.2**	**5**	**6.9**	**1.5**
Dactylis polygama	**8.8**	**5.9**	**5.9**	**0.7**
Leaf area ratio (m^2 kg^{-1} dry mass)				
Dactylis glomerata	**4**	**11.7**	**12.7**	**38.0**
Dactylis polygama	**11.2**	**15.0**	**10**	**38.5**
Specific leaf area (m^2 kg^{-1} dry mass)				
Dactylis glomerata	**28.5**	**36.4**	**33.7**	**66.6**
Dactylis polygama	**31.7**	**36.4**	**40.4**	**74.9**
Leaf mass ratio (g g^{-1})				
Dactylis glomerata	**0.26**	**0.34**	**0.37**	**0.57**
Dactylis polygama	**0.36**	**0.41**	**0.42**	**0.52**
Leaf mass density (kg dry mass m^{-3})				
Dactylis glomerata	**217**	**217**	**217**	**142**
Dactylis polygama	**247**	**248**	**244**	**155**
Root length ratio (m g^{-1} dry mass)				
Dactylis glomerata	**141**	**105**	**102**	**59**
Dactylis polygama	**110**	**92**	**88**	**96**
Specific root length (m g^{-1} dry mass)				
Dactylis glomerata	**287**	**282**	**303**	**416**
Dactylis polygama	**278**	**277**	**279**	**407**

***Source*: Ryser & Eek (2000).**

that this shade acclimation is more extreme in shade-adapted species (Fig. 10).

At a very low irradiance, such as under a dense canopy, many shade-avoiding plants do not survive, even though they may exhibit a positive RGR in short-term growth experiments (Table 3). Thus, there must be additional factors that account for the distribution of sun-adapted and shade-adapted species. First, **leaf longevity** appears to be important. Shade-tolerant species tend to keep their leaves for a longer time and so increase the potential photosynthetic return (Reich et al. 1991, 1992a,b). When grown in shade, fast-growing tropical trees show a higher LAR and lower RMR, as well as a greater mortality than do slower-growing ones (Kitajima 1994). Shade-tolerant plants also minimize leaf loss through their greater allocation to chemical defenses against pathogens and herbivores than in shade-avoiding species (Chapter 9B on ecological biochemistry). In addition, the enhanced rate of stem elongation (Sect. 5.1.1.3) may weaken the shade-avoiding plants.

5.1.1.2 Adaptations to Shade

In addition to **acclimation** to a specific light environment, there are also specific **adaptations**. That is, there are species with a genetic constitution that restricts their distribution to an environment with a specific light climate. To put it simply, three "plant strategies" are discerned:

1. Plants avoiding shade, or obligate sun plants
2. Plants tolerating shade, or facultative sun or shade plants
3. Plants requiring shade, or obligate shade plants

Many weedy species and most crop species are **obligate sun species**. **Obligate shade plants** include some mosses, ferns, club mosses, and a few higher plant species in tropical rainforests

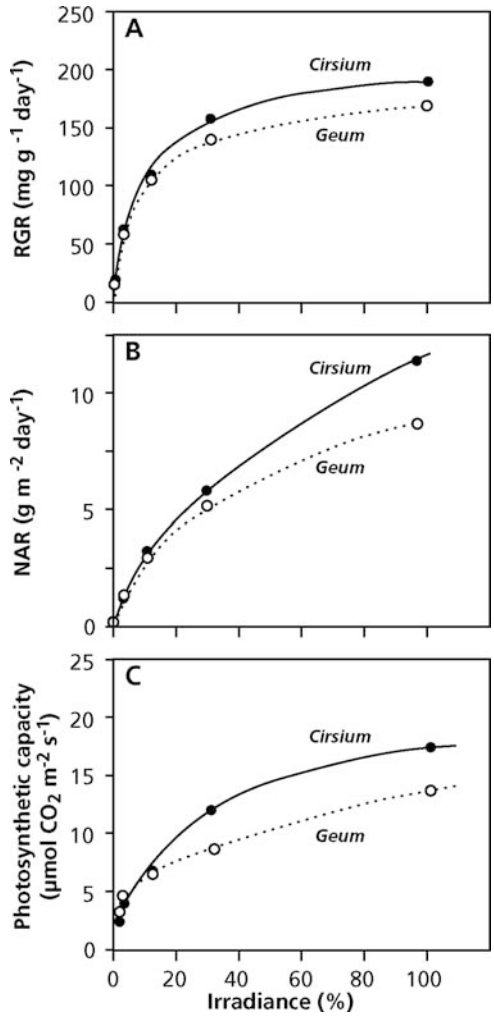


FIGURE 10. The relative growth rate (RGR), net assimilation rate (NAR), and photosynthetic capacity of the shade-avoiding *Cirsium palustre* (marsh thistle) and the shade-tolerant *Geum urbanum* (avens), grown at a range of light intensities. Full daylight is 100% (after Pons 1977).

(e.g., young individuals of *Monstera* and *Philodendron* species). Among higher plants, obligate shade species are rare in temperate regions and will not be discussed here. Most understory species are **facultative** rather than obligate shade plants.

5.1.1.3 Stem and Petiole Elongation: The Search for Light

Stem and petiole elongation of **shade-avoiding** plants growing in the shade are greatly enhanced, branching is reduced (increased apical dominance), total leaf area and **leaf thickness** are less, and **SLA** is increased. The effects of leaf canopy shade can be separated into those due to **reduced irradiance** and those affected by the **red/far-red ratio**.

Plants that tolerate shade do not respond with increased stem elongation; instead, they increase their leaf area. Their leaf thickness is reduced to a smaller extent than it is in shade-avoiding species, and their chlorophyll concentration per unit leaf area often increases. The increased chlorophyll concentration gives these plants [e.g., *Hedera* spp. (ivy) and species from the understory of tropical rain forests] their dark-green color. Less extreme shade-tolerant species [e.g., *Geum urbanum* (avens)] also enhance their chlorophyll concentration per unit fresh mass. Because their SLA is increased at the same time, however, the chlorophyll concentration per unit area is not enhanced (sometimes even less), and they do not appear dark-green.

The **red/far-red ratio** (R/FR) is the ratio of the irradiance at 655–665 nm and that at 725–735 nm. Comparison of a number of species from open habitats [e.g., *Chamaenerion angustifolium* (fireweed), *Sinapis alba* (white mustard), *Senecio vulgaris* (groundsel)], from intermediate habitats [*Urtica dioica* (stinging nettle)], and from closed habitats (shade in forest understory) [*Geum urbanum* (avens), *Oxalis acetosella* (soursop), *Silene dioica* (red campion)] shows that the stem elongation of sun-adapted species responds much more strongly to R/FR than does that of shade species. The effect of a change in R/FR on stem elongation can be recorded within 10–15 min, e.g., in *Sinapis alba* (white mustard) (Fig. 11).

5.1.1.4 The Role of Phytochrome

Perception of R/FR involves the **phytochrome** system (Box 7.2 and Sect. 2.2.2). In *Vigna sinensis* (cowpea) the response of **stem elongation** to R/FR is similar to that of **gibberellins** (GAs). In fact, inhibition of stem elongation by light is associated with a decrease in tissue responsiveness to GAs (Olszewski et al. 2002). *Arabidopsis thaliana* (thale cress) plants that have mutations affecting GA- and/or phytochrome action show that a fully functional GA system is necessary for full expression of the phytochrome response (Peng & Harberd 1997). The phytochrome responses clearly demonstrate that many of the light responses of shade plants are hormonally mediated (sink-controlled) rather than direct responses to irradiance level.

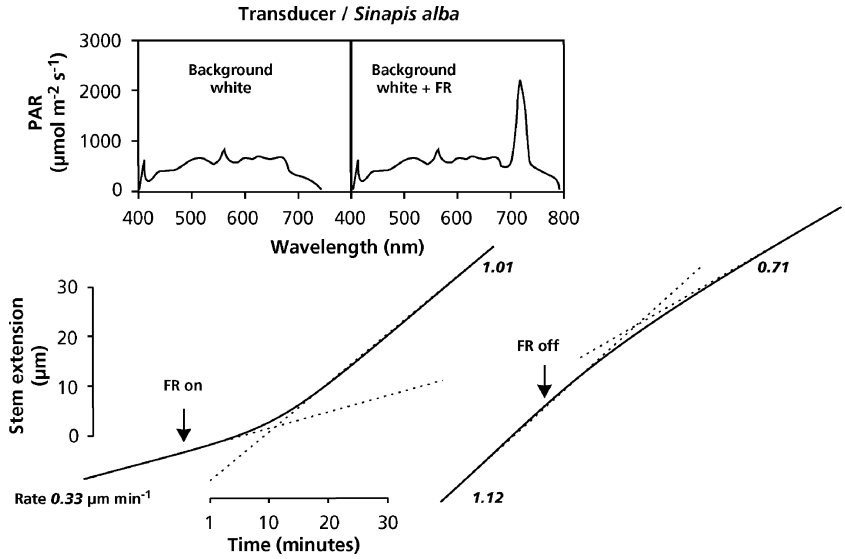


FIGURE 11. Continuous measurements of stem extension rate by a position-sensitive transducer. A seedling attached to the transducer and exposed to background white fluorescent light was given far-red (FR) light via a fiberoptic probe. The FR source was switched on and off as indicated. *Solid lines* show the observed stem extension, and the *dotted lines* show the best-fit initial and final extension rates, the values of which are presented next to the lines. The *insets* show the spectral composition of the irradiance of the background white light with and without FR (data of D.C. Morgan, as presented in Smith 1981).

5.1.1.5 Phytochrome and Cryptochrome: Effects on Cell-Wall Elasticity Parameters

Both red light and **blue light** inhibit stem elongation. A blue photoreceptor (**cryptochrome**) is involved in the perception of blue light. Both red light and blue light affect cell-wall properties rather than the osmotic or turgor potential of the cells (Table 4). As explained in Sect. 2.2, stem elongation is the result of cell expansion ($dV/V \cdot t$), which is related to the cell-wall yield coefficient, the turgor pressure, and the yield threshold. Red light inhibits elongation mainly by lowering the **cell-wall yield coefficient** (ϕ), whereas blue light predominantly acts by enhancing the **yield threshold** (Y) (Table 4). This indicates that shade affects growth through **feedforward responses** rather than through direct supply of photosynthate.

5.1.1.6 Effects of Total Level of Irradiance

The total level of irradiance is the major factor that determines the LAR and SLA of shade-avoiding species, but the spectral composition of the irradiance also has an effect in some species. Shade-avoiding species respond to the spectral composition in the shade primarily with enhanced stem elongation, at the expense of their leaf mass ratio. Shade-tolerant species tend to invest relatively more resources in

TABLE 4. Effects of darkness, red light, and blue light on in vivo cell wall properties of stems of etiolated pea (*Pisum sativum*) seedlings. *

	Dark	Red light	Blue light
Elongation rate (μm m^{-1} s^{-1})	9.2	3.3	3.0
Turgor potential (MPa)	0.53	0.59	0.58
Osmotic potential (MPa)	0.84	0.82	0.83
Yield threshold, Y (MPa)	0.05	0.16	0.33
Yield coefficient, ϕ (Pa^{-1} s^{-1})	19.1	8	15.6

Source: Kigel & Cosgrove (1991).
* In darkness the P_{fr} configuration of phytochrome reverts to the P_r configuration.

their leaves when exposed to shade, primarily as a response to the level of irradiance (Smith 1981).

These responses to the level of irradiance are most likely mediated through **sugar-sensing systems** (Sects. 4.3 and 12.1 of Chapter 2A on photosynthesis and Sect. 4.4 of Chapter 2B on plant respiration).

5.1.2 Effects of the Photoperiod

The length of the photoperiod affects the flowering response of long-day and short-day plants (Sect. 3.3.1 of Chapter 8 on life cycles), tuber formation [e.g., in *Solanum tuberosum* (potato)], as well as aspects of vegetative plant development that are not directly related to reproduction. These effects are mediated by the **phytochrome** system and differ from those that result from changes in the total level of irradiance received by the plants. It is interesting that a leaf from a tobacco plant (*Nicotiana tabacum*) that is induced to flower induces a potato plant (*Solanum tuberosum*) to tuberize when the tobacco leaf is grafted on the potato plant. Antisense phytochrome B potato plants have provided evidence for the role of phytochrome B (Box 7.2) in tuberization (Jackson et al. 1998).

For temperate species, the length of the photoperiod is an important signal for acclimation to low temperatures (cold hardening), especially in woody species (Sect. 3.5 of Chapter 4B on effects of radiation and temperature). In a Norwegian ecotype of *Dactylis glomerata* (cocksfoot) dry matter production is enhanced under long days at low temperature, compared with short days at the same low temperature (Fig. 12). In a Portuguese ecotype at higher temperatures, photoperiod has little effect. The greater production at a low temperature and long days in the Norwegian ecotype reflects a higher RGR, because of a higher SLA. The net assimilation rate is reduced in long days, at all temperatures and in both ecotypes (Fig. 12). Leaves tend to be thinner in long days and their cells are longer. It is common for populations of a species from different latitudes to differ in their photoperiodic cues, indicating that changes in photoperiodic requirement are a relatively easy evolutionary adjustment that is differentially selected at different latitudes.

Increased levels of endogenous **gibberellins**, possibly in combination with an enhanced sensitivity to these hormones, are involved in the growth response of *Poa pratensis* (Kentucky bluegrass) to

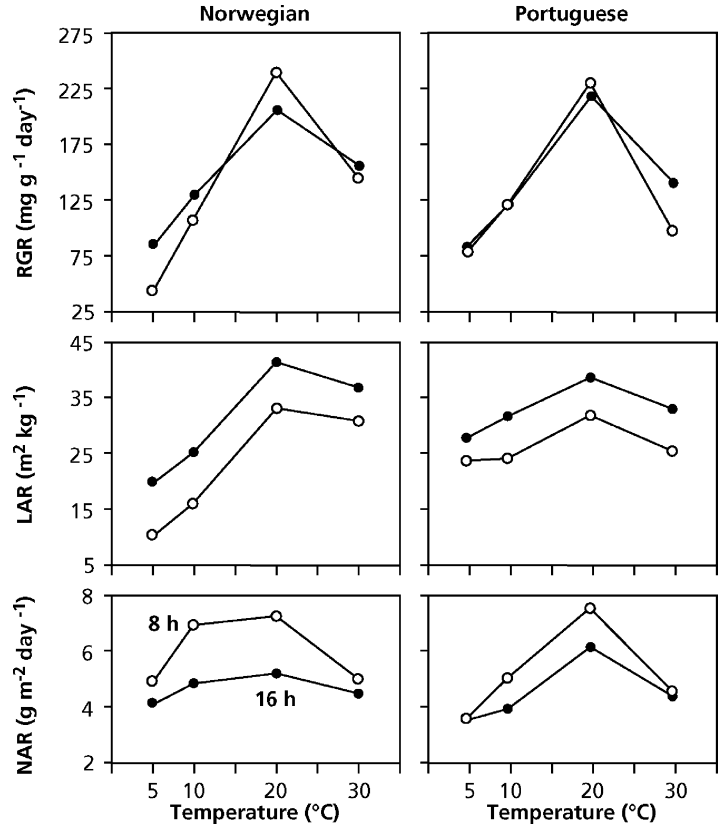


FIGURE 12. Results of a growth analysis of seedlings of *Dactylis glomerata* (cocksfoot) from two different origins at four temperatures and two daylengths (Eagles 1971, as cited in Hay 1990). Copyright Trustees of The New Phytologist.

long days (Juntilla et al. 1997). The photoperiod also affects the plant's chemical composition, again independent of the total level of irradiance received by the plant. The percentage of total N in dry matter declines with increasing photoperiod, which is the likely cause for a decrease in NAR at long days (Fig. 12).

5.2 Growth as Affected by Temperature

Temperature affects a range of enzymatically catalyzed and membrane-associated processes in the plant and is a major factor affecting plant distribution. The **activation energy** of different reactions may differ widely. Growth, development, and allocation are affected in different ways in different species. Effects of temperature on plant development are commonly related to **degree days**, computed as the integral of a function of time that varies with temperature. The number of degree days accumulated over a period of time is often related to the phenological development of plants. Degree days are used to predict the date a flower will bloom or a crop will reach maturity (Leon et al. 2001).

The temperature optimum of root growth tends to be lower than that of the shoot. In spring, therefore, roots start growing before the leaves do. Temperature also affects the uptake of nutrients and water by the roots. The optimum temperature for root growth of plants from temperate regions is between 10 and 30°C, but growth may continue around 0°C. Subtropical species have a higher optimum temperature for root growth, and growth may cease below 10–15°C (Bowen 1991). In tropical species damage may occur at temperatures of 12°C or less. How exactly does a low temperature affect root and leaf growth and the pattern of allocation to roots and leaves? This is a highly relevant question, in view of the current rise in global temperature.

5.2.1 Effects of Low Temperature on Root Functioning

Exposure to a low temperature reduces **root extension**, without an effect on turgor in the elongation zone. In *Zea mays* (corn) the reduction in elongation rate is associated with a decrease in cell-wall extensibility, more specifically in the **cell-wall yield coefficient**. Reduced elongation may lead to an increased number of rather small cells, immediately behind the root tip. These resume expansion upon exposure of the roots to a more favorable temperature (Pritchard 1994).

For a proper functioning of roots at low temperature, their membranes must remain fluid and semipermeable. The **lipid composition** of the membranes in the roots affects membrane fluidity and interactions with membrane-bound proteins and, therefore, the transport of both ions and water. Cold-acclimated plants tend to have a higher degree of unsaturation of phospholipids, which causes their membranes to remain fluid at lower temperatures.

The major resistances for **water flow** in the roots are in the **exodermis**, if present, and the **endodermis**. At the exodermis or endodermis, water must enter the **symplast** before it can arrive in the xylem vessels. Water passes the membranes in a single file through specific water-channel proteins (**aquaporins**) (Sect. 5.2 of Chapter 3 on plant water relations). The effect of temperature on the rate of water uptake by roots, therefore, possibly reflects direct effects on these water-channel proteins and indirect effects on membrane fluidity.

The effects of temperature on the roots' capacity to absorb water largely account for temperature effects on plant growth. Increasing the root temperature of *Glycine max* (soybean) in the range that is suboptimal for growth, while maintaining a constant shoot temperature, increases the water potential of the whole plant (Kuo & Boersma 1971). It is likely that the effects of temperature on the relative investment of biomass in roots and leaves reflect the roots' capacity to take up water, at least in the range of temperatures around the optimum (Li et al. 1994). Capacity to take up water is, in turn, probably influenced by plant hormones (Sect. 5.3).

Does this imply that effects of temperature on the allocation pattern are accounted for by an effect of root temperature on the roots' capacity to transport water and that temperature effects on nutrient uptake are not a cause for changes in the allocation pattern? Current evidence does indeed support this contention. Whereas growth at a low root temperature does affect the rate of absorption of both NO_3^- and NH_4^+, this appears to be a response to the decline in growth rate (Clarkson et al. 1992). That is, the decline in the rate of nutrient absorption at low root temperatures is, in part, a response to the decreased nutrient demand of the plant (Sect. 2.2.3.2 of Chapter 6 on mineral nutrition).

5.2.2 Changes in the Allocation Pattern

Variation in growth rate with temperature is associated with changes in plant carbon balance. A

positive carbon balance can be maintained at adverse temperatures by changes in the pattern of resource allocation to leaves and nonphotosynthetic plant parts. Acclimation to different temperatures, therefore, may affect the rate of photosynthesis per unit leaf area (Fig. 2A.25 in Chapter 2A on photosynthesis) or the plant's allocation pattern. In very general terms, the effect of temperature on biomass allocation in the vegetative stage is that the relative investment of biomass in roots is lowest at a certain optimum temperature, and that it increases at both higher and lower temperatures. This is found both when the temperature of the entire plant is varied and when only root temperature is changed (constant shoot temperature) (Bowen 1991).

It has been suggested that an increase in root temperature in the suboptimal range increases the demand for respiratory substrate in roots, which results in lower carbohydrate concentrations in the whole plant or in the shoots. These effects of root temperature on root respiration are often only transient, however, with values returning to control rates within a day (Sect. 4.5 of Chapter 2B on respiration).

Temperature strongly affects the uptake of both nutrients and water by the roots. Although **nutrient uptake** does depend on root temperature, at least in short-term experiments, it is unlikely that long-term temperature effects on biomass partitioning are due to effects on nutrient uptake. Upon prolonged exposure to low root temperature, the uptake system acclimates (Sect. 2.2.3.3 of Chapter 6 on mineral nutrition); there is compelling evidence that, at a low root temperature, **growth controls the rate of nutrient uptake**, rather than being controlled by it (Clarkson et al. 1988). Effects of root temperature, through the plant's water relations, are probably mediated by **ABA** (Sect. 5.3), but further evidence is needed to support this contention.

There are also indirect effects of temperature on nutrient availability, in that rates of mineralization decline at low temperatures (e.g., in arctic and alpine environments).

5.3 Growth as Affected by Soil Water Potential and Salinity

Many processes in the plant are far more sensitive to a low water potential than are stomatal conductance and photosynthesis (Sect. 5.2 of Chapter 2A on photosynthesis). The growth reduction at a low soil water potential is largely due to inhibition of more sensitive processes, such as **leaf cell elongation** and **protein synthesis**. At a low soil water potential, the

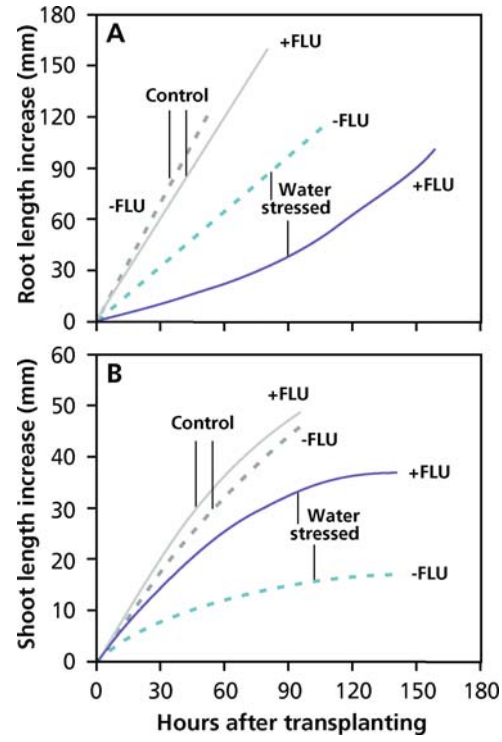


FIGURE 13. Elongation of the primary root and shoot of *Zea mays* (corn) seedlings that were well watered or grown at a low water potential. Also shown is the effect of fluridone, which is an inhibitor of the synthesis of ABA. (*Top*) Root growth of seedlings soaked in water for 36 hours and then transplanted to –1.6 MPa; (*Bottom*) shoot growth of seedlings soaked in water for 60 hours and then transplanted to –0.3 MPa (after Saab et al. 1990). Copyright American Society of Plant Biologists.

rate of leaf expansion decreases, whereas the rate of **root elongation** is much less affected (Fig. 13). In glycophytes [e.g., *Zea mays* (corn)] root elongation is inhibited by exposure to high concentrations of NaCl. This inhibition is not associated with a loss of turgor of the growing tip, but with an **increased yield threshold pressure** (Neumann et al. 1994).

Maintenance of root elongation at a low soil water potential may occur despite a (transient) decline in turgor of the root cells, suggesting that the yielding capacity of the elongating cells has increased due to an increase in the **amount** and **activity** of **expansins** in the root tip of plants grown at low soil water potential and an increase in the sensitivity of the cell wall to expansins (Wu et al. 1996).

Although it is tempting to think that the reduction in leaf expansion (Fig. 13) is due to a loss in turgor of the leaf cells, such a turgor loss usually

does not occur, and the reduction in leaf growth is due primarily to leaf cell-wall stiffening (Van Volkenburgh & Boyer 1985) in response to (**chemical**) **signals** arriving from the roots in contact with the drying soil (Davies & Zhang 1991). How do we know that chemical signals play a role?

5.3.1 Do Roots Sense Dry Soil and Then Send Signals to the Leaves?

To answer this question, Passioura (1988) used a pressure vessel placed around the roots of a *Triticum aestivum* (wheat) seedling growing in drying soil. As the soil dries, the hydrostatic pressure in the vessel is increased to maintain shoot water relations similar to those of well watered plants. The treated wheat plants show reductions in leaf growth similar to those of plants in drying soil without a pressure chamber. Additional evidence comes from experiments with small apple trees (*Malus* × *domestica*) with their roots growing in two separate containers, one with moist and one with dry soil. Soil drying in one container restricts leaf expansion and initiation, although the roots in the moist soil continue to maintain shoot water relations similar to those of control plants. Leaf growth recovers upon severing the roots in contact with the drying soil (Gowing et al. 1990). These effects on leaves of wheat seedlings and apple trees must therefore be attributed to effects of soil drying that do not require a change in shoot water status (Davies et al. 1994).

As with effects of soil drying on stomatal conductance (Sect. 5.1 of Chapter 2A on photosynthesis and Sect. 5.4.1 of Chapter 3 on plant water relations), **hydraulic** and **electric signals**, in addition to **chemical messengers** from the roots, possibly play a role in effects of drying soils on leaf growth (Dodd & Davies 1996, Dodd 2005). Thus, there are multiple signal-transduction pathways by which water shortage reduces plant growth.

5.3.2 ABA and Leaf Cell-Wall Stiffening

The effect of water stress on leaf elongation is mediated by the phytohormone abscisic acid (**ABA**) (Dodd 2005). Soil drying and salinity enhance the concentration of this hormone in the leaves (Tardieu et al. 1992, He & Cramer 1996). The **pH of the xylem sap** also affects leaf elongation, and this effect is, again, mediated via ABA (Bacon et al. 1998).

Above-ground plant parts respond more strongly to a decreased soil water potential than do roots. This is due to a greater **inhibition by ABA of leaf growth**, as compared with that of the roots (Saab et al. 1990), at least during the initial phase of imposed water stress. At a later stage, ABA acts to maintain leaf growth, albeit at a slower rate than in well-watered plants (Sharp 2002). If, and to what extent, ABA is responsible for the decline in cell-wall acidification upon water stress (Van Volkenburgh & Boyer 1985) and acid-induced wall loosening (Cleland 1967) remains to be investigated (Munns & Sharp 1993). We do know that leaves tend to have stiffer walls when the plants are exposed to water stress (Chimenti & Hall 1994). The leaves also show higher endogenous ABA concentrations and reduced leaf growth. ABA most likely affects the growth of roots and leaves through its inhibitory effect on **ethylene** biosynthesis (Sharp 2002, Dodd 2005).

Salt-sensitive species respond more strongly, both in terms of ABA level and in leaf expansion, than do resistant species (He & Cramer 1996). ABA seems to harden the cell wall of leaf cells by increasing the yield threshold, Y, and decreasing wall extensibility, ϕ. Both the carbohydrate and the protein component of cell walls are affected (Munns & Cramer 1996).

5.3.3 Effects on Root Elongation

Roots that experience a moderate water stress may loosen their walls and increase their extension growth rate. **Wall loosening** is probably due to an increase in activity of **expansins** (Sect. 2.2.4; Cosgrove 2000). An increase in expansin proteins and wall-loosening capacity in the root apex in response to water stress is widespread and presumably an adaptation to growth in drying soils that allows exploitation of a falling water table. The size of the root meristem is also reduced under water stress, so fewer root cells contribute to the elongation process (Sharp et al. 2004). As in leaves, osmotic stress has no effect on the **turgor** of *Zea mays* (corn) root cells; however, it increases the **concentration of osmotic solutes** to the extent that the difference in cell water potential and that of the root environment is restored (Pritchard et al. 1996).

Lowering the water potential around the roots also enhances sugar transport to the roots, probably due to the growth reduction of the leaves. Because photosynthesis is less affected than leaf growth, sugar transport as well as root growth may be enhanced in both a relative and an absolute sense, at least in the early stages of the stress. The unresolved question remains, however: how does an increased concentration of sugars affect the growth of roots? This probably requires a sugar-sensing mechanism similar to the one discussed for leaves

where a specific hexokinase senses hexose levels and affects the repression of genes that encode photosynthetic enzymes (Sect. 4.3 of Chapter 2A on photosynthesis). Gene transcription in roots is indeed affected by sugar levels, as discussed for respiratory enzymes (Sect. 4.4 of Chapter 2B on plant respiration), but the search continues for genes that affect root elongation. We are still far from understanding the entire signal-transduction pathway from elevated sugar levels in roots cells on the one hand to stimulation of root elongation on the other. This is clearly a major challenge for molecular ecophysiologists!

5.3.4 A Hypothetical Model That Accounts for Effects of Water Stress on Biomass Allocation

The effects of water stress on phytohormone production in the roots, leaf expansion, and root growth are summarized in Fig. 14. Whatever the exact signal-transduction pathway, the overall effect of inhibition of leaf area expansion while root elongation is inhibited less, or even stimulated, is that the LAR and/or the LMR decrease, and that the RMR increases in response to a decrease in soil water potential. The increased respiratory costs of such an increase in RMR may contribute to reduced growth of desiccated plants; they also reduce the dry mass gain per unit of water lost in transpiration (Van den Boogaard et al. 1996).

5.4 Growth at a Limiting Nutrient Supply

Plants allocate relatively less biomass to leaves and more to their roots when N or P is in short supply (e.g., Brouwer 1963, 1983). Like the response to water stress (Sect. 5.3), the response to nutrient shortage is also functional. In both situations the investment in plant parts that acquire the limiting resource is favored, at the expense of allocation to plant parts that have a high requirement for the limiting resource. The opposite and equally functional response is found when plants are growing at a low irradiance (Sect. 5.1).

In this section we focus on the response to N shortage because the effect of N shortage on biomass allocation is stronger than that of other nutrients. P may have similar effects, possibly acting through an effect on N acquisition (Kuiper et al. 1989). This may also be the case for S, whereas the pattern is less clear for other nutrients. Leaf expansion rates are decreased at a low N supply (Gastal et al. 1992). Leaves of plants grown with a limiting N supply are smaller, compared with those of plants grown with an optimum nutrient supply, predominantly due to an effect on **meristem size** and **cell number** (Fig. 2B) (Terry 1970). How are the changes in biomass allocation pattern brought about?

5.4.1 Cycling of Nitrogen Between Roots and Leaves

NO_3^- can act as a signaling molecule that affects local root proliferation (Sect. 2.2.8 of Chapter 6 on mineral nutrition). NO_3^- probably also plays a signaling role in the control of biomass partitioning between roots and leaves (Scheible et al. 1997). Since plants respond to NH_4^+ supply in much the same way as they do to NO_3^-, however, additional signals must be involved. In vegetative plants, whether grown with an

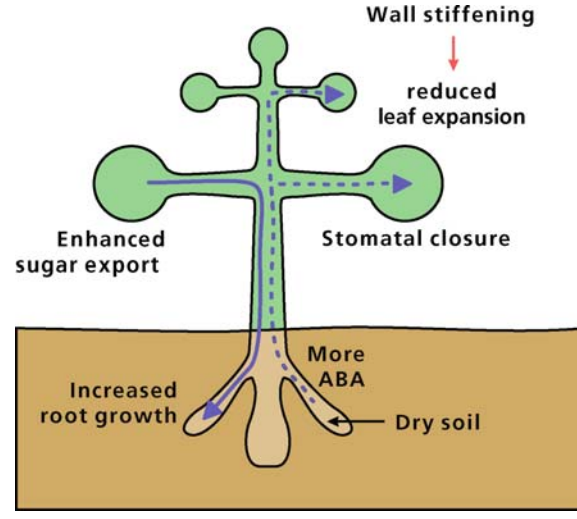


FIGURE 14. Hypothetical model to account for the effects of water stress on plant growth and biomass allocation. Roots sensing dry soil enhance the production of ABA, which is exported in the xylem and moves to the leaves. Here, ABA reduces stomatal conductance and wall extensibility of growing cells. The effects are a reduction in the rate of transpiration and photosynthesis as well as in leaf expansion. As long as photosynthesis is affected less than leaf expansion, the export of assimilates to the roots is enhanced. The increased import of assimilates in combination with ABA-enhanced wall loosening of growing roots cell may enhance the rate of root growth.

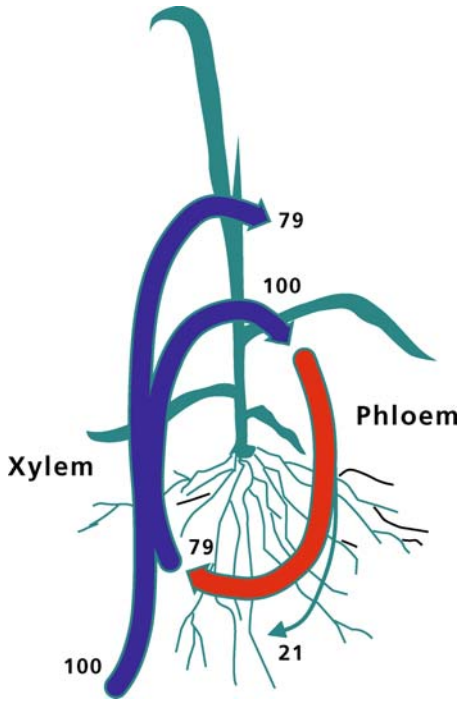


FIGURE 15. "Cycling" of nitrogen in a vegetative wheat plant (*Triticum aestivum*). Much of the N (NO_3^-, amino acids, and amides) that arrives in the leaves via the xylem is exported again in the phloem (amino acids and amides). Upon arrival in the roots, some of the nitrogen may be used for root growth, whereas the remainder cycles back to the shoot (Simpson et al. 1982a). Copyright Physiologia Plantarum.

optimum or a limiting N supply, much of the N transported from the roots via the xylem to the leaves is exported back to the roots, as amino acids and amides, via the phloem (Fig. 15). Such a process of continuous **N cycling** between roots and leaves makes it highly unlikely that the transport of N to the leaves itself is a controlling factor. Rather, we should search for signals, in addition to NO_3^-, that change concomitantly with the N supply.

5.4.2 Hormonal Signals That Travel via the Xylem to the Leaves

The response of plants to a low N or P supply is akin to that to a limiting supply of water: reduced leaf growth while root growth is maintained or enhanced. This response is generally described in terms of a **functional equilibrium** between leaves and roots (Brouwer 1963, 1983). That is, when resources that are acquired by the roots are in short supply, the growth of the roots is favored over that of the leaves so that the RMR is increased. Transgenics that have a very low nitrate reductase activity (1–5% of wild-type levels) also exhibit an increased RMR when NO_3^- is in short supply, which shows that **NO_3^-** itself, rather than a product of its assimilation, is the primary signal that induces this response (Scheible et al. 1997). We have encountered a similar **signaling role of NO_3^-** in the proliferation of roots in response to a local NO_3^- supply (Sect. 2.2.8 of Chapter 6 on mineral nutrition). We know less about the signaling pathways in plants from environments with low nitrification potential. It is interesting that N deficiency reduces the roots' **hydraulic conductivity**; it is very likely that this is controlled by a decreased expression or activity of **aquaporins**, water-channel proteins involved in water uptake by the roots (Sect. 5.2 of Chapter 3 on plant water relations; Clarkson et al. 2000). The rapid decline (within hours) in leaf growth of *Zea mays* (corn) upon transfer to a low-nutrient solution is associated with a decreased extensibility of the cell walls of expanding leaf cells. Transfer to high-nutrient conditions enhances this extensibility. The transfer has no effect on the osmotic potential of the leaf cells or on cell production (Snir & Neumann 1997).

Contrary to what has been found for plants exposed to water stress, there is no evidence that ABA plays a role as a signal between roots and leaves of plants exposed to a nutrient supply that is limiting to plant growth (Munns & Cramer 1996). Rather, a reduced nutrient supply to the roots reduces the synthesis of **cytokinins** in the root tips and their subsequent export to the leaves (Fetene & Beck 1993, Van der Werf & Nagel 1996). N appears to be the predominant nutrient that leads to this response (Kuiper et al. 1989). Due to the lower cytokinin import into leaves of plants grown with a limiting N supply, growth of the leaves is reduced (Simpson et al. 1982b). Cytokinins affect the growth of leaves and roots in an opposite manner (Sect. 2.2.2); root growth is either stimulated or unaffected by a low N supply.

In plants grown with a limiting supply of nutrients, the level of cytokinin can be maintained, by the addition of benzyladenine, a synthetic **cytokinin**, to the roots (Table 5). This maintains the RGR of the leaves of plants transferred to a low nutrient supply to a rate close to that in plants grown with a full nutrient supply; this effect can only last for a few days, after which the plants start to collapse. On the other hand, addition of cytokinin reduces the root growth to the level of plants well supplied with nutrients.

What kind of effects do cytokinins have on leaf metabolism? First, cytokinins promote the synthesis of

Table 5. Cytokinin (zeatin) concentrations (pmol g^{-1} FM) and the relative growth rate (RGR, mg g^{-1} day^{-1}) of *Plantago major* (common plantain) plants, exposed to a full-nutrient solution or transferred to a diluted solution, plus or minus 10^{-8} M benzyladenine (BA), a synthetic cytokinin.

	Cytokinin concentration		Growth (RGR)	
Treatment	Shoot	Roots	Shoot	Roots
Full nutrients	110	160	220	160
Diluted solution				
Without BA	25	23	150	180
With BA	100	140	190	160

Source: Kuiper & Staal (1987) and Kuiper et al. (1989).

several proteins that are involved in photosynthesis. **Cytokinins** also have a specific effect on a gene encoding a protein involved in the cell cycle and promote cell division and cell expansion (Sect. 2.2.2). To put it simply, cytokinins promote **leaf cell division** and **leaf cell expansion**, increase the **photosynthetic capacity**, **delay leaf senescence**, and enhance **leaf expansion**. Thus, as with water and temperature, nutrient supply governs growth through hormonal signals (**feedforward control**) rather than through a direct effect on the availability of substrates for protein synthesis (source control). The hormonal signals that regulate growth in response to nutrient shortage (cytokinins), however, differ from those associated with water and salinity stress (ABA) and light shortage (phytochrome-induced changes in gibberellins).

5.4.3 Signals That Travel from the Leaves to the Roots

Leaves that experience a low import of nutrients probably send signals back to the roots, which account for their enhanced growth. What is the nature of these signals? The signal might well be the amount of **carbohydrates** exported via the phloem (Van der Werf & Nagel 1996). When the low nutrient supply reduces leaf growth, products of photosynthesis accumulate. These probably affect the **sugar-sensing mechanism** (Sect. 4.3 of Chapter 2A on photosynthesis). Genes encoding photosynthetic enzymes are subsequently suppressed, leading to down-regulation of photosynthesis. The increased level of carbohydrates in the leaves, however, implies that more photosynthate is available for translocation to the roots. There it may act as a signal and affect sugar-sensing mechanisms. Rather than suppressing genes, it is likely to de-repress genes encoding respiratory enzymes (Sect. 4.4 of Chapter 2B on plant respiration) and possibly others (Farrar 1996).

5.4.4 Integrating Signals from the Leaves and the Roots

The results presented in Sect. 5.4.2 lead to the model depicted in Fig. 16 (Van der Werf & Nagel 1996). An

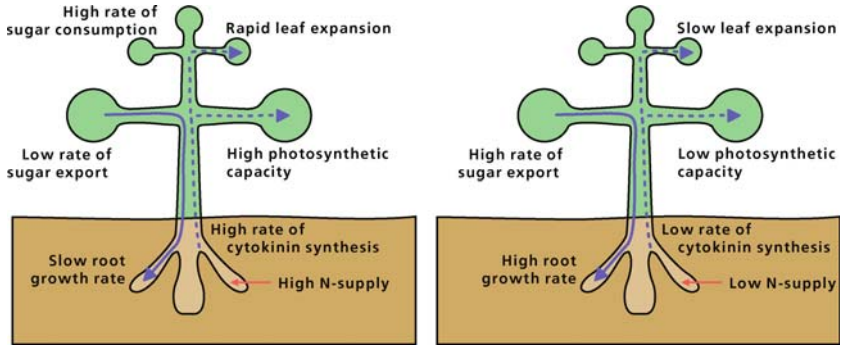


Figure 16. Hypothetical model to account for the effects of N supply on plant growth and biomass allocation. (*Left*) Roots sensing a high N availability produce large amounts of cytokinins, which are exported via the xylem to the leaves. Here the cytokinins enhance the photosynthetic capacity and leaf expansion. Hence, a large fraction of the photosynthates are consumed in the leaves, and a relatively small fraction is available for export to the roots. (*Right*) Roots sensing a low N availability produce only small amounts of cytokinins. The import of cytokinins into leaves is small, so that their photosynthetic capacity and rate of leaf expansion are reduced. Only a small fraction of the photosynthates are consumed in the leaves, so that the concentration of sugars in the leaves is high and a relatively large fraction is available for export to the roots. The high level of sugars in leaves suppresses genes encoding photosynthetic enzymes. In roots, high sugar levels induce genes encoding respiratory and possibly other enzymes.

early response of a plant to a decline in the N supply is the decrease in synthesis and export of **cytokinins**. This reduces the rate of protein synthesis, cell division, and expansion in the growing leaves. Carbohydrates accumulate, leading to suppression of photosynthetic genes and down-regulation of photosynthesis. Plenty of carbohydrates are available for export to the roots. In the roots they derepress genes that encode respiratory and possibly other enzymes. The roots may either grow at the same rate as those of control plants or their growth may be increased (Van der Werf 1996).

It appears that the relative increase in biomass allocation to roots with N shortage is largely accounted for by the decrease in production of **cytokinins** in the roots. This phytohormone then sets the change in biomass partitioning in motion which leads to a new **functional equilibrium** between roots and leaves. Roots appear to have very little *direct* control over the rate of carbon import from the leaves. They do exert *indirect* control, however, via their effect on leaf growth, which depends on the supply of cytokinins from the roots.

5.4.5 Effects of Nitrogen Supply on Leaf Anatomy and Chemistry

In a comparison of four congeneric grass species [*Poa annua* (annua meadow-grass), *Poa trivialis* (rough bluegrass), *Poa compressa* (Canada bluegrass), and *Poa pratensis* (Kentucky bluegrass)] grown at both an optimum and a limiting N supply, RGR and N concentrations decrease with low N supply (Van Arendonk et al. 1997). The decrease in RGR is accounted for by the decrease in **LAR** (both **SLA** and **LMR**). The changes are largest in the fastest-growing *Poa annua*. N shortage invariably enhances the proportion of leaf tissue that is occupied by **sclerenchymatic cells**, from about 0.5 to 6%, predominantly due to an increase in the number of these sclerenchymatic cells. The area occupied by **veinal tissue** doubles, from approximately 4.5 to 9%, whereas that occupied by epidermal cells is more or less constant (25%), despite a substantial decrease in **size of the epidermal cells**, especially in *Poa annua*. Mesophyll + intercellular spaces occupy a variable area of about 60% in all species and treatments. N stress decreases the concentration of protein and enhances that of (hemi)cellulose and lignin.

It is not known whether cytokinins are involved in the control of these anatomical and chemical features by nutrient supply. The anatomical changes are probably ecologically important, however, in that the increase in sclerenchymatic and veinal tissue likely gives better protection of leaves from herbivores and desiccation (Lambers & Poorter 2004).

N shortage also has a major effect on allocation to nonstructural secondary metabolites such as **lignin and tannins** (Sect. 4.1 of Chapter 9B on ecological biochemistry). Because these compounds slow down the rate of litter decomposition, this response aggravates the N shortage in the environment (Sects. 2 and 3 of Chapter 10A on decomposition).

5.4.6 Nitrogen Allocation to Different Leaves, as Dependent on Incident Irradiance

Different leaves of a plant may differ widely with respect to their N concentration, perhaps due to **N withdrawal** from older, senescing leaves (Sect. 4). Leaves also adjust their N concentration to the **level of incident irradiance**; leaves at the top of the canopy that are exposed to full daylight have higher N concentrations per unit leaf area than leaves near the ground surface, where they are shaded by higher leaves (Hirose & Werger 1987a).

Most of the leaf N is associated with the photosynthetic apparatus (Sect. 3.2.3 of Chapter 2A on photosynthesis). Because light intensity is higher for the top leaves than for the bottom ones, the observed **gradient in leaf N concentration** enables the plant to optimize its use of N to fix C (Hirose & Werger 1987b, Pons et al. 1989, Field 1991). Mathematical models have been developed to assess the significance of a gradient in leaf N concentration, as opposed to a uniform distribution (Box 5.1).

What might be the physiological mechanism to achieve a N gradient that tends to follow the gradient of irradiance in the canopy? Leaves exposed to higher levels of irradiance, high in the canopy, will have higher rates of transpiration than the shaded ones lower in the canopy. This occurs partly because stomata respond to the level of irradiance (Sect. 5.4.4 of Chapter 3 on plant water relations), partly because of the greater vapor pressure difference between leaf and air higher in the canopy, and possibly also because the temperature of the top leaves is higher which increases the partial pressure of water vapor inside the leaf. The higher rate of transpiration causes a greater influx of solutes imported via the xylem, including amino acids and root-produced phytohormones. The greater N influx is probably not the immediate cause of enhanced incorporation of N into the photosynthetic apparatus, because far more N is imported via the xylem in leaves than is required for biosynthesis (Fig. 15). It is more likely that other xylem-transported compounds

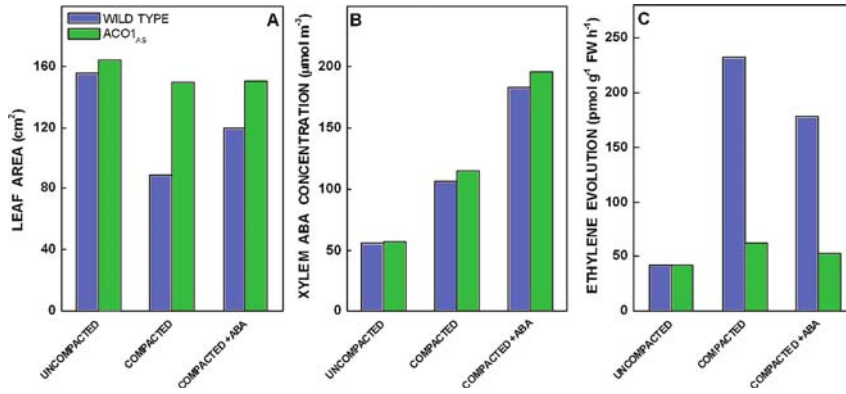


FIGURE 17. Effects of soil compaction on leaf growth, xylem ABA concentration, and ethylene production in wild type and a transgenic with a low capacity to produce ethylene of *Solanum lycopersicum* (tomato). (A) Total leaf area; (B) xylem sap ABA concentration; (C) leaf ethylene evolution at 21 days after emergence. Plants were well watered and grown in a split-pot system in which either both compartments contained uncompacted soil or one compartment contained uncompacted soil and the other contained compacted soil. The compartment containing compacted soil was supplied either with water or with 100 nM ABA (compacted +ABA) twice daily from day 5 (modified from Hussain et al. 2000).

control the differential incorporation of N in the leaves. **Cytokinins** are probably transported in greater amounts to rapidly transpiring leaves that are exposed to high levels of irradiance, compared with slowly transpiring leaves that are lower in the canopy (Fig. 16). In the top leaves, the greater inflow of cytokinins enhances the net incorporation of N into the photosynthetic apparatus (Sect. 5.4.4, Fig. 17). Other factors likely play an additional role, especially in trees where leaves in the outer canopy may have an extra layer of palisade parenchyma (Sect. 3.2.2 of Chapter 2A on photosynthesis), which may be programmed well before the leaf has developed and begins to transpire (Sect. 5.1.1.1) (Fig. 18).

The mechanism depicted in Fig. 17 leads us to the following question: to what extent does the plant achieve its N allocation to different leaves so as to maximize its rate of photosynthesis? To answer this question, ecophysiological experiments have to be combined with a modeling approach.

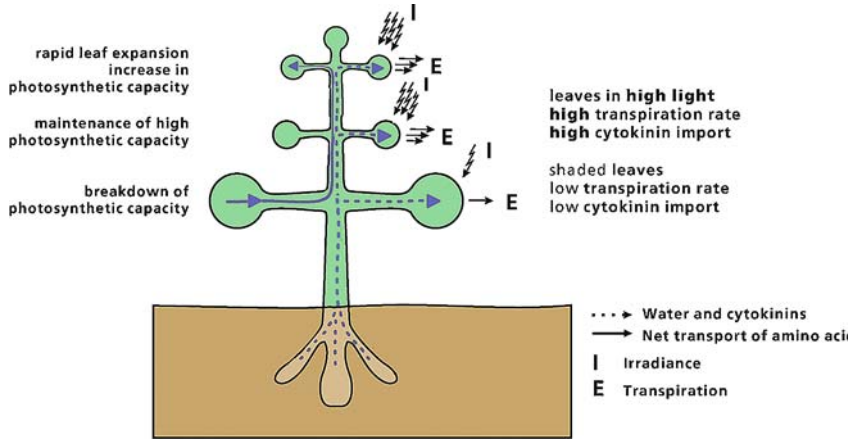


FIGURE 18. A hypothetical model to account for the differential allocation of N to leaves exposed to high or low levels of irradiance. Cytokinins are imported in greater amounts by rapidly transpiring leaves high in the canopy than by leaves lower in the canopy, which have lower rates of transpiration. Cytokinins then promote N incorporation into the photosynthetic apparatus. In the absence of a large inflow of cytokinins, much of the nitrogenous compounds imported via the xylem are exported again via the phloem. Based on information in Pons & Bergkotte (1996).

To assess whether plants optimize the allocation of N to the different leaves, we need to know (1) the gradient of light within the canopy, (2) the relationship between photosynthesis and the level of irradiance, and (3) the relationship between photosynthesis and leaf N concentration. The optimal pattern of N distribution is the one that maximizes the rate of photosynthesis of the entire plant (Box 5.1). The outcome can be summarized as follows. Although plants do not quite achieve the pattern of N allocation to their leaves that would yield the highest possible rate of canopy photosynthesis, both monocotyledons and dicotyledons, and both C_3 and C_4 plants, have a N allocation pattern that approaches the optimal pattern. In this way the plants have a higher rate of canopy photosynthesis than could have been achieved with a uniform N allocation pattern (Hirose & Werger 1987a,b, Pons et al. 1989, Anten et al. 1995).

5.5 Plant Growth as Affected by Soil Compaction

Soil structure affects plant performance in many ways, both reducing leaf growth and changing root morphology. Roots are smooth and cylindrical in friable soil, but they become **stubby** and **gnarled** with soil compaction and explore less soil, with potentially deleterious effects on the supply of water and nutrients (Bengough & Mullins 1990a,b).

5.5.1 Effects on Biomass Allocation: Is ABA Involved?

Plants that grow in compacted soil have a **reduced LMR**, even in the presence of adequate nutrients and water. Soil compaction tends to enhance the concentration of ABA in the xylem sap (Sharp 2002). ABA is probably responsible for a reduced stomatal conductance (Hussain et al. 1999), but is it also the cause of the reduction in leaf growth, as it is under water stress? This is unlikely, because ABA-deficient mutants of both *Solanum lycopersicum* (tomato) and *Zea mays* (corn) show exactly the same response as wild-type plants (Munns & Cramer 1996).

Hussain et al. (2000) compared a wild-type tomato (*Solanum lycopersicum*), an ABA-deficient mutant, and a transgenic genotype with a reduced capacity to produce **ethylene**. They grew their plants in pots with soil that was noncompacted, compacted, or layered in such a way that the plants first encountered noncompacted and then compacted soil. The wild type and the transgenic with a low capacity to produce ethylene show a similar increase in ABA concentration in the xylem sap. Because the leaf area expansion of the wild-type tomatoes is reduced to a greater extent than that of the transgenics, ABA can be discounted as the root-produced signal that affects leaf growth in compacted soil. Leaf expansion is invariably less in the ABA-deficient mutant. Reductions in leaf area expansion in wild-type and ABA-deficient mutants are associated with increased ethylene production. Application of ABA enhances the leaf expansion of the ABA-deficient mutant, and to a lesser extent that in the wild type. These results suggest that antagonistic interactions between ABA and ethylene regulate leaf expansion in tomato when the roots simultaneously encounter uncompacted and compacted soil (Fig. 17).

The responses of plants that grow in compacted soil are similar to those of plants that are **pot-bound** (i.e., grown in pots that are too small for their roots). The roots somehow sense the walls of the pots to be "impenetrable soil". Leaf area expansion is reduced, even when sufficient water and nutrients are provided. The xylem sap of pot-bound sunflower (*Helianthus annuus*) plants contains far more ABA than does the sap of control plants (Table 6), but in bean (*Phaseolus vulgaris*) no such effect is observed (Munns & Cramer 1996). These responses can also be expected in plants that encounter rocks or a hardpan. However, root growth of *Hakea* species adapted to ironstone soils and a Mediterranean climate in Western Australia, typically do not show inhibition of root growth when reaching the hard surface. Instead, they continue growth and thus maximize chances to reach cracks in the rocks which are essential for survival in their natural habitat (Poot & Lambers 2003, 2008).

5.5.2 Changes in Root Length and Diameter: A Modification of the Lockhart Equation

Mechanical resistance (impedance) of the soil can be an important factor that limits root growth in cropping as well as natural systems (Hamza & Anderson 2005). The resulting increase in the rate of **ethylene** production is the most likely cause for the observed reduction in root elongation and an increase in root diameter and (sometimes) number of cortical cells (Harpham et al. 1991). There is also a change in the branching pattern. When ethylene production is inhibited, however, soil compaction still induces the same root morphology. The effects of soil compaction on root morphology may therefore also be accounted for by physical effects.

TABLE 6. Effects of root confinement on yield and physiology of 14-day-old *Helianthus annuus* (sunflower) plants.*

Treatment	Fresh mass (mg)			Transpiration (mm day^{-1})	K^+ transport (pmol g^{-1} s^{-1})	Plant water potential (MPa)	[ABA] in xylem (nM)
	Shoot	Root	RMR				
Control	163	9.5	0.055	0.054	97	−0.51	10
Confined	112	3	0.061	0.053	136	−0.51	70

Source: Ternesi et al. (1994).
* The root mass ratio (RMR) is the root fresh mass as a fraction of total plant mass; K^+ transport (expressed per unit root fresh mass) was calculated from the concentration of K^+ in the xylem exudate and the rate of exudation. Plants were grown in such a way as to ensure that water and nutrients were supplied at an optimum level.

For the roots to be able to elongate, the mechanical impedance of the soil matrix acting against the cross-section of the root tip must be less than the pressure exerted by the root itself. To expand on Equation (6) (Sect. 2.2), the proportional root elongation (r) is the result of cell expansion, which is related to the cell-wall yield coefficient (ϕ, MPa^{-1} s^{-1}), the turgor pressure (Ψ_p, Pa), the **yield threshold of the root** (Ψ_r, MPa), and the **yield threshold of the soil** (Ψ_s, MPa) (Pritchard 1994):

$$r = \phi(\Psi_P - Y_r - Y_s) \qquad (10)$$

Maximum axial and radial root growth pressures range from 0.24 to 1.45 and from 0.51 to 0.90 MPa, respectively, and vary with plant species. Because it is impractical to measure the mechanical impedance of the soil directly by using actively growing roots, a **penetrometer** has been developed that measures the pressure required to force a steel probe, with a 60° or 30° conical tip (i.e., 30° or 15° semiangle), into the soil.

Root elongation is primarily determined by the rate at which files of cells are produced and by the cell elongation rate in the apex. Root elongation and total root length are reduced by mechanical impedance (Fig. 19), due to inhibition of cell elongation. The root diameter commonly increases because of radial cell expansion of cortical cells (Fig. 20) and the solute concentration of the root cells is enhanced (Atwell 1989). Thicker and more rigid roots which result from radial root expansion are thought to exert higher pressure on the surrounding soil and deform the soil ahead of the root which facilitates subsequent penetration (Pritchard 1994). Turgor measurements show **turgor pressures** of 0.78 MPa in impeded root tips of *Pisum sativum* (pea), as compared with 0.55 MPa in unimpeded root tip cells (Clark et al. 1996).

The smaller root system under conditions of soil compaction may be detrimental for the uptake of

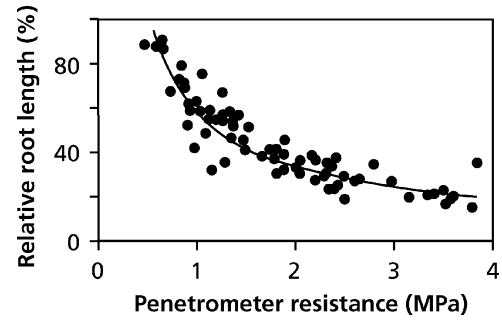


FIGURE 19. The relative root length of 70-day-old plants of *Zea mays* (corn), *Gossypium hirsutum* (cotton), *Triticum aestivum* (wheat), and *Arachis hypogaea* (groundnut) as dependent on mechanical impedance of the soil, as determined with a penetrometer (after Bennie 1996).

nutrients and water, and hence reduce the plant's growth rate and productivity. There are also effects on leaf expansion, however, that are not accounted for by the plant's water or nutrient status. Roots perceive soil compaction as such, and they send inhibitory signals to the leaves which cause a **feed-forward response** (Stirzaker et al. 1996). There is no conclusive evidence that species differ in their capacity to grow in compacted soil. Rather, they differ in their capacity to find less compacted sites in the same soil (Sect. 5.5.1; Bennie 1996). They may also differ in the size of their root system and hence in the extent to which they explore the soil, including the compacted part (Materechera et al. 1993).

5.6 Growth as Affected by Soil Flooding

Flooding or inundation of the soil leads to filling with water of the soil pores that are normally filled with air. This reduces the supply of soil O_2 which may reduce aerobic respiration (Sect. 4.1 of Chapter

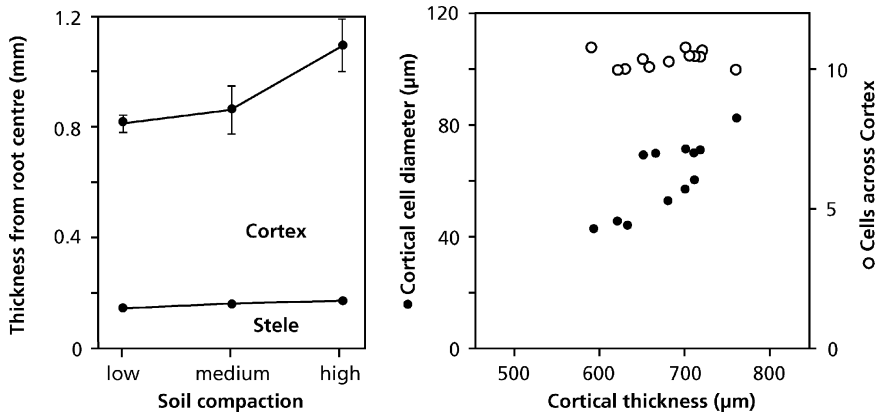


FIGURE 20. The radius of the stele and cortex in roots of *Lupinus angustifolius* (narrow-leaved lupin), (*left*) grown at three levels of soil compaction and (*right*) the diameter and number of cortical cells and mean cortical cell diameter of the same plants. Increasing cortical thickness on the abscissa in the right-hand figure is the result of increased soil compaction, as illustrated in the left-hand figure (Atwell 1989).

2B on plant respiration). Flooding also affects the roots' hormone metabolism. Concentrations of **ethylene** in the roots increase, largely because this gas diffuses more slowly in a flooded soil than it does in a well aerated soil, so that it gets trapped in the roots, and partly because of an enhanced production of this hormone (Colmer 2003).

5.6.1 The Pivotal Role of Ethylene

Ethylene inhibits root elongation and induces the formation of **aerenchyma** in roots (Fig. 21). **Lysigenous aerenchyma** formation, which involves death and dissolution of cortical cells, is preceded by enhanced transcription of a gene that encodes a **xyloglucan endotransglycosylase**, which is a cell-wall loosening enzyme involved in the hydrolysis of cell walls (Sect. 2.2) and ultimately in the **lysis** of some **cortical cells** (Saab & Sachs 1996): **programmed cell death**. The ethylene-induced aerenchyma facilitates **gas diffusion** between roots and aerial parts (Sect. 4.1.4 of Chapter 2B on plant respiration), because the large cross-sectional area of gas space reduces the physical resistance to gas movement. Many hydrophytes such as *Oryza sativa* (rice) and *Senecio congestus* (marsh fleabane) possess extensive aerenchyma even when growing in well-drained conditions. In mesophytes such as *Zea mays* (corn) and *Helianthus annuus* (sunflower), however, cortical aerenchyma formation by cell breakdown is minimal in well-aerated conditions and is promoted by poor aeration (Colmer 2003).

Ethylene also increases the **elongation of the coleoptile** in seedlings of *Oryza sativa* (rice), and, at later growth stages, stem internodes, so that shoots reach the surface of the water more rapidly. In the flood plains of Bangladesh, internodal growth rates of up to 25 cm day^{-1} have been recorded. Submergence induces accumulation of mRNA that encodes **expansins** before the rate of growth starts to increase (Cho & Kende 1997c). The "snorkeling" response is characteristic of most flood-tolerant species. A similar response has been found for petioles and lamina in the flood-tolerant *Rumex palustris* (marsh dock) during submergence of entire plants. The flood-sensitive *Rumex acetosa* (sorrel), on the other hand, responds to flooding with enhanced ethylene concentrations in the shoot, but not with enhanced elongation rates (Peeters et al. 2002). This indicates that it is the greater **responsiveness to ethylene**, and not the enhanced ethylene production, that increases petiole elongation in the flood-tolerant *Rumex* species (Banga et al. 1996). The increased responsiveness of the flood-tolerant *Rumex* species is associated with an increased transcription of the gene encoding for an ethylene receptor upon submergence. High concentrations of ethylene and exposure to high concentrations of CO_2 and low concentrations of ethylene increase the levels of transcripts encoding for the ethylene receptor. Therefore, flood-tolerant *Rumex* species respond to flooding stress by increasing their number of **ethylene receptors** which subsequently enhances their responsiveness to ethylene, leading to leaf elongation (Vriezen et al. 1997). The interaction of three hormones (ethylene, ABA, and GA) determines the growth rate of the shoot. Ethylene renders the internode more responsive to GA by

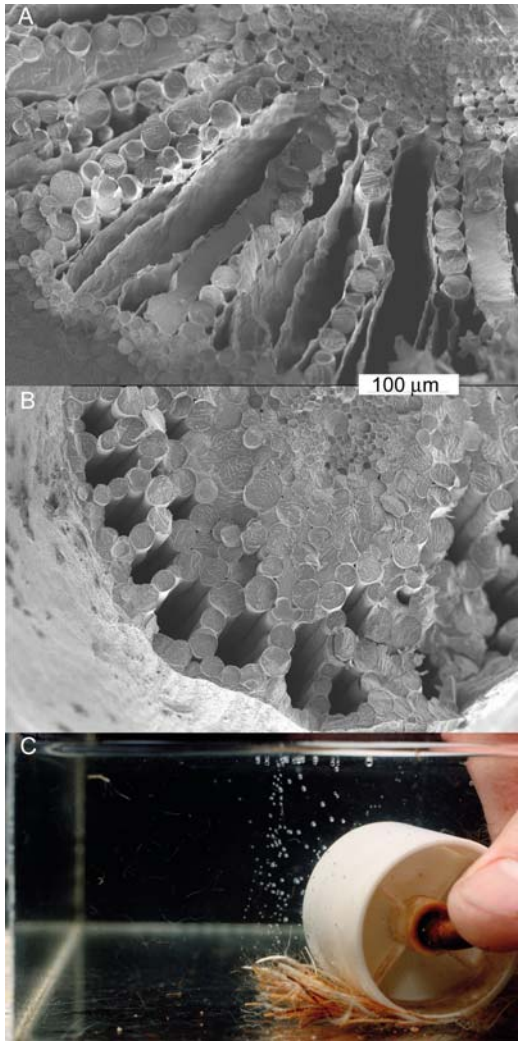


FIGURE 21. Aerenchyma in roots. Scanning electron micrograph of (A) constitutive, lysigenous aerenchyma of *Juncus effusus* (soft rush) and (B) constitutive, schyzogenous aerenchyma of *Rumex palustris* (marsh dock). The horizontal bars indicate a length of 100 µm (courtesy L. Mommer, Department of Ecology, Radboud University Nijmegen, the Netherlands). (C) Evidence of air-filled aerenchyma in roots of *Oryza sativa* (rice) is provided by bubbles coming from cut ends of roots squeezed gently with a roller under water. The rice plants were grown in waterlogged soil [courtesy T. L. Setter, Department of Agriculture and Food Western Australia, Perth, Australia; Setter & Belford (1990)].

lowering the level of endogenous ABA. GA is the immediate growth-promoting hormone and acts by enhancing cell elongation and, probably indirectly, by increasing cell-division activity in the intercalary meristem. Rice internodes contain two **expansins** that may mediate acid-induced wall extension (Cho & Kende 1997a,b).

In *Potamogeton pectinatus* (water chestnut) it is the root that shows a "snorkeling" response to flooding; it reaches the surface of the water by growing upward, rather than showing the normal positive gravitropism (Summers & Jackson 1994).

5.6.2 Effects on Water Uptake and Leaf Growth

The responses of leaf growth and metabolism to soil inundation are similar to those of water-stressed plants. Flooding delays the normal daily increase in root **hydraulic conductance** in flooding-sensitive *Solanum lycopersicum* (tomato) plants (Else et al. 1995). This is probably due to **cytosol acidosis** and the inhibitory effect of a low pH on **aquaporins** (Sect. 5.2 of Chapter 3 on plant water relations). **Stomatal conductance** declines and the rate of **leaf elongation** is reduced (Fig. 22). If the lower hydraulic conductance is compensated by

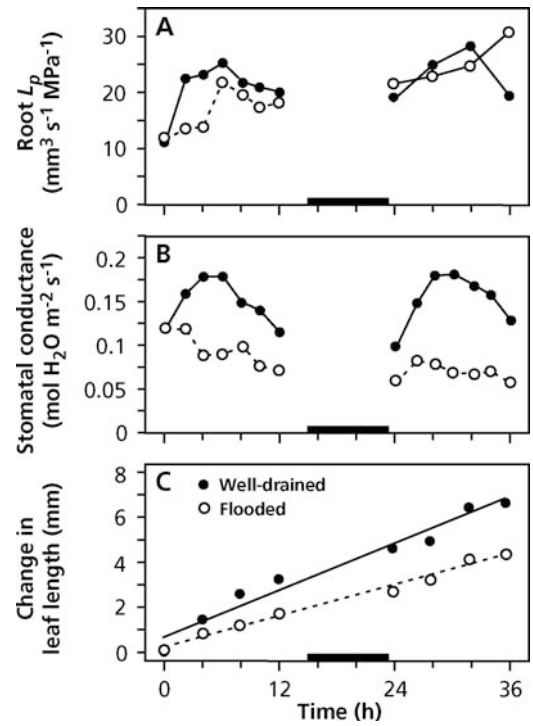


FIGURE 22. Effects of soil flooding for 24–36 hours on (A) root hydraulic conductance, (B) stomatal conductance, and (C) leaf elongation of *Solanum lycopersicum* (tomato) (after Else et al. 1995). Copyright American Society of Plant Biologists.

pressurizing the roots (Sect. 5.3), however, both the stomatal conductance and the rate of leaf expansion remain low. As in plants exposed to water shortage, **chemical signals** are responsible for the early responses to flooding in sensitive plants. **ABA** is one of the chemical signals arriving from the roots that cause stomatal closure (Else et al. 1996). Exposure of roots to hypoxia also reduces leaf **cell-wall extensibility**, and it is paralleled by a decreased capacity to **acidify leaf cell walls** (Van Volkenburgh 1994).

5.6.3 Effects on Adventitious Root Formation

When the effects of soil flooding become too severe, plants with some degree of flooding tolerance make new, aerenchymatous adventitious roots with air channels to the shoot that permit O_2 diffusion to the new roots (Colmer 2003). Endogenous **auxin** is the phytohormone that is generally responsible for adventitious root formation, even in flooding-sensitive plants. Auxin accumulates at the base of the shoot, possibly due to inhibition of the energy-dependent transport of auxin to the roots. In the flood-tolerant *Rumex palustris* (marsh dock) both **ethylene** and **auxin** enhance the formation of new adventitious roots (Table 7). Because ethylene has no effect in the presence of an inhibitor of auxin transport, it must exert its effect through auxin. Because the concentration of auxin is not increased, ethylene, which accumulates upon flooding the plants, must enhance the tissue's sensitivity for endogenous auxin, allowing root primordia to develop where they would otherwise remain dormant (Visser et al. 1996).

Table 7. The effect of exposure to hypoxia and treatment with auxin, ethylene, or a combination of ethylene and an inhibitor of auxin transport on the formation of adventitious roots in the flooding-tolerant *Rumex palustris* (marsh dock).

Treatment	Number of adventitious roots
Aerobic control	4
Anaerobic control	43
Auxin	45
Ethylene	44
Ethylene + inhibitor	8

***Source*: Visser et al. (1996).**

5.6.4 Effects on Radial Oxygen Loss

Aerenchyma provides a low-resistance internal pathway for the exchange of gases between the atmosphere and the submerged plant parts. Respiration by tissues along the pathway in aerenchymatous roots decreases the amount of O_2 that is available for the growing root apex, eventually restricting the maximum length of these roots in an O_2-free environment. A potentially greater sink for O_2 along the pathway is the **radial loss of O_2** to the soil. Many wetland species prevent excessive O_2 loss from the basal root zones by forming a complete or partial **barrier to radial O_2 loss** (Armstrong 1971, 1979). Radial O_2 loss tends to be less in species that are adapted to waterlogging than in waterlogging-sensitive species (McDonald et al. 2002, Garthwaite et al. 2003). The barrier for radial O_2 loss may be constitutive [e.g., in *Carex acuta* (slender tufted sedge) and *Juncus effusus* (common rush)] or inducible [e.g., in *Caltha palustris* (marsh marigold) and *Oryza sativa* (rice)] (Colmer et al. 1998, Visser et al. 2000).

5.7 Growth as Affected by Submergence

Flooding of terrestrial plants may also submerge aerial parts, restricting gas exchange not only of the roots but also of the leaves. Two alternative responses can be observed under different flooding regimes: (1) dormancy, characterized by tolerance of the stress and reduced metabolic activity; (2) escape, due to shoot elongation, which establishes aerial contact. The **elongation response** requires energy expenditure, which is only "paid back" when aerial contact is established. Under conditions of deep or short-lasting floods tolerance of **hypoxia** and reduced metabolic activity are favored (Setter & Laureles 1996, Voesenek et al. 2004).

Plants that escape **submergence** occur in habitats that are temporarily and shallowly flooded and where the water table rises gradually. Plants with a rosette habit typically show hyponastic growth (upward curving) of petioles and leaves and increased extension of petioles (Fig. 23). When a stem is present, internodes elongate strongly upon submergence. The increased growth toward the surface re-establishes or maintains aerial contact that facilitates gas exchange and increases survival (Voesenek et al. 2004). Flood-prone environments with long-lasting submergence periods are found in river floodplains where depressions and embankments can trap water, causing continued submergence after the flood has receded. *Rumex palustris* (marsh dock) is a typical example of a species that

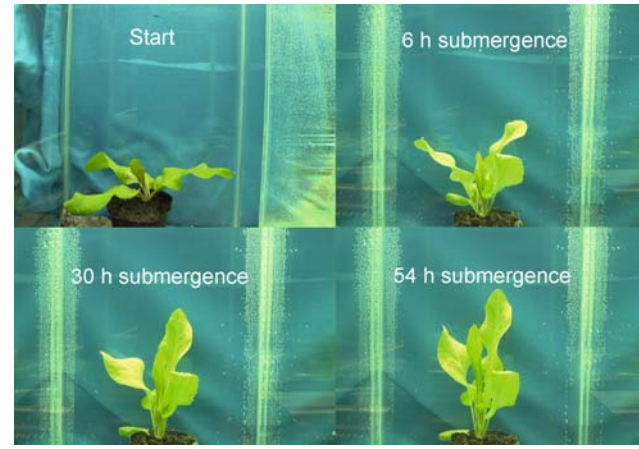


FIGURE 23. Submergence-induced hyponastic growth and petiole elongation in *Rumex palustris* (marsh dock). At the start of the submergence treatment plants had an age of 28 days. Plants were submerged up to 54 hours (Voesenek et al. 2003). Courtesy M.C.H. Cox & L.A.C.J. Voesenek, Department of Biology, Utrecht University, Utrecht, the Netherlands.

shows the above-mentioned "snorkeling" behavior, whereas the closely related *Rumex acetosa* (sorrel) from higher, better-drained sites does not show such a response to submergence (Voesenek et al. 2004). Deepwater rice (*Oryza sativa*) is also adapted to seasonal floods; its internodes elongate to such an extent that the shoots keep pace with the rising water levels in the monsoon season in river deltas in south-east Asia. Leaves and panicles can thus be in contact with air above water of several meters deep (Kende et al. 1998).

Tolerance of the conditions after the water level drops is part of the **suite of traits** that allow survival in occasionally flooded areas. Protection against desiccation and damage as a result of the sudden exposure to O_2 after a prolonged period of hypoxia is an important aspect.

5.7.1 Gas Exchange

Net photosynthetic CO_2 uptake essentially stops upon submergence of terrestrial plants at the low ambient CO_2 concentrations in water (Vervuren et al. 2003). Only higher CO_2 concentrations allow net CO_2 assimilation (and thus net O_2 production). The capability of CO_2 exchange is improved after a period of acclimation under water. Leaves of *Rumex palustris* (marsh dock) that develop under water are thinner with a thin cuticle. Furthermore, chloroplasts in the mesophyll cells orient toward the epidermis, indicating that **diffusion of CO_2** takes place predominantly through the **cuticle**, rather than through the stomata that are closed under water. Although net photosynthetic CO_2 uptake may be absent under water, photosynthetic electron transport continues, as evidenced by **chlorophyll fluorescence** (Mommer et al. 2005). There is apparently recycling of CO_2 derived from (photo)respiration in photosynthesis which may produce some ATP and help dissipate excess energy in strong light.

Although photosynthetic O_2 evolution may be restricted under low ambient CO_2 conditions, it can be substantial at elevated CO_2 in flood water. Moreover, O_2 can diffuse into the leaf at sufficiently high concentrations (Mommer et al. 2004). Hence, provided the water is sufficiently clear and gas concentrations are suitable, the internal O_2 can facilitate aerobic respiration. Internal diffusion through aerenchyma to below-ground parts can further improve O_2 conditions and contribute to long-term survival of submergence-tolerant plants.

5.7.2 Perception of Submergence and Regulation of Shoot Elongation

Ethylene accumulates under submergence conditions (Sect. 5.6). Normal internal concentrations are in the range of 0.02–0.05 μmol mol^{-1}, but they can increase to 1 μmol mol^{-1} within an hour after submergence (Bailey-Serres & Voesenek 2008) and enhance further by increased ethylene production (Kende et al. 1998). Exposure of a responsive plant to a high ethylene concentration without submergence is sufficient to initiate shoot elongation. Reduced internal O_2 levels further promote the submergence-avoidance response and increased CO_2 concentrations also contribute to the signal in deepwater rice (*Oryza sativa*). Ethylene accumulates also upon submergence in *Rumex acetosa* (sorrel), but this flood-intolerant species does not respond to submergence or high ethylene concentration with enhanced shoot elongation.

The first reaction of *Rumex palustris* (marsh dock) upon submergence is **hyponastic growth**, i.e., a more vertical orientation of the petiole and leaf

blade (Fig. 23) which is a condition for further petiole extension. Ethylene-stimulated petiole and internode elongation in *Rumex palustris* and *Oryza sativa* (rice) depends on a reduced level of the inhibitor ABA relative to the stimulator of extension growth GA (Kende et al. 1998, Voesenek et al. 2006). The ABA:GA ratio quickly changes upon submergence by increased breakdown of ABA and de novo synthesis of GA. A further essential step is that cell-wall extensibility is enhanced both by increased expression of specific **expansins** and **acidification** of the cell wall. These events downstream of the signal perception allow the rapid (within a few hours) onset of extension growth toward the water surface.

5.8 Growth as Affected by Touch and Wind

Some plants can "move" when touched. Unless *Mimosa pudica* (touch-me-not) has just been assaulted by a classroom of school children, its petioles and pinnate leaves will respond to touch, due to the movement of ions in the pulvinus (Sect. 5.4.6 of Chapter 3 on plant water relations). These movements in response to touch are *not* related to growth. The growth of some plant organs, however, does respond to touch (e.g., the **tendrils** of climbing plants like *Clematis* or *Lathyrus*). Upon contact, these tendrils enhance their growth at the side away from the point of contact, sometimes in combination with a growth reduction at the side where contact occurred. Another response of the tendril to contact may be a strong reduction in the rate of elongation, as in the tendrils of *Cucumis sativus* (cucumber) (Ballaré et al. 1995). Susceptibility of plants to contact was already recognized by Theophrastus, around 300 BC, and by Darwin (1880), who described this phenomenon for the apex of the radicle of *Vicia faba* (broad bean). Since then, it has been shown that wind, vibrations, rain, and turbulent water flow affect a plant's physiology and morphology which is a phenomenon generally termed **thigmomorphogenesis** (Esmon et al. 2005). Wind exposure may make plants less susceptible to other forms of stress. Mechanical stimulation of young internodes of *Bryonia dioica* (Cretan bryony) reduces their elongation and increases their radial expansion. This is associated with an acceleration of lignification and a transient increase in **ethylene** production, preceded by a redistribution of Ca^{2+} within the cell and expression of specific proteins (Thonat et al. 1997). An extreme form of thigmomorphogenesis is found in trees at high altitude, which show the typical "**Krumholz**" sculpture (i.e., a wind-induced deformation). Trees at the edge of a plantation or forest tend to be hardened by wind and have thicker and shorter trunks. Whenever these trees are removed, the weaker, slender trees are easily knocked over (Jaffe & Forbes 1993).

Plant growth may decline in response to careful touching or stroking of leaves, much to the disappointment of some students who have tried to carry out a **nondestructive growth analysis**. Although not all species or genotypes of a species show thigmomorphogenesis to the same extent, it is a common and often underestimated phenomenon, generally associated with a reduction in plant growth. Canopy effects on stem growth are usually ascribed to shading, but reduced mechanical stress also plays a role. This canopy effect on *Nicotiana tabacum* (tobacco) is that plants produce shorter but thicker and more flexible stems (Table 8). Touching the leaves may also affect leaf respiration, in some species by as much as 56% (Todd et al. 1972), transpiration, and chemical composition, even in plants whose growth may not be reduced by such a treatment (Kraus et al. 1994). Roots show thigmotropic reactions when encountering obstacles in soil and grow around these (Fasano et al. 2002).

Exposure of the grasses *Lolium perenne* (perennial ryegrass) and *Festuca arundinacea* (tall fescue) to a high wind speed of 8.4 m s^{-1}, as compared with 1.0 m s^{-1} for control plants, reduces their rate of leaf elongation by about 25% which is partially reversible. The wind-exposed plants are shorter and less leafy. Although wind speed reduces leaf temperature of these grasses, this effect is small and cannot account for the large effects on leaf elongation. Wind speed reduces the LAR, mainly due to a decrease in SLA. The RGR of the grasses is also reduced, although not to the same extent, due to a 15% increase in NAR by this wind treatment (Russel & Grace 1978, 1979).

Thigmomorphogenetic effects may vary among genotypes of the same species (Table 8). An alpine ecotype of *Stellaria longipes* (longstalk starwort), which is characterized by a short erect habit, produces substantial amounts of **ethylene** in response to wind, and stem growth is inhibited by ethylene (Emery et al. 1994). By contrast, the prairie ecotype produces substantial amounts of ethylene even in the absence of wind stress, but stem growth is not inhibited by ethylene. This demonstrates that ethylene dwarfs stems in alpine *Stellaria longipes* primarily as a result of increased sensitivity to the ethylene produced during wind stress. To an alpine plant, wind is an important selective force, whereas in the prairie habitat it is important that stems elongate rapidly, in order to avoid being overtopped by

Table 8. Stem characteristics measured on control and flexed *Nicotiana tobacco* (tobacco) plants grown either in isolation or in a mixed stand.*

	Isolated plants		Mixed stand	
	Control	Flexed	Control	Flexed
Mechanical properties				
Height (cm)	84	67	61	27
Diameter	13.3	14.8	8.4	1
σ_b	10.7	9.3	10.1	4.3
E	1.6	0.9	1.1	0.1
Growth data				
Leaf mass ratio	0.47	0.49	0.49	0.54
Stem mass ratio	0.38	0.35	0.38	0.34
Root mass ratio	0.15	0.16	0.13	0.11

***Source*: Anten et al. (2005).**

* **In the mixed stand, flexed and control plants were mixed together. The properties σ_b and E are the breaking stress and Young's modulus (a measure for stiffness) of the stem, respectively; both σ_b and E are expressed in N m^{-2}.**

competitors. Such genetic differentiation likely affects a genotype's success in contrasting environments, as further discussed in Chapter 9E on interactions among plants.

Exposure of *Arabidopsis thaliana* (thale cress) to wind, rain, or touch led to the serendipitous discovery that these stimuli rapidly (within 10 min) induce several **touch-specific** (*TCH*) **genes**, three of which encode **calmodulin**, which is a Ca-binding protein that turns on several cellular processes, or calmodulin-related proteins (Braam & Davis 1990). The gene *TCH4* encodes XET (**xyloglucan endotransglycolase**, an enzyme that breaks cross-links among cell-wall carbohydrates and promotes wall loosening) (Braam et al. 1996). It is interesting that overall XET levels decline after wind stimulation, whereas TCH4 (i.e., the product of the gene *TCH4*) increases (Antosiewicz et al. 1997). Using *in planta* expression of the jellyfish apoaequorin gene, which encodes a Ca-dependent luminescent protein, Knight et al. (1991, 1992) showed that touch immediately increases cytosolic free Ca levels. Calcium has therefore been implicated as the **second messenger** that induces the expression of the *TCH* genes (Esmon et al. 2005). The increased production of calmodulin and calmodulin-related proteins probably starts many Ca-regulated events. For example, wind-induced production of calmodulin reduces the rate of elongation of petioles and of bolting in *Arabidopsis thaliana*, modifies callose deposition, and induces auxin-enhanced growth and mitosis. Up-regulation of the XET-encoding gene may play a critical role in determining properties of the cell wall, including extensibility (Sect. 2.2).

5.9 Growth as Affected by Elevated Concentrations of CO_2 in the Atmosphere

On average, the final mass of C_3 plants, grown at high nutrient supply without shading by neighboring plants, increases by 47% when the atmospheric CO_2 concentration is doubled to 700 μmol mol^{-1} (70 Pa) (Poorter et al. 1996). When plants have **numerous sinks**, such as tillers or side shoots, this stimulation can be even higher (several hundred percent). The average enhancement is, however, much less than the extent of the stimulation of the rate of **photosynthesis** in short-term experiments (Fig. 6, Sect. 2.2.1 of Chapter 2A on photosynthesis). To explain why growth is less sensitive to CO_2 than is photosynthesis, it is helpful to examine the impact of elevated [CO_2] on each growth parameter (Sect. 2.1.1):

$$\mathrm{RGR} = \frac{(A_a \cdot \mathrm{SLA} \cdot \mathrm{LMR} - \mathrm{LR_m} \cdot \mathrm{LMR} - \mathrm{SR_m} \cdot \mathrm{SMR} - \mathrm{RR_m} \cdot \mathrm{RMR})}{[\mathrm{C}]} \qquad (11)$$

where A_a is the rate of photosynthesis per unit leaf area; RGR is the plant's relative growth rate; SLA is the specific leaf area; LMR, SMR, and RMR are the leaf mass ratio, stem mass ratio, and root mass ratio, respectively; LR_m, SR_m, and RR_m are the rate of respiration per unit mass of the leaves, stems, and

roots, respectively; [C] is the carbon concentration of the plant biomass. If the RGR and final mass of the plants are enhanced less than expected from the increase in rate of photosynthesis, one or more of the parameters in the equation must have been affected by elevated atmospheric CO_2 concentrations. In other words, growth at 700 µmol mol^{-1} CO_2 leads to a number of changes in the plant that may compensate for the higher rate of photosynthesis as found in A vs. C_c curves. Photosynthetic **acclimation** to high CO_2 concentrations was addressed in Sect. 12.1 of Chapter 2A on photosynthesis. Here we discuss some additional changes that counteract the initial stimulation of photosynthesis.

There are numerous examples where exposure of plants to a high atmospheric CO_2 concentration transiently enhances the plant's RGR, followed by a return to the RGR found in control plants (e.g., Wong 1993, Fonseca et al. 1996). The **transient increase in RGR** may account entirely for the increase in final mass of the plants grown at elevated [CO_2] (Fig. 24). Some species show a sustained enhancement of RGR, but some degree of acclimation is common. Which component(s) of the growth equation accounts for such acclimation?

A **decrease in SLA** is the major adjustment found upon prolonged exposure to 700 µmol mol^{-1} CO_2. This is partly due to the accumulation of nonstructural carbohydrates (Sect. 3.4 of Chapter 2C on long-distance transport). LMR, SMR, and RMR are not, or are only marginally, affected (Stulen & Den Hertog 1993). If they are affected, then it is due to the more rapid depletion of nutrients in the soil of the faster-growing plants exposed to elevated [CO_2].

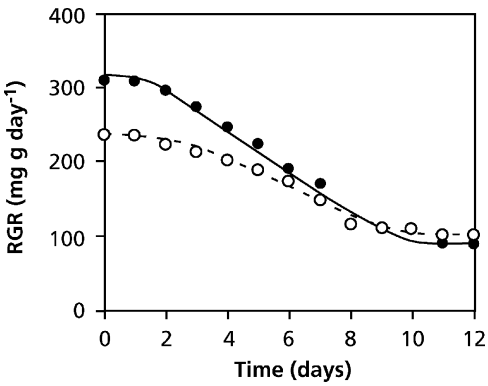


FIGURE 24. The relative growth rate (expressed on a fresh mass basis) of *Plantago major* (common plantain) grown at 350 µmol mol^{-1} CO_2 (*open symbols*) or at 700 µmol mol^{-1} CO_2 from day zero onward, when the plants were 4 weeks old (Fonseca et al. 1996). Copyright Trustees of *The New Phytologist*.

Leaf respiration is increased by long-term exposure to high [CO_2] (Sect. 4.7 of Chapter 2B on plant respiration). The carbon concentration varies with CO_2 concentration, but without a distinct trend (Poorter et al. 1992). Results from short-term measurements on single leaves clearly cannot simply be extrapolated to the growth of whole plants over a long period. About two-thirds of all studies show enhanced biomass production at elevated [CO_2] (Luo et al. 2006).

Different types of plants may respond to varying degrees to elevated [CO_2]. For example, **C_4 plants**, whose rate of photosynthesis is virtually saturated at 350 µmol mol^{-1} CO_2, respond to a smaller extent (Poorter et al. 1996). Elevated [CO_2] does not consistently affect the **competitive balance between C_3 and C_4 plants** (Sect. 5.4 of Chapter 9E on interactions among plants).

6. Adaptations Associated with Inherent Variation in Growth Rate

6.1 Fast- and Slow-Growing Species

In **unpredictable but productive environments**, where "catastrophes" like fire, inundation, or other forms of disturbance occur, **fast-growing short-lived species** are common. In more **predictable environments** with a low incidence of disturbance, **longer-lived slow-growing species** predominate. Apart from their life span, these short- and long-lived species differ in many other traits and, broadly generalizing, have been termed **r-species** and **K-species**, where r and K are constants in a logistic growth curve (McArthur & Wilson 1967, Pianka 1970). Such a classification, once proposed for both plants and animals, has been questioned, but it provides a useful context in which to understand the ecological performance of vastly different species (Table 9).

Grime (1979) extended this concept by suggesting that there are two major categories of selective factors: **stress**, which is an environmental factor that reduces the growth rate of plants, and **disturbance**, which is a factor that destroys plant biomass. High-stress environments include those with low availability of water, nutrients, and light or where other conditions are unfavorable for growth (low

TABLE 9. Some of the characteristics of r- and K-species and the habitats in which they occur.

	r selection	K selection
Climate	Variable and/or unpredictable; uncertain	Fairly constant and/or predictable; more certain
Mortality	Often catastrophic; density independent	Density dependent
Population size	Variable; usually well below carrying capacity; frequent recolonization	Fairly constant; at or near carrying capacity; no recolonization required
Intra- and interspecific competition	Variable; often minor	Usually severe
Traits favored by selection	Rapid development High growth rate Early reproduction Single reproduction	Slower development Competitive ability Delayed reproduction Repeated reproductions
Life span	Relatively short	Longer

temperature, high salinity, low oxygen, heavy metal contamination). Disturbance can result from herbivory or from environmental factors like fire or wind. Grime describes three extreme types of plant strategies: **competitors**, which exist under conditions of low stress and low disturbance; **stress-tolerant** species, which occupy habitats with high stress and low disturbance; and **ruderals** (=weeds), which occur in highly disturbed nonstressful environments. There is no viable plant strategy that can deal with the combination of high stress and high disturbance. Most plants actually fall at intermediate points along these continua of stress and disturbance, so it is most useful to use the scheme in a comparative sense, with some species being more stress-tolerant than others, some species more tolerant of disturbance than others. Although this classification has also been seriously questioned, it has led to the recognition that plants characteristic of low-resource and stressful environments consistently have a lower RGR than do plants from more favorable environments (Box 9E.1).

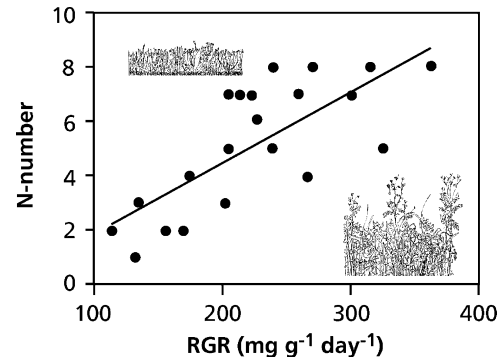


FIGURE 25. The relationship between the relative growth rate (RGR) of 24 herbaceous C_3 species and the "N-number" of the species' habitat (high values correspond to habitats of high N availability). The RGR was determined under identical conditions for all species: free access to nutrients and an irradiance of 320 μmol m^{-2} s^{-1} (Poorter & Remkes 1990).

The close association between a species' growth potential and the quality of its natural habitat (Fig. 25) raises two questions. First, how are the differences in growth rate between species brought about? Second, what ecological advantage is conferred by a plant's growth potential? These two questions are in fact closely related. Before evaluating the **ecological significance** of the inherent RGR of a species, it is important to analyze the **physiological basis** of the genetic variation in RGR (Lambers & Poorter 2004). Numerous plant characteristics contribute to a plant's absolute growth rate in its natural habitat (e.g., seed size, germination time, or plant size after overwintering). In view of the close correlation between a plant's inherent RGR and environmental parameters (Fig. 25), we restrict the present discussion to traits that contribute to variation in RGR. Finally, we discuss the ecological implications of inherent differences in the various traits and in the growth rate itself.

6.2 Growth of Inherently Fast- and Slow-Growing Species Under Resource-Limited Conditions

In Sect. 2.1 we compared plants under conditions favorable for growth. How do fast- and

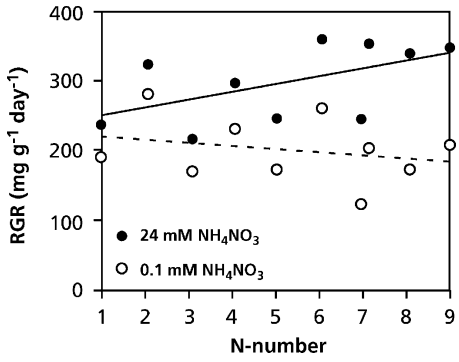


FIGURE 26. The RGR of 10 annual herbaceous C_3 species grown at a high and a low N supply. The 10 species were from habitats differing in "N-number" (higher values indicating a higher N availability as well as an inherently higher RGR_{max}) (Fichtner & Schulze 1992).

slow-growing species perform at a low nutrient concentration?

6.2.1 Growth at a Limiting Nutrient Supply

Although the RGR of potentially fast-growing species is reduced more than that of slow-growing ones, when nutrients are in short supply, the inherently fast-growing species still tend to grow fastest (Fig. 26). Similar results are obtained in a situation where a fast-growing species competes with a slow-growing one under nutrient stress, at least when the duration of the experiment is short, relative to the plant's life span.

The higher RGR of inherently fast-growing species at a low nutrient supply, in comparison with slow-growing ones, is largely "explained" by differences in LAR (SLA) which is similar to the situation with free access to nutrients (Table 10). (Note that "explained" is used here in a statistical sense and that it does not refer to physiological mechanisms.)

6.2.2 Growth in the Shade

In a comparison of tropical tree species, fast-growing species with a high LAR and low RMR maintain a higher RGR when grown in the shade; however, they also show greater mortality (Kitajima 1994). This trend can be accounted for by greater investment in defense against herbivores and pathogens (dense and tough leaves) in the slower-growing trees, which have a large root system and a high wood density (Kitajima 1996).

6.3 Are There Ecological Advantages Associated with a High or Low RGR?

The ecological advantage of a high RGR seems straightforward: fast growth results in the rapid occupation of space, which is advantageous in a situation of competition for limiting resources. A high RGR may also maximize the reproductive output in plants with a short life span, which is particularly important for ruderals. What is the possible survival value of slow growth? Grime and Hunt (1975) and Chapin (1980, 1988) offered several explanations, which we review in this section.

6.3.1 Various Hypotheses

It has been suggested that slow-growing species make modest demands and are therefore less likely to exhaust the available nutrients (Parsons 1968). This is not a stable evolutionary strategy, however, because a neighboring individual with a faster nutrient uptake could absorb most nutrients (Schulze & Chapin 1987). In addition, these modest demands cannot explain slow growth as an adaptation to saline environments or other situations where conditions are stressful for reasons other than low resource supply.

TABLE 10. The effect of a nutrient solution with a high or a low NO_3^- concentration on some growth parameters of an inherently slow-growing species [*Deschampsia flexuosa* (tufted hair-grass)] and a fast-growing one [*Holcus lanatus* (common velvet grass)]

Parameter	High [NO_3] *Deschampsia*	*Holcus*	Low [NO_3] *Deschampsia*	*Holcus*
RGR	97	172	47	66
NAR	6.9	8.5	5.2	4.6
LAR	13	20	9	14
SLA	28	51	24	44

Source: Poorter et al. (1995).

Slow-growing species have also been suggested to function closer to their optimum than fast-growing ones in an adverse environment (Chapin 1980). This explanation suggests that allocation or some other aspects of the plant's physiology at a low nutrient supply is closer to the optimal pattern for inherently slow-growing species than for fast-growing ones. Information on the pattern of allocation, however, indicates that both fast- and slow-growing species allocate their carbon and N in a manner that maximizes their RGR (Van der Werf et al. 1993).

Slow-growing species were thought to incorporate less photosynthates and nutrients into structural biomass. This might allow them to form reserves for later growth, thereby enabling them to maintain physiological integrity during periods of low nutrient availability. As we discuss in Sects. 5.3.3 and 5.4.3, however, under such adverse conditions, growth is restricted before photosynthesis is, and sugars tend to accumulate. Hence, it is unlikely that survival during periods of nutrient shortage depends on storage of photosynthates.

There is also no evidence that slow-growing species have a greater capacity to accumulate nutrients, perhaps with the exception of P. Finally, it has been suggested that a high growth rate cannot be realized in a low-resource environment; therefore, a high potential RGR is a selectively neutral trait. As discussed in Sect. 6.2, however, potentially fast-growing species still grow faster than potentially slow-growing ones, even in low-resource environments. This indicates that the potential RGR is not a selectively neutral trait. Even in low-resource environments, fast-growing species attain a larger size more rapidly, which has advantages in terms of their competitive ability and fitness. Although a very high RGR is not attainable, a slightly higher RGR might, therefore, still be advantageous.

6.3.2 Selection on RGR_{max} Itself, or on Traits That Are Associated with RGR_{max}?

Having scrutinized the various hypotheses accounting for variation in growth potential, 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 unfavorable habitats than do fast-growing ones? An alternative explanation for the observed differences in potential growth rate is that one of the **components linked with RGR**, and not RGR itself, has been the target of selection (Lambers & Poorter 2004).

The most likely traits selected for are those that protect the tissue (**quantitative defense**; Sect. 3.2 of Chapter 9B on ecological biochemistry). In leaves this is associated with a **low SLA**, which is accounted for by variation in **leaf mass density** (i.e., the amount of dry mass per unit fresh mass). Variation in leaf mass density is largely accounted for by variation in cell-wall thickness, number of sclerenchymatic cells, and the concentration of quantitatively important secondary plant compounds (Sects. 3.2 and 3.3). Variation in these traits is closely correlated with that in RGR (Figs. 3 and 4). In a situation where nutrients are limiting, conservation of the scarce resource is at least as important as its capture (Sect. 4 of Chapter 6 on mineral nutrition). Hence, plants growing under severe nutrient limitation are expected to **conserve their nutrients**. Indeed, low-productivity species are more successful due to less leaf turnover; therefore, nutrient losses are restricted (Sects. 4.3 and 4.4 of Chapter 6 on mineral nutrition). Comparing tree seedlings, a close negative correlation exists between relative growth rate and leaf life span (Reich et al. 1992a,b).

How can **leaf longevity** be increased? This depends on the environmental factor that affects leaf longevity. Herbivory can be reduced by increasing leaf toughness and accumulating palatability-reducing compounds (Sect. 3 of Chapter 9B on ecological biochemistry; Wright et al. 2005). The abrasive effects of high wind speeds can be reduced by investment in fiber and sclerenchyma (Sect. 3.3). Trampling resistance may be the result of a large amount of cell-wall material per cell. Transpiration can be decreased and water-use efficiency can be increased by the construction of leaf hairs or epicuticular waxes (Sect. 2 of Chapter 4A on the plant's energy balance). Epicuticular waxes may also confer disease resistance and diminish deleterious effects of salt spray. Each of these additional investments increases the leaf's longevity, but each also decreases SLA, and therefore diminishes the plant's growth potential, but positively influences its fitness under adverse conditions.

There is considerably less information on root turnover than on leaf turnover, and not enough to generalize about inherent differences associated with a plant's growth potential. We do know, however, that the **tissue mass density** tends to be higher in roots of slow-growing grass species, when compared with that in fast-growing ones which is similar to what has been found for leaves (Ryser & Lambers 1995); this higher root mass density is associated with thicker cell walls. The high tissue mass density might be associated with slow root turnover, but this remains speculative.

Is there any indication that plants without the types of leaf and root adjustment discussed in this

section could not survive in unfavorable habitats? This would require introduction of plants that only differ in one specific trait in different environments. Such isogenic genotypes are rarely available, however, and variation in one trait could be expected to affect related traits. The best ecological information available does support the contention that a decrease in SLA enhances the capacity to survive in more stressful environments (Lambers & Poorter 2004).

6.3.3 An Appraisal of Plant Distribution Requires Information on Ecophysiology

A plant's growth potential is part of a strategy that explains the distribution of a species (Sect. 3). Various hypotheses have been proposed to account for the ecological advantage of a high or low RGR_{max}. As we learned before, however, when discussing the ecology and physiology of C_4 and CAM plants (Sects. 9 and 10 of Chapter 2A on photosynthesis), and of cluster-root-producing species (Sect. 2.2.5.2 of Chapter 6 on mineral nutrition), detailed information on biochemistry and physiology is essential to fully appreciate a plant's functioning in different environments as well as a species' distribution.

In the present context, we conclude that a thorough **ecophysiological analysis** of inherent variation in RGR has led to greater insight in the **ecological significance** of this trait. Rather than RGR per se, one or more underlying components have been the target of natural selection. This natural selection has inevitably led to variation in maximum RGR and an associated **suite of traits** (Table 11). This analysis also serves to illustrate that a thorough ecophysiological analysis is essential for a full appreciation of a species' strategy.

Table 11. Typical characteristics of inherently fast-growing and slow-growing herbaceous C_3 species, summarizing information presented in the text.

Characteristic	Fast-growing species	Slow-growing species
Habitat		
Nutrient supply	High	Low
Potential productivity	High	Low
Morphology and allocation		
Leaf area ratio	High	Low
Specific leaf area	High	Low
Leaf mass ratio	Higher	Lower
Root mass ratio	Lower	Higher
Physiology		
Photosynthesis		
(per unit leaf area)	Equal	Equal
(per unit leaf mass)	High	Low
Carbon use in respiration		
(% of total C fixed)	Low	High
Ion uptake rate		
(per unit root mass)	High	Low
Chemical composition		
Concentration of quantitative secondary compounds	Low	High
Concentration of qualitative secondary compounds	Variable	Variable
Other aspects		
Leaf mass density	Low	High
Root mass density	Low	High
Leaf turnover	High	Low
Root turnover	High?	Low?
Leaf longevity	Low	High
Root longevity	Low?	Low?

Note: Unless stated otherwise, the differences refer to plants grown with free access to nutrients. A ? indicates that further study is needed.

7. Growth and Allocation: The Messages About Plant Messages

The numerous examples in this chapter provide a wealth of information on how plants cope with their environment. Plant responses to mild stress are not merely the direct effect of resource deprivation on growth rate. Intricate physiological adjustments that minimize major disturbances in plant metabolism take place. Upon sensing water or nutrient shortage in the root environment, signals are sent to the leaves, which respond in such a way as to minimize deleterious effects. This is a **feedforward response**: an anticipating response in which the rate of a process is affected before large deleterious effects of that process have occurred. Low levels of irradiance are similarly detected, both in developing and in mature leaves, and the signals lead to a feedforward response that minimizes the effect of growth in the shade.

What do all these examples have in common? They demonstrate that a plant is continuously **sensing** its changing **environment** and using this information to control its physiology and allocation pattern. They indicate that, in general, environment affects growth via chemical or hydraulic messages (**sink control**). We may assume that all plants have this capacity to sense their environment. What makes species different from one another is perhaps the manner in which they are able to **respond**, and not so much the variation in their capacity to sense the environments. The typical response of a ruderal species upon sensing nutrient shortage is to slow down leaf expansion and allocate more resources to root growth; it will promote leaf senescence and so withdraw nutrients from older leaves and use these for its newly developing tissues. A species naturally occurring on nutrient-poor sandplains will use the same signal to slow down the production of new tissues, with less dramatic effects on leaf senescence and allocation pattern. Upon sensing water shortage some plants may similarly respond by severely reducing leaf expansion, and others by shedding some leaves, whereas facultative CAM plants switch from the C_3 or C_4 pathway to the CAM mode. Shade is perceived by shade-avoiding and shade-tolerant plants, but the response to promote stem elongation is typical only for shade-avoiding species.

It is the **variation in responses**, rather than the actual sensing mechanism itself, that must be of paramount importance accounting for a species' **ecological amplitude** as well as in such ecological processes as **succession** and **competition** (Aphalo & Ballaré 1995). Ignoring the capacity of plants to process and respond to environmental information (and assuming that plants grow until they run out of resources) leads to a distorted view of the process of competition (Ballaré 1999). As neighbors interact, how do the continuous changes in plant form and function, elicited by information-sensing systems, contribute to competitive success? To what extent does the capacity of an individual to adjust its allocation and development contribute to the outcome of competition?

It is not our aim to promote the "Panglossian" view, which is referred to in Chapter 1 on assumptions and approaches, that just because a species exhibits certain traits in a particular environment, these traits must be beneficial and have resulted from natural selection in that environment. We do wish to stress, however, that plants are **information-acquiring systems**, rather than passively responding organisms, and that this capability must not be ignored, as we discuss in Chapter 9E on interactions among plants.

If we aim to understand plant functioning in different environments, information at the cellular and molecular level is of vital importance. Perception of the environment by specific molecules (e.g., phytochrome), followed by transduction of the information and effects on cell growth (e.g., through cell-wall acidification), allows the plant to acclimate to its environment (e.g., shade). In the past decade our understanding of numerous intricate processes has increased enormously. It is to be expected that fascinating progress will be made in the next decade that will allow us both to deepen our understanding of plant performance in an ecological context and to apply this information in breeding new varieties for adverse environments.

References

Anten, N.P.R., Schieving, F., & Werger, M.J.A. 1995. Patterns of light and nitrogen distribution in relation to whole canopy carbon gain in C_3 and C_4 mono- and dicotyledonous species. *Oecologia* **101:** 504–513.

Anten, N.P.R., Casado-Garcia, R., & Nagashima, H. 2005. Effects of mechanical stress and plant density on mechanical characteristics, growth, and lifetime reproduction of tobacco plants. *Am. Nat.* **166:** 650–660.

Antosiewicz, D.M., Purugganan, M.M., Polisensky, D.H., & Braam, J. 1997. Cellular localization of *Arabidopsis* xyloglucan endotransglycosylase-related proteins during development and after wind stimulation. *Plant Physiol.* **115:** 1319–1328.

Antúnez, I., Retamosa, E.C., Villar, R. 2001. Relative growth rate in phylogenetically related deciduous and evergreen woody species. *Oecologia* **128:** 172–180.

Aphalo, P.J. & Ballaré, C.L. 1995. On the importance of information-acquiring systems in plant–plant interactions. *Funct. Ecol.* **9:** 5–14.

Armstrong, W. 1971. Radial oxygen losses from intact rice roots as affected by distance from the apex, respiration and waterlogging. *Physiol. Plant.* **25:** 192–19

Armstrong, W. 1979. Aeration in higher plants. In: Advances in botanical research, Vol. 7, H.W. Woolhouse (ed.). Academic Press, London, pp. 225–332.

Atkin, O.K. 1996. Reassessing the nitrogen relations of arctic plants: A mini-review. *Plant Cell Environ.* **19:** 695–704.

Atkin, O.K., Botman, B, & Lambers, H. 1996. The causes of inherently slow growth in alpine plants: An analysis based on the underlying carbon economies of alpine and lowland *Poa* species. *Funct. Ecol.* **10:** 698–700.

Atwell, B.J. 1989. Physiological responses of lupin roots to soil compaction. In: Structural and functional aspects of transport in roots, B.C. Loughman, O. Gasparikova, & J. Kolek (eds.). Kluwer Academic Publishers, Dordrecht, pp. 251–255.

Avice, J.-C., Ourry, A., Volenec, J.J., Lemaire, G., & Boucaud, J. 1996a. Defoliation-induced changes in abundance and immuno-localization of vegetative storage proteins in taproots of *Medicago sativa*. *Plant Physiol. Biochem.* **34:** 561–570.

Avice, J.-C., Ourry, A., Lemaire. G., & Boucaud, J. 1996b. Nitrogen and carbon flows estimated by 15n and 13c pulse-chase labeling during regrowth of alfalfa. *Plant Physiol.* **112:** 281–290.

Ayling, S.M. & Topa, M.A. 1998. Phosphorus compartmentation in *Pinus serotina* Michx. (pond pine); observations from in vivo nuclear magnetic resonance spectroscopy. *Plant Cell Environ.* **21:** 723–730.

Bacon, M.A., Wilkinson, S., & Davies, W.J. 1998. pH-regulated leaf cell expansion in droughted plants is abscisic acid dependent. *Plant Physiol.* **118:** 1507–1515.

Bailey-Serres, J. & Voesenek, L.A.C.J. 2008. Flooding stress: Acclimations and genetic diversity. *Annu. Rev. Plant Biol.*, **59:** 313–339.

Ball, M.C. & Pidsley, S.M. 1995. Growth responses to salinity in relation to distribution of two mangrove species, *Sonneratia alba* and *S. lanceolata*, in northern Australia. *Funct. Ecol.* **9:** 77–85.

Ballaré, C.L. 1999. Keeping up with the neighbours: Phytochrome sensing and other signalling mechanisms. *Trends Plant Sci.* **4:** 97–102.

Ballaré, C.L., Scopel, A.L., Roush, M.L., & Radosevich, S.R. 1995. How plants find light in patchy canopies. A comparison between wild-type and phytochrome-B-deficient mutant plants of cucumber. *Funct. Ecol.* **9:** 859–868.

Banga, M., Blom, C.W.P.M., & Voesenek, L.A.C.J. 1996. Sensitivity to ethylene: The key factor in ethylene production by primary roots of *Zea mays* L. in submergence-induced shoot elongation of *Rumex*. *Plant Cell Environ.* **19:** 1423–1430.

Bausenwein, U., Millard, P., Thornton, B., & Raven, J.A. 2001. Seasonal nitrogen storage and remobilization in the forb *Rumex acetosa*. *Funct. Ecol.* **15:** 370–37

Bell, T.L., Pate, J.S., & Dixon. K.W. 1996. Relationship between fire response, morphology, root anatomy and starch distribution in south-west Australian Epacridaceae. *Ann. Bot.* **77:** 357–364.

Bennie, A.T.P. 1996. Growth and mechanical impedance. In: Plant roots: The hidden half, 2nd edition, Y. Waisel, A. Eshel, & U. Kafkaki (eds.). Marcel Dekker, New York, pp. 453–470.

Bengough, A.C. & Mullins, C.E. 1990a. The resistance experienced by roots growing in a pressurized cell. *Plant Soil* **123:** 73–82.

Bengough, A.C. & Mullins, C.E. 1990b. Mechanical impedance to root growth: A review of experimental techniques and root growth responses. *J. Soil Sci.* **41:** 341–358.

Berger, S., Bell, E., Sadka, A., & Mullet, J.E. 1995. *Arabidopsis thaliana Atvsp* is homologous to soybean *vspA* and *vspB*, genes encoding vegetative storage protein acid phosphatases, and is regulated similarly by methyl jasmonate, wounding, sugars, light and phosphate. *Plant Mol. Biol.* **27:** 933–942.

Bloom, A.J., Chapin III, F.S., & Mooney, H.A. 1985. Resource limitation in plants – An economic analogy. *Annu. Rev. Ecol. Syst.* **16:** 363–392.

Bowen, G.D. 1991. Soil temperature, root growth, and plant function. In: Plant roots: The hidden half, 1st edition. Y. Waisel, A. Eshel, & U. Kafkaki (eds.). Marcel Dekker, New York, pp. 309–330.

Braam, J. & Davis, R.W. 1990. Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in *Arabidopsis*. *Cell* **60:** 357–364.

Braam, J., Sistrunk, M.L., Polisensky, D.H., Xu, W., Purugganan, M.M., Antosiewicz, D.M., Campbell, P., & Johnson, K.A. 1996. Life in a changing world: *TCH* gene regulation of expression and responses to environmental signals. *Physiol. Plant.* **98:** 909–91

Brouwer, R. 1963. Some aspects of the equilibrium between overground and underground plant parts. *Meded. Inst. Biol. Scheikd. Onderzoek Landbouwgewassen* **213:** 31–39.

Brouwer R. 1983. Functional equilibrium: Sense or nonsense? *Neth. J. Agric. Sci.* **31:** 335–348.

Butler, W.L., Norris, H.W., & Hendricks, S.B. 1959. Detection, assay, and preliminary purification of the pigment controlling photoresponsive developments of plants. *Proc. Natl. Acad. Sci. USA* **45:** 1703–1708.

Carpita, N.C. & Gibeaut, D.M. 1993. Structural models of primary cell walls in flowering plants: Consistency of molecular structure with the physical properties of the walls during growth. *Plant J.* **3:** 1–30.

Castro-Díez, P., Puyravaud, J.P., & Cornelissen, J.H.C. 2000. Leaf structure and anatomy as related to leaf mass per area variation in seedlings of a wide range of woody plant species and types. *Oecologia* **124:** 476–486.

Ceulemans, R. 1989. Genetic variation in functional and structural productivity components in *Populus*. In: Causes and consequences of variation in growth rate and productivity of higher plants, H. Lambers, M.L. Cambridge, H. Konings, & T.L. Pons (eds.). SPB Academic Publishing, The Hague, pp. 69–85.

Chapin III, F.S. 1980. The mineral nutrition of wild plants. *Annu. Rev. Ecol. Syst.* **11:** 233–260.

Chapin III, F.S. 1988. Ecological aspects of plant nutrition. *Adv. Min. Nutr.* **3:** 161–191.

Chapin III, F.S., Follet, J.M., & O'Connor, K.F. 1982. Growth, phosphate absorption, and phosphorus chemical fractions in two *Chionochloa* species. *J. Ecol.* **70:** 305–321.

Chapin III, F.S., Shaver, G.R., & Kedrowski, R.A. 1986. Environmental controls over carbon, nitrogen and phosphorus fractions in *Eriophorum* in Alaskan tussock tundra. *J. Ecol.* **74:** 167–195.

Chapin III, F.S., Schulze, E.-D., & Mooney, H.A. 1990. The ecology and economics of storage in plants. *Annu. Rev. Ecol. Syst.* **21:** 423–44

Chimenti, C.A. & Hall, A.J. 1994. Responses to water stress of apoplastic water fraction and bulk elastic modulus of elasticity in sunflower (*Helianthus annuus* L.) genotypes of contrasting capacity for osmotic adjustment. *Plant Soil* **166:** 101–10

Cho, H.-T. & Kende, H. 1997a. Expansins in deepwater rice internodes. *Plant Physiol.* **113:** 1137–1143.

Cho, H.-T. & Kende, H. 1997b. Expansins and internodal growth of deepwater rice. *Plant Physiol.* **113:** 1145–1151.

Cho, H.-T. & Kende, H. 1997c. Expression of expansin genes is correlated with growth in deepwater rice. *Plant Cell* **9:** 1661–1671.

Clark, L.J., Whalley, W.R., Dexter, A.R., Barraclough, P.B., & Leigh, R.A. 1996. Complete mechanical impedance increases the turgor of cells in the apex of pea roots. *Plant Cell Environ.* **19:** 1099–1102.

Clarkson, D.T., Earnshaw, M.J., White, P.J., & Cooper, H.D. 1988. Temperature dependent factors influencing nutrient uptake: An analysis of responses at different levels of organization. In: Plants and temperature, S.P. Long & F.I. Woodward (eds). Company of Biologists, Cambridge, pp. 281–309.

Clarkson, D.T., Jones, L.H.P., & Purves, J.V. 1992. Absorption of nitrate and ammonium ions by *Lolium perenne* from flowing solution cultures at low root temperatures. *Plant Cell Environ.* **15:** 99–106.

Clarkson, D.T., Carvajal, M., Henzler, T., Waterhouse, R.N., Smyth, A.J., Cooke, D.T., & Steudle, E. 2000. Root hydraulic conductance: Diurnal aquaporin expression and the effects of nutrient stress. *J. Exp. Bot.* **51:** 61–70.

Cleland, R.E. 1967. Extensibility of isolated cell walls: Measurements and changes during cell elongation. *Planta* **74:** 197–209.

Coleman, G.D., Chen, T.H.H., & Fuchigami, L.H. 1992. Complementary DNA cloning of poplar bark storage protein and control of its expression by photoperiod. *Plant Physiol.* **98:** 687–693.

Colmer, T.D. 2003. Long-distance transport of gases in plants: A perspective on internal aeration and radial oxygen loss from roots. *Plant Cell Environ.* **26:** 17–36.

Colmer, T.D., Gibberd, M.R., Wiengweera, A., & Tinh, T.K. 1998. The barrier to radial oxygen loss from roots of rice (*Oryza sativa* L.) is induced by growth in stagnant solution. *J. Exp. Bot.* **49:** 1431–1436.

Comas, L.H. & Eissenstat, D.M. 2004. Linking fine root traits to maximum potential growth rate among 11 mature temperate tree species. *Funct. Ecol.* **18:** 388–39

Cornelissen, J.H.C., Castro-Díez, P., & Hunt, R. 1996. Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *J. Ecol.* **84:** 755–765.

Cosgrove, D.J. 1999. Enzymes and other agents that enhance cell wall extensibility. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **50:** 391–41

Cosgrove, D.J. 2000. Loosening of plant cell walls by expansins. *Nature* **407:** 321–326.

Cunningham, S.A., Summerhaye, B., & Westoby, M. 1999. Evolutionary divergences in leaf structure and chemistry, comparing rainfall and soil nutrient gradients. *Ecology* **69:** 569–588.

Cyr, D.R. & Bewley, J.D. 1990. Proteins in the roots of perennial weeds chicory (*Cichorium intybus* L.) and dandelion (*Taraxacum officinale* Weber) are associated with overwintering. *Planta* **182:** 370–374.

Darwin, C. 1880. The power of movement in plants. John Murray, London.

Davies, P.J. 2004. (ed.). Plant hormones; biosynthesis, signal transduction, action! Kluwer Academic Publishers, Dordrecht.

Davies, W.J. & Zhang, J. 1991. Root signals and the regulation of growth and development of plants in drying soil. *Annu. Rev. Plant Physiol. Mol. Biol.* **42:** 55–76.

Davies, W.J., Tardieu, F., & Trejo, C.L. 1994. How do chemical signals work in plants that grow in drying soil? *Plant Physiol.* **104:** 309–314.

Dodd, I.C. & Davies, W.J. 1996. The relationship between leaf growth and ABA accumulation in the grass leaf elongation zone. *Plant Cell Environ.* **19:** 1047–1056.

Dodd, I.C. 2005. Root-to-shoot signalling: Assessing the roles of "up" in the up and down world of long-distance signalling in planta. *Plant Soil* **274:** 251–270.

Else, M.A., Davies, W.J., Malone, M., & Jackson, M.B. 1995. A negative hydraulic message from oxygen-deficient roots of tomato plants? Influence of soil flooding on leaf water potential. Leaf expansion, and synchrony between stomatal conductance and root hydraulic conductivity. *Plant Physiol.* **109:** 1017–1024.

Else, M.A., Tiekstra, A.E., Croker, S.J., Davies, W.J., & Jackson, M.B. 1996. Stomatal closure in flooded tomato plants involves abscisic acid and a chemically unidentified anti-transpirant in xylem sap. *Plant Physiol.* **1012:** 239–24

Emery, R.J.N., Reid, D.M., & Chinnappa 1994. Phenotypic plasticity of stem elongation in two ecotypes of *Stellaria longipes*: The role of ethylene and response to wind. *Plant Cell Environ.* **17:** 691–700.

Esmon, C.A., Pedmale, U.V., & Liscum, E. 2005 Plant tropisms: Providing the power of movement to a sessile organism. *Int. J. Dev. Biol.* **49:** 665–674.

Evans, G.C. 1972. The quantitative analysis of plant growth. Blackwell Scientific Publications, Oxford.

Evans, L.T. 1980. The natural history of crop yield. *Am. Sci.* **68**: 388–39

Evans, J.R. 1989. Photosynthesis and nitrogen relationships in leaves of C_3 plants. *Oecologia* **78:** 9–19.

Farrar, J.F. 1996. Regulation of root weight ratio is mediated by sucrose. *Plant Soil* **185:** 13–19.

Fasano, J.M., Massa, G.D., & Gilroy, S. 2002. Ionic signaling in plant responses to gravity and touch. *J. Plant Growth Regul.* **21:** 71–88.

Fetene, M. & Beck, E. 1993. Reversal of direction of photosynthate allocation in *Urtica dioica* L. plants by increasing cytokinin import into the shoot. *Bot. Acta.* **106:** 235–240.

Fichtner, K. & Schulze, E.-D. 1992. The effect of nitrogen nutrition on growth and biomass partitioning of annual plants originating from habitats of different nitrogen availability. *Oecologia* **92:** 236–241.

Field, C.B. 1991. Ecological scaling of carbon gain to stress and resource availability. In: Integrated responses of plants to stress, H.A. Mooney, W.E. Winner, & E.J. Pell (eds.). Academic Press, San Diego, pp. 35–65.

Fondy, B.R. & Geiger, D.R. 1985. Diurnal changes in allocation of newly fixed carbon in exporting sugar beet leaves. *Plant Physiol.* **78:** 753–75

Fonseca, F., Den Hertog, J., & Stulen, I. 1996. The response of *Plantago major* ssp. *pleiosperma* to elevated CO_2 is modulated by the formation of secondary shoots. *New Phytol.* **133:** 627–635.

Franklin, K.A. & Whitelam, G.C. 2004. Light signals, phytochromes and cross-talk with other environmental cues. *J. Exp. Bot.* **55:** 271–276

Fry, S.C. 2004. Primary cell wall metabolism: Tracking the careers of wall polymers in living plant cells. *New Phytol.* **161:** 641–675.

Garnier, E. 1991. Resource capture, biomass allocation and growth in herbaceous plants. *Trends Ecol. Evol.* **6:** 126–131.

Garnier, E. 1992. Growth analysis of congeneric annual and perennial grass species. *J. Ecol.* **80:** 665–675.

Garnier, E. & Laurent, G. 1994. Leaf anatomy, specific leaf mass and water content in congeneric annual and perennial grass species. *New Phytol.* **128:** 725–736.

Garnier, E. & Vancaeyzeele, S. 1994. Carbon and nitrogen content of congeneric annual and perennial grass species: Relationships with growth. *Plant Cell Environ.* **17:** 399–40

Garnier, E., Gobin, O., & Poorter, H. 1995. Interspecific variation in nitrogen productivity depends on photosynthetic nitrogen use efficiency and nitrogen allocation within the plant. *Ann. Bot.* **76:** 667–672.

Garthwaite, A.J., Von Bothmer, R., & Colmer, T.D. 2003. Diversity in root aeration traits associated with waterlogging tolerance in the genus *Hordeum*. *Funct. Plant Biol.* **30:** 875–889.

Gastal, F., Belanger, G., & Lemaire, G. 1992. A model of the leaf extension rate of tall fescue in response to nitrogen and temperature. *Ann. Bot.* **70:** 437–442.

Goulas, E., Richard-Molard, C., Le Dily, F., Le Dantec, C., Ozouf, J., & Ourry, A. 2007. A cytosolic vegetative storage protein (TrVSP) from white clover is encoded by a cold-inducible gene. *Physiol. Plant.* **129:** 567–57

Gowing, D.J.G., Davies, W.J., & Jones, H.G. 1990. A positive root-sourced signal as an indicator of soil drying in apple, *Malus* x *domestica* Borkh. *J. Exp. Bot.* **41:** 1535–1540.

Green, P.B. 1976. Growth and cell pattern formation on an axis: Critique of concepts, terminology, and mode of study. *Bot. Gaz.* **137:** 187–202.

Grime, J.P. 1979. Plant strategies and vegetation processes. John Wiley, Chichester.

Grime, J.P. & Hunt, R. 1975. Relative growth-rate: Its range and adaptive significance in a local flora. *J. Ecol.* **63:** 393–422.

Groeneveld, H.W. & Bergkotte, M. 1996. Cell wall composition of leaves of an inherently fast- and a slow-growing grass species. *Plant Cell Environ.* **19:** 1389–1398.

Hamza, M.A. & Anderson, W.K. 2005. Soil compaction in cropping systems: A review of the nature, causes and possible solutions. *Soil & Tillage Research* **82:** 121–145.

Harpham, N.V.J., Berry, A.W., Knee, E.M., Roveda-Hoyos, G., Raskin, I., Sanders, I.O., Smith, A.R., Wood, C.K. & Hall, M.A. 1991. The effect of ethylene on the growth and development of wild-type and mutant *Arabidopsis thaliana* (L.) Heynh. *Ann. Bot.* **68:** 55–61.

Hart, R. 1977. Why are biennials so few? *Am. Nat.* **111:** 792–799.

Hay, R.K.M. 1990. The influence of photoperiod on the dry-matter production of grasses and cereals. *New Phytol.* **116:** 233–254.

He, T. & Cramer, G.R. 1996. Abscisic acid concentrations are correlated with leaf area reductions in two salt-stressed rapid-cycling *Brassica* species. *Plant Soil* **179:** 25–33.

Heilmeier, H. & Monson, R.K. 1994. Carbon and nitrogen storage in herbaceous plants. In: A whole-plant perspective on carbon-nitrogen interactions, J. Roy & E. Garnier (eds.) SPB Academic Publishing, The Hague, pp. 149–171.

Heilmeier, H., Schulze, E.-D., & Whale, D.M. 1986. Carbon and nitrogen partitioning in the biennial monocarp *Arctium tomentosum* Mill. *Oecologia* **70:** 466–474.

Hirose, T. & Werger, M.J.A. 1987a. Maximizing daily canopy photosynthesis with respect to leaf nitrogen allocation pattern in the canopy. *Oecologia* **72:** 520–526.

Hirose, T. and Werger, M.J.A. 1987b. Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. *Physiol. Plant.* **70:** 215–222.

Hsiao, T.C., French, J., & Rojas-Lara, B.A. 1998. The pressure-jump technique shows maize leaf growth to be enhanced by increases in turgor only when water status is not too high. *Plant Cell Environ.* **21:** 22–42.

Hübel, F. & Beck, E. 1996. Maize root phytase. Purification, characterization, and localization of enzyme activity and its putative substrate. *Plant Physiol.* **112:** 1429–1436.

Hussain, A., Black, C.R., Taylor, I.B., Mulholland, B.J., & Roberts, J.A. 1999. Novel approaches for examining the effects of differential soil compaction on xylem sap abscisic acid concentration, stomatal conductance and growth in barley (*Hordeum vulgare* L.). *Plant Cell Environ.* **22:** 1377–1388.

Hussain, A., Black, C.R., Taylor, I.B., & Roberts, J.A. 2000. Does an antagonistic relationship between ABA and

ethylene mediate shoot growth when tomato (*Lycopersicon esculentum* Mill.) plants encounter compacted soil? *Plant Cell Environ.* **23:** 1217–1226.

Jackson, S.D., James, P., Prat, S. & Thomas, B. 1998. Phytochrome B affects the levels of a graft-transmissible signal involved in tuberization. *Plant Physiol.* **117:** 29–32.

Jaffe, M.J. & Forbes, S. 1993. Thigmomorphogenesis: The effects of mechanical perturbation on plants. *Plant Growth Regul.* **12:** 313–324.

Jiao, Y., Lau, O.S., & Deng, X.W. 2007. Light-regulated transcriptional networks in higher plants. *Nature* **8:** 217–230.

Jonasson, S. & Chapin III, F.S. 1985. Significance of sequential leaf development for nutrient balance of the cotton sedge, *Eriophorum vaginatum* L. *Oecologia* **67:** 511–518.

Juntilla, O., Heide, O.M., Lindgard, B., & Ernstein, A. 1997. Gibberellins and the photoperiodic control of leaf growth in *Poa pratensis*. *Physiol. Plant.* **101:** 599–605.

Kende H., Van der Knaap, E., & Cho H.T. 1998. Deepwater rice: A model plant to study stem elongation. *Plant Physiol.* **118:** 1105–1110.

Kigel, J. & Cosgrove, D.J. 1991. Photoinhibition of stem elongation by blue and red light. Effects on hydraulic and cell wall properties. *Plant Physiol.* **95:** 1049–1056.

Kitajima, K. 1994. Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98:** 419–428.

Kitajima, K. 1996. Ecophysiology of tropical tree seedling. In: Tropical forest plant ecophysiology, S. Mulkey, R. Chazdon, & A. Smith (eds.). Chapman & Hall, New York, pp. 559–596.

Knight, M.R., Campbell, A.K., Smith, S.M., & Trewawas, A.J. 1991. Transgenic plant aequorin reports the effects of touch and cold-shock and elicitors on cytoplasmic calcium. *Nature* **352:** 524–526.

Knight, M.R., Smith, S.M., & Trewawas, A.J. 1992. Wind-induced plant motion immediately increases cytosolic calcium. *Proc. Natl. Acad. Sci. USA* **89:** 4967–4971.

Kraus, E., Kollöffel, C., & Lambers, H. 1994. The effect of handling on photosynthesis, transpiration, respiration, and nitrogen and carbohydrate content of populations of *Lolium perenne*. *Physiol. Plant.* **91:** 631–638.

Kuiper, D. & Staal, M. 1987. The effect of exogenously supplied plant growth substances on the physiological plasticity in *Plantago major* ssp *major*: Responses of growth, shoot to root ratio and respiration. *Physiol. Plant.* **69:** 651–658.

Kuiper, D., Kuiper, P.J.C., Lambers, H., Schuit, J.T., & Staal, M. 1989. Cytokinin contents in relation to mineral nutrition and benzyladenine addition in *Plantago major* ssp. *pleiosperma*. *Physiol. Plant.* **75:** 511–51

Kuo, T. & Boersma, L. 1971. Soil water suction and root temperature effects on nitrogen fixation in soybeans. *Agron. J.* **63:** 901–904.

Lambers, H. & Poorter, H. 2004. Inherent variation in growth rate between higher plant: A search for physiological causes and ecological consequences. *Adv. Ecol. Res.* **34:** 283–362.

Lambers, H., Cambridge, M.L., Konings, H., & Pons, T.L. (eds.) 1989. Causes and consequences of variation in growth rate and productivity of higher plants. SPB Academic Publishing, The Hague.

Langheinrich, U. & Tischner, R. 1991. Vegetative storage proteins in poplar. Induction and characterization of a 32- and a 36-kilodalton polypeptide. *Plant Physiol.* **97:** 1017–1025.

Lee, R.B., Ratcliffe, R.G., & Southon, T.E. 1990. ^{31}P NMR measurements of the cytoplasmic and vacuolar P_i content of mature maize roots: Relationships with phosphorus status and phosphate fluxes. *J. Exp. Bot.* **41:** 1063–1078.

Leigh, R.A. & Tomos, A.D. 1983. An attempt to use isolated vacuoles to determine the distribution of sodium and potassium in cells of storage roots of red beet (*Beta vulgaris* L.). *Planta* **159:** 469–475.

Leon, A.J., Lee, M., & Andrade, F.H. 2001. Quantitative trait loci for growing degree days to flowering and photoperiod response in sunflower (*Helianthus annuus* L.).*Theor. Appl. Genet.* **102:** 497–503.

Leverenz, J.W. 1992. Shade shoot structure and productivity of evergreen conifer stands. *Scand. J. For. Res.* **7:** 345–353.

Li, X., Feng, Y., & Boersma, L. 1994. Partitioning of photosynthates between shoot and root in spring wheat (*Triticum aestivum* L.) as a function of soil water potential and root temperature. *Plant Soil* **164:** 43–50.

Luo, Y., Hui, D., & Zhang, D. 2006. Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: A meta-analysis. *Ecology* **87**: 53–63.

MacAdam, J.W., Volenec, J.J., & Nelson, C.J. 1989. Effects of nitrogen supply on mesophyll cell division and epidermal cell elongation in tall fescue leaf blades. *Plant Physiol.* **89:** 549–556.

McDonald, M.P., Galwey, N.W., & Colmer, T.D. 2002. Similarity and diversity in adventitious root anatomy as related to root aeration among a range of wetland and dryland grass species. *Plant Cell Environ.* **25:** 441–451.

Maranon, T. & Grub, P.J. 1993. Physiological basis and ecological significance of the seed size and relative growth rate relationship in Mediterranean annuals. *Funct. Ecol.* **7:** 591–599.

Materechera, S.A., Alston, A.M., Kirby, J.M., & Dexter, A.R. 1993. Field evaluation of laboratory techniques for predicting the ability of roots to penetrate strong soil and of the influence of roots on water absorptivity. *Plant Soil* **149:** 149–158.

McArthur, R.H. & Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press, Princeton.

Meuriot, F., Noquet, C., Avice, J.-C., Volenec, J.J., Cunningham, S.M., Sors, T.G., Caillot, S., & Ourry, A. 2004. Methyl jasmonate alters N partitioning, N reserves accumulation and induces gene expression of a 32-kDa vegetative storage protein that possesses chitinase activity in *Medicago sativa* taproots. *Physiol. Plant.* **120:** 113–123.

Millard, P. 1988. The accumulation and storage of nitrogen by herbaceous plants. *Plant Cell Environ.* **11:** 1–8.

Mommer, L., Pedersen, O., & Visser, E.J.W. 2004. Acclimation of a terrestrial plant to submergence facilitates gas exchange under water. *Plant Cell Environ.* **27:** 1281–128

Mommer, L., Pons, T.L., Wolters-Arts, M., Venema, J.H., & Visser, E.J.W. 2005. Submergence-induced morphological, anatomical, and biochemical responses in a terrestrial species affect gas diffusion resistance and photosynthetic performance. *Plant Physiol.* **139:** 497–508.

Mooney, H.A. & Rundel, P.W. 1979. Nutrient relations of the evergreen shrub, *Adenostoma fasciculatum*, in the California chaparral. *Bot. Gaz.* **140:** 109–113.

Morvan-Bertrand, A., Pavis, N., Boucaud, J., & Prud'homme, M.-P. 1999. Partitioning of reserve and newly assimilated carbon in roots and leaf tissue of *Lolium perenne* during regrowth after defoliation: Assessment by ^{13}C steady-state labelling and carbohydrate analysis. *Plant Cell Environ.* **22:** 1097–1108.

Munns, R. & Cramer, G.R. 1996. Is coordination of leaf and root growth mediated by abscisic acid? *Plant Soil* **185:** 33–49.

Munns, R. & Sharp, R.E. 1993. Involvement of abscisic acid in controlling plant growth in soil of low water potential. *Aust. J. Plant Physiol.* **20:** 425–43

Neumann, P.M., Azaizeh, H., & Leon, D. 1994. Hardening of root cell walls: A growth inhibitory response to salinity stress. *Plant Cell Environ.* **17:** 303–309.

Okamoto, A. & Okamoto, H. 1995. Two proteins regulate the cell-wall extensibility and the yield threshold in glycerinated hollow cylinders of cowpea hypocotyl. *Plant Cell Environ.* **18:** 827–830.

Okamoto, A., Katsumi, M., & Okamoto, H. 1995. The effects of auxin on the mechanical properties in vivo of cell wall in hypocotyl segments from gibberellin-deficient cowpea seedlings. *Plant Cell Physiol.* **36:** 645–651.

Olszewski, N., Sun, T., & Gubler, F. 2002. Gibberellin signaling: Biosynthesis, catabolism, and response pathways. *Plant Cell Suppl.* S61–S80.

Parsons, R.F. 1968. The significance of growth-rate comparisons for plant ecology. *Am. Nat.* **102:** 595–59

Passioura, J.B. 1988. Root signals control leaf expansion in wheat seedlings growing in drying soil. *Aust. J. Plant Physiol.* **15:** 687–693.

Passioura, J.B. 1994. The physical chemistry of the primary cell wall: Implications for the control of expansion rate. *J. Exp. Bot.* **45:** 1675–1682.

Passioura, J.B. & Fry, S.C. 1992. Turgor and cell expansion: Beyond the Lockhart equation. *Aust. J. Plant Physiol.* **19:** 565–576.

Peeters, A.J.M., Cox, M.C.H., Benschop, J.J., Vreeburg, R.A.M., Bou, J., Voesenek, L.A.C.J. 2002. Submergence research using *Rumex palustris* as a model; looking back and going forward. *J. Exp. Bot.* **53:** 391–398.

Peng, J. & Harberd, P. 1997. Gibberellin deficiency and response mutations suppress the stem elongation phenotype of phytochrome-deficient mutants of *Arabidopsis*. *Plant Physiol.* **113:** 1051–1058.

Pianka, E.R. 1970. On r and K selection. *Am. Nat.* **104:** 592–59

Pons, T.L. 1977. An ecophysiological study in the field layer of ash coppice. II. Experiments with *Geum urbanum* and *Cirsium palustre* in different light intensities. *Acta Bot. Neerl.* **26:** 29–42.

Pons, T.L. & Bergkotte, M. 1996. Nitrogen allocation in response to partial shading of a plant: Possible mechanisms. *Physiol. Plant.* **98:** 571–57

Pons, T.L., Schieving, F., Hirose, T., & Werger, M.J.A. 1989. Optimization of leaf nitrogen allocation for canopy photosynthesis in *Lysimachia vulgaris*. In: Causes and consequences of variation in growth rate and productivity of higher plants, H. Lambers, M.L. Cambridge, H. Konings, & T.L. Pons (eds.). SPB Academic Publishing, The Hague, pp. 175–186.

Poorter, H. & Remkes, C. 1990. Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia* **83:** 553–559.

Poorter, H. Remkes, C., & Lambers, H. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiol.* **94:** 621–72

Poorter, H., Gifford, R.M., Kriedemann, P.E., & Wong, S.C. 1992. A quantitative analysis of dark respiration and carbon content as factors in the growth response of plants to elevated CO_2. *Aust. J. Bot.* **40:** 501–513.

Poorter, H., Van de Vijver, C.A.D.M., Boot, R.G.A., & Lambers, H. 1995. Growth and carbon economy of a fast-growing and a slow-growing grass species as dependent on nitrate supply. *Plant Soil* **171:** 217–22

Poorter, H., Roumet, C., & Campbell, B.D. 1996. Interspecific variation in the growth response of plants to elevated CO_2: A search for functional types. In: Biological biversity in a CO_2-rich world, C. Körner & F.A. Bazzaz (eds.). Physiological ecology series, Academic Press, San Diego, pp. 375–412.

Poot, P. & Lambers, H. 2003. Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the SW Australian flora. *J. Ecol.* **91:** 58–6

Poot, P. & Lambers, H. 2008 Shallow-soil endemics: Adaptive advantages and constraints of a specialized root-system morphology. *New Phytol.* **175:** 371–381.

Pritchard, J. 1994. The control of cell expansion in roots. *New Phytol.* **127:** 3–2

Pritchard, J., Fricke, W., & Tomos, D. 1996. Turgor-regulation during extension growth and osmotic stress of maize roots. An example of single-cell mapping. *Plant Soil* **187:** 11–21.

Quail, P.H., Boylan, M.T., Parks, B.M., Short, T.W., Xu, Y., & Wagner, D. 1995. Phytochromes: Photosensory perception and signal transduction. *Science* **268:** 675–680.

Rappoport, H.F. & Loomis, R.S. 1985. Interaction of storage root and shoot in grafted sugarbeet and chard. *Crop Sci.* **25:** 1079–1084.

Reich, P.B., Uhl, C., Walters, M.B., & Ellsworth, D.S. 1991. Leaf life-span as a determinant of leaf structure and function among 23 Amazonian tree species. *Oecologia* **86:** 16–24.

Reich, P.B., Walters, M.B., & Ellsworth, D.S. 1992a. Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Monogr.* **62:** 365–392.

Reich, P.B., Walters, M.B., & Ellsworth, D.S. 1992b. Leaf life-span in relation to leaf, plant and stand characteristics among diverse ecosystems. *Ecol. Monogr.* **62:** 365–392.

Reski, R. 2006. Small molecules on the move: Homeostasis, crosstalk, and molecular action of phytohormones. *Plant Biol.* **8:** 277–280.

Rosnitschek-Schimmel, I. 1983. Biomass and nitrogen partitioning in a perennial and an annual nitrophilic species of *Urtica*. *Z. Pflanzenphysiol.* **109:** 215–225.

Russel, G. & Grace, J. 1978. The effects of wind on grasses. V. Leaf extension, diffusive conductance, and photosynthesis in the wind tunnel. *J. Exp. Bot.* **29:** 1249–1258.

Russel, G. & Grace, J. 1979. The effects of windspeed on the growth of grasses. J. *Appl. Ecol.* **16:** 507–514.

Ryser, P. & Lambers, H. 1995. Root and leaf attributes accounting for the performance of fast- and slow-growing grasses at different nutrient supply. *Plant Soil* **170:** 251–265.

Ryser, P. & Eek, L. 2000. Consequences of phenotypic plasticity vs. interspecific differences in leaf and root traits for acquisition of aboveground and belowground resources. *Am. J. Bot.*. **87:** 402–411.

Saab, I.N. & Sachs, M.N. 1996. A flooding-induced xyloglucan endo-transglycosylase homolog in maize is responsive to ethylene and associated with aerenchyma. *Plant Physiol.* **112:** 385–391.

Saab, I.N., Sharp, R.R., Pritchard, J., & Voetberg, G.S. 1990. Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. *Plant Physiol.* **93:** 1329–1336.

Sauter, J.J. & Van Cleve, B. 1990. Biochemical, immunochemical, and ultrastructural studies of protein storage in poplar (*Populus* x*canadensis "robusta"* wood. *Planta* **183:** 92–100.

Scheible, W.-R., Lauerer, M, Schulze, E.-D., Caboche, M., & Stitt, M. 1997. Accumulation of nitrate in the shoot acts as a signal to regulate shoot-root allocation in tobacco. *Plant J.* **11:** 671–691.

Schnyder, H. & De Visser, R. 1999. Fluxes of reserve-derived and currently assimilated carbon and nitrogen in perennial ryegrass recovering from defoliation. The regrowing tiller and its component functionally distinct zones. *Plant Physiol.* **119:** 1423–1436.

Schulze, E.-D. & Chapin III, F.S. 1987. Plant specialization to environments of different resource availability. In: Potentials and limitations of ecosystem analysis, E.-D. Schulze & H. Zwölfer (eds.). Springer-Verlag, Berlin. pp. 120–148.

Setter, T.L. & Belford, B. 1990. Waterlogging: How it reduces plant growth and how plants can overcome its effects. *W.A. J. Agric.* **31**: 51–55

Setter, T.L. & Laureles, E.V. 1996. The beneficial effect of reduced elongation growth on submergence tolerance of rice. *J. Exp. Bot.* **47:** 1551–1559.

Sharp, R.E. 2002. Interaction with ethylene: Changing views on the role of abscisic acid in root and shoot growth responses to water stress. *Plant Cell Environ.* **25:** 211–222.

Sharp, R.E., Poroyko, V., Hejlek, L.G., Spollen, W.G., Springer, G.K., Bohnert, H.J., & Nguyen, H.T. 2004. Root growth maintenance during water deficits: Physiology to functional genomics. *J. Exp. Bot.* **55:** 2343–2351.

Siefritz, F., Otto, B., Bienert, G.P., Van der Krol, A., & Kaldenhoff, R. 2004. The plasma membrane aquaporin NtAQP1 is a key component of the leaf unfolding mechanism in tobacco. *Plant J.* **37:** 147–155.

Simpson, R.J., Lambers, H., Beilharz, V.C., & Dalling, M.J. 1982a. Translocation of nitrogen in a vegetative wheat plant (*Triticum aestivum*). *Physiol. Plant.* **56:** 11–1

Simpson, R.J., Lambers, H., & Dalling, M.J. 1982b. Kinetin application to roots and its effects on uptake, translocation and distribution of nitrogen in wheat (*Triticum aestivum*) grown with a split root system. *Physiol. Plant.* **56:** 430–435.

Simpson, R.J., Lambers, H., & Dalling, M.J. 1983. Nitrogen redistribution during grain growth in wheat (*Triticum aestivum* L.). IV. development of a quantitative model of the translocation of nitrogen to the grain. *Plant Physiol.* **71:** 7–14.

Smith, H. 1981. Adaptation to shade. In: Physiological processes limiting plant productivity, C.B. Johnson (ed.). Butterworths, London, pp. 159–173.

Smith, H. 2000. Phytochromes and light signal perception by plants – An emerging synthesis. *Nature* **407:** 585–591.

Snir, N. & Neumann, P.M. 1997. Mineral nutrient supply, cell wall adjustment and the control of leaf growth. *Plant Cell Environ.* **20:** 239–246.

Staswick, P.E. 1988. Soybean vegetative storage protein structure and gene expression. *Plant Physiol.* **87:** 250–254.

Staswick, P.E. 1990. Novel regulation of vegetative storage protein genes. *Plant Cell* **2:** 1–6.

Staswick, P.E., Huang, J.-F., & Rhee, Y. 1991. Nitrogen and methyl jasmonate induction of soybean vegetative storage protein genes. *Plant Physiol.* **96:** 130–136.

Steingröver, E. 1981. The relationship between cyanide-resistant root respiration and the storage of sugars in the taproot in *Daucus carota* L. *J. Exp. Bot.* **32:** 911–919.

Stirzaker, R.J., Passioura, J.B., & Wilms, Y. 1996. Soil structure and plant growth: Impact of bulk density and biopores. *Plant Soil* **185:** 151–162.

Stulen, I. & Den Hertog, J. 1993. Root growth and functioning under atmospheric CO_2 enrichment. *Vegetatio* **104/105:** 99–115.

Summers, J.E., & Jackson, M.B. 1994. Anaerobic conditions strongly promote extension by stems of overwintering tubers of *Potamogeton pectinatus* L. *J. Exp. Bot.* **45:** 1309–1318.

Tardieu, F., Zhang, J., Katerji, N., Bethenod, O., Palmer, S., & Davies, W.J. 1992. Xylem ABA controls the stomatal conductance of field-grown maize subjected to soil compaction or soil drying. *Plant Cell Environ.* **15:** 193–19

Terashima, I., Hanba, Y.T., Tazoe, Y., Vyas, P., & Yano, S. 2006. Irradiance and phenotype: Comparative eco-development of sun and shade leaves in relation to photosynthetic CO_2 diffusion. *J. Exp. Bot.***57:** 343–354.

Ternesi, M., Andrade, A.P., Jorrin, J., & Benloloch, M. 1994. Root-shoot signalling in sunflower plants with confined root systems. *Plant Soil* **166:** 31–36.

Terry, N. 1970. Developmental physiology of sugar-beet. II. Effect of temperature and nitrogen supply on the

growth, soluble carbohydrate content and nitrogen content of leaves and roots. *J. Exp. Bot.* **21:** 477–496.

Thonat, C., Mathieu, C., Crevecoeur, M., Penel, C., Gaspar, T., & Boer, N. 1997. Effects of a mechanical stimulation on localization of annexin-like proteins in *Bryonia dioica* internodes. *Plant Physiol.* **114:** 981–988.

Todd, G.W., Chadwick, D.L., & Tsai, S.-D. 1972. Effect of wind on plant respiration. *Physiol. Plant.* **27:** 342–346.

Touraine, B., Clarkson, D.T., & Muller, B. 1994. Regulation of nitrate uptake at the whole plant level. In: A whole-plant perspective on carbon-nitrogen interactions, J. Roy & E. Garnier (eds.), SPB Academic Publishing, The Hague, pp. 11–30.

Tyerman, S.D., Niemietz, C.M., & Bramley, H. 2002. Plant aquaporins: Multifunctional water and solute channels with expanding roles. *Plant Cell Environ.* **25:** 173–194.

Van Arendonk, J.J.C.M. & Poorter, H. 1994. The chemical composition and anatomical structure of leaves of grass species differing in relative growth rate. *Plant Cell Environ.* **17:** 963–970.

Van Arendonk, J.J.C.M., Niemann, G.J., Boon, J.J., & Lambers, H. 1997. Effects of N-supply on anatomy and chemical composition of leaves of four grass species, belonging to the genus *Poa*, as determined by image-processing analysis and pyrolysis-mass spectrometry. *Plant Cell Environ.* **20:** 881–89

Van den Boogaard, R., Goubitz, S., Veneklaas, E.J., & Lambers, H. 1996. Carbon and nitrogen economy of four *Triticum aestivum* cultivars differing in relative growth rate and water use efficiency. *Plant Cell Environ.* **19:** 998–1004.

Van der Werf, A. 1996. Growth analysis and photoassimilate partitioning. In: Photoassimilate distribution in plants and crops: Source-sink relationships, E. Zamski & A.A. Schaffer (eds.). Marcel Dekker, New York, pp. 1–20.

Van der Werf, A. & Nagel, O.W. 1996. Carbon allocation to shoots and roots in relation to nitrogen supply is mediated by cytokinins and sucrose. *Plant Soil* **185:** 21–32.

Van der Werf, A., Schieving, F. & Lambers, H. 1993. Evidence for optimal partitioning of biomass and nitrogen at a range of nitrogen availabilities for a fast- and slow-growing species. *Funct. Ecol.* **7:** 63–74.

Van Volkenburgh, E. 1994. Leaf and shoot growth. In: Physiology and determination of crop yield, K.J. Boote, J.M. Bennet, T.R. Sinclair, & G.M. Paulsen (eds.). American Society of Agronomy, Crop Science Society of America, Soil Science Society of America, Madison, pp. 101–120.

Van Volkenburgh, E. & Boyer, J.S. 1985. Inhibitory effects of water deficit on maize leaf elongation. *Plant Physiol.* **77:** 190–194.

Vervuren, P.J.A., Blom, C.W.P.M., & De Kroon, H. 2003. Extreme flooding events on the Rhine and the survival and distribution of riparian plant species. *J. Ecol.* **91:** 135–146.

Visser, E.J.W., Cohen, J.D., Barendse, G.W.M., Blom, C.W. P.M., & Voesenek, L.A.C.J. 1996. An ethylene-mediated increase in sensitivity to auxin induces adventitious root formation in flooded *Rumex palustris* Sm. *Plant Physiol.* **112:** 1687–1692.

Visser, E.J.W., Colmer, T.D., Blom, C.W.P.M., & Voesenek, L.A.C.J. 2000. Changes in growth, porosity, and radial oxygen loss from adventitious roots of selected mono- and dicotyledonous wetland species with contrasting types of aerenchyma. *Plant Cell Environ.* **23:** 1237–1245.

Voesenek, L.A.C.J., Benschop, J.J., Bou i Torrent, J., Cox, M. C.H., Groeneveld, H.W., Millenaar, F.F., Vreeburg, R.A. M., Peeters, A.J.M. 2003. Interactions between plant hormones regulate submergence-induced shoot elongation in the flooding tolerant dicot *Rumex palustris*. *Ann. Bot.* **91:** 205–211.

Voesenek, L.A.C.J., Rijnders, J.H.G.M., Peeters, A.J.M., Van de Steeg, H.M.V., & De Kroon, H. 2004. Plant hormones regulate fast shoot elongation under water: From genes to communities. *Ecology* **85:** 16–2

Voesenek, L.A.C.J., Colmer, T.D., Pierik, R., Millenaar, F.F., & Peeters, A.J.M. 2006. How plants cope with complete submergence. *New Phytol.* **170:** 213–226.

Vriezen, W.H., Van Rijn, C.P.E., Voesenek, L.A.C.J., & Mariani, C. 199 A homologue of the *Arabidopsis thaliana ERS* gene is actively regulated in *Rumex palustris* upon flooding. *Plant J.* **11:** 1265–1271.

Went, F.W. 1926. On growth-accelerating substances in the coleoptile of Avena sativa. *Proc. Koninkl. Ned. Akad. Wetensch. Ser. C.* **30:** 10–19.

Wahl, S. & Ryser, P. 2000. Root tissue structure is linked to ecological strategies of grasses. *New Phytol.* **148:** 459–471.

Wong, S.C. 1993. Interaction between elevated atmospheric concentration of CO_2 and humidity on plant growth: Comparison between cotton and radish. *Vegetatio* **104/5:** 211–221.

Witkowski, E.T.F. & Lamont, B.B. 1991. Leaf specific mass confounds leaf density and thickness. *Oecologia* **88:** 486–493.

Wright, I.J., Reich, P.B., Cornelissen, J.H.C., Falster, D.S., Groom, P.K., Hikosaka, K., Lee, W., Lusk, C.H., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Warton, D.I., & Westoby, M. 2005. Modulation of leaf economic traits and trait relationships by climate. *Global Ecol. Biogeog.* **14:** 411–421.

Wu, Y., Sharp, R.E., Durachko, D.M., & Cosgrove, D.J. 1996. Growth maintenance of the maize primary root at low water potentials involves increases in cell-wall extension properties, expansin activity, and wall susceptibility to expansins. *Plant Physiol.* **111:** 765–772.

Yano, S. & Terashima, I. 2001. Separate localization of light signal perception for sun or shade type chloroplast and palisade tissue differentiation in *Chenopodium album*. *Plant Cell Physiol.* **42:** 1303–1310.

Yano, S. & Terashima, I. 2004. Developmental process of sun and shade leaves in *Chenopodium album* L. *Plant Cell Environ.* **27:** 781–793.

Yokota, T. 1997. The structure, biosynthesis and function of brassinosteroids. *Trends Plant Sci.* **2:** 137–143.

Zhu, G.L. & Boyer, J.S. 1992. Enlargement in *Chara* studied with a turgor clamp. Growth rate is not determined by turgor. *Plant Physiol.* **100:** 2071–2080.