Chapter 6 - Growth analysis: a quantitative approach

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Growth is an irreversible increase in plant size accompanied by a *quantitative* change in biomass (weight). Development is more subtle and implies an additional *qualitative* change in plant form or function such as a phase change from vegetative to reproductive growth.

Growth analysis is a conceptual framework for resolving the nature of genotype x environment interactions on plant growth and development.

In natural environments, growth and development cycles have to be completed within a time frame dictated by environmental conditions where light, moisture and nutrients often limit expression of genetic potential. Adaptive features that counter such constraints and help sustain relative growth rate can be revealed via growth analysis under contrasting conditions.



At the right is a highly productive rice crop with the grain-bearing panicles emerging from the canopy. The dry mass of the grain will be 50% of the total above-ground biomass - a harvest index of 0.5. (Photograph courtesy R. Munns)

In managed environments, crop plants commonly experience similar restrictions, but in addition their economic yield is often only a small portion of total biomass at harvest and subject to genetic control. Crop scientists need to explore plant growth and reproductive development in quantitative terms. Sources of variation in productivity can then be resolved into those processes responsible for converting external resources into biomass and those responsible for partitioning biomass into usable sinks such as cereal ears or pumpkins. Both aspects are addressed here.

6.1 - Concepts and components of RGR

The most useful and widely used analysis is the concept of relative growth rate (RGR) and the simple RGR equation, which derives from the growth of cell populations with unrestricted resources – that is where light, space and nutrient supply are not limiting.

Growth models developed from populations of single cells can be extended mathematically to cover complex multicellular organisms where whole-plant growth is expressed in terms of leaf area and nutrient resources. Such growth indices are not intrinsic properties of plants, but rather mathematical constructs with functional significance. These concepts can be traced to the early 1900s and have proved increasingly useful for studies of growth and developmental responses in natural and managed environments.

6.1.1 - Cell populations

A small population of unicellular organisms presented with abundant resources and ample space will increase exponentially (Figure 6.1a). Population doubling time T_d (hours or days) is a function of an inherent capacity for cell division and enlargement which is expressed according to environmental conditions. In Figure 6.1(a) doubling times for these two populations are 1 and 2 d for fast and slow strains respectively.

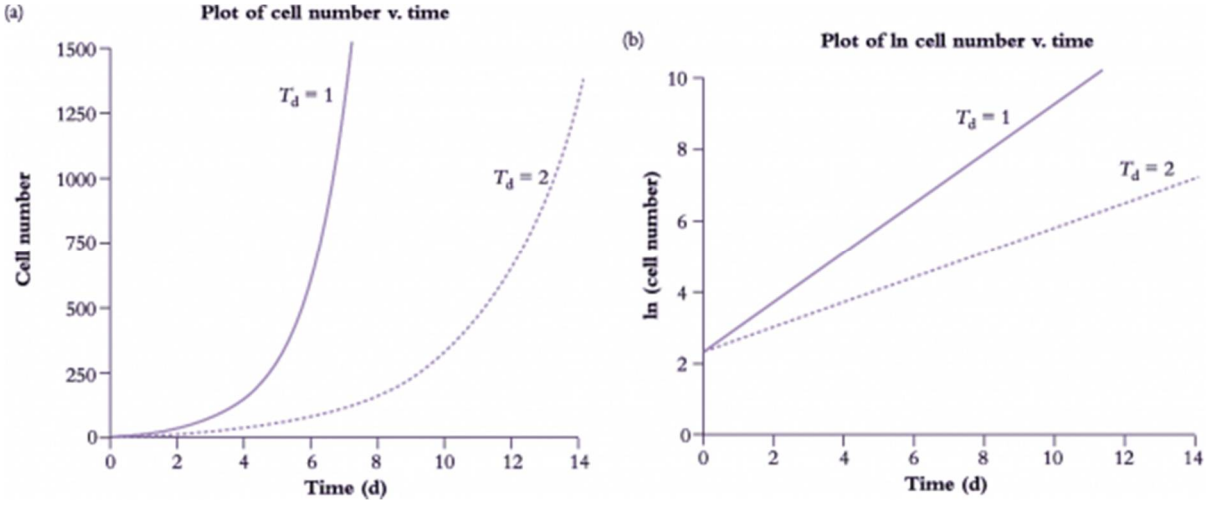


Figure 6.1 A population of cells unrestricted by space or substrate supply will grow exponentially. In this hypothetical case, a fast-growing strain of a single-celled organism with a doubling time of 1 d starts on day 0 with a population of n cells which increases to 120.*n* by day 7. In this example, n=10. The slow-growing strain with a doubling time of 2 d takes

twice as long to reach that same size. When data for cell numbers are ln transformed, exponential curves (a) become straight lines (b) where slope = r.

Exponential curves such as those in Figure 6.1(a) are described mathematically as

$$N(t) = N_0 e^{rt} \qquad (6.1)$$

where $N(t)$ is the number of cells present at time t, N_0 is the population at time 0, r determines the rate at which the population grows, and e is the base of the natural logarithm. By derivation from Equation 6.1

$$r = \frac{1}{N}\frac{dN(t)}{dt} \qquad (6.2)$$

and is called *relative growth rate* with units of 1/time. The doubling time is $T_d = (\ln 2)/r$.

If a population or an organism has a constant relative growth rate then doubling time is also constant, and that population must be growing at an exponential rate given by Equation 6.1. The 'fast' strain in Figure 6.1(a) is doubling every day whereas the 'slow' strain doubles every 2 d, thus r is 0.69 d^{-1} and 0.35 d^{-1}, respectively.

If cell growth data in Figure 6.1(a) are converted to natural logarithms (i.e. ln transformed), two straight lines with contrasting slopes will result (Figure 6.1b). For strict exponential growth where $N(t)$ is given by Equation 6.1,

$$\ln N(t) = \ln N_0 + rt \qquad (6.3)$$

which is the familiar slope-intercept form of a linear equation, so that a plot of ln $N(t)$ as a function of time t is a straight line whose slope is relative growth rate r, and intercept is ln N_0

In practice, r is inferred by assessing cell numbers N_1 and N_2 on two occasions, t_1 and t_2 (separated by hours or days depending on doubling time — most commonly days in plant cell cultures), and substituting those values into the expression

$$r = \frac{\ln N_2 - \ln N_1}{t_2 - t_1} \qquad (6.4)$$

which expresses r in terms of population numbers N_1 and N_2 at times t_1 and t_2, respectively.

If growth is exponential, Eq. 6.3 will be linear and any two time points and the natural logarithm of their corresponding population sizes will give an estimate of the growth rate, r. However, if relative growth rate r is not constant, then growth is not exponential but the concept of relative growth rate is still useful for analysis of growth dynamics in populations or organisms. Equation 6.3 is then used to compute average relative growth rate between times t_1 and t_2 even though population growth might not follow Equation 6.1 in strict terms. In that case plots analogous to Figure 6.1(b) will not be straight lines.

6.1.2 - Plant biomass

In whole plants, cell number is an impractical measure of growth. Instead, fresh or oven-dried biomass (W) is generally taken as a surrogate for cell growth and referenced to the number of days elapsed between successive observations. Relative growth rate is now known as RGR rather than r and measured in days or weeks rather than hours.

Relative growth rate, RGR (d^{-1}), can be expressed in terms of differential calculus as $RGR = (1/W)\,(dW/dt)$ (compare Equation 6.2.) so that RGR is increment in dry mass (dW) per increment in time (dt) divided by existing biomass (W). Averaged over a time interval t_1 to t_2 during which time biomass increases from W_1 to W_2, RGR (d^{-1}) can be calculated from

$$\mathrm{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \qquad (6.5)$$

which is analogous to Eq, 6.4. Net gain in biomass (W) is the outcome of CO_2 assimilation by leaves minus respiratory loss by the entire plant. Leaf area can therefore be viewed as a driving variable, and biomass increment (dW) per unit time (dt) can then be divided by leaf area (A) to yield the net assimilation rate, NAR (g m^{-2} d^{-1}), where

$$\mathrm{NAR} = \frac{1}{A}\frac{dW}{dt} \qquad (6.6)$$

Averaged over a short time interval (t_1 to t_2 days) and provided whole-plant biomass and leaf area are linearly related (see Radford 1967),

$$\mathrm{NAR} = \left(\frac{W_2 - W_1}{t_2 - t_1}\right)\left(\frac{\ln A_2 - \ln A_1}{A_2 - A_1}\right) \qquad (6.7)$$

NAR thus represents a plant's net photosynthetic effectiveness in capturing light, assimilating CO_2 and storing photoassimilate. Variation in NAR can derive from differences in canopy architecture and light interception, photosynthetic activity of leaves, respiration, transport of photoassimilate and storage capacity of sinks, or even the chemical nature of stored products.

The following treatment assumes for simplicity that photosynthesis and the assimilation of CO_2 occurs only in leaves, even though for many herbaceous or succulent species it occurs to a lesser degree also in stems. Since leaf area is a driving variable for whole-plant growth, the proportion of plant biomass invested in leaf area will have an important bearing on RGR, and can be conveniently defined as leaf area ratio, LAR (m^2 g^{-1}), where

$$\mathrm{LAR} = \frac{A}{W} \qquad (6.8)$$

LAR can be factored into two components: specific leaf area (SLA) and leaf weight ratio (LWR). SLA is the ratio of leaf area (A) to leaf mass (W_L) (m^2 g^{-1}) and LWR is the ratio of leaf mass (W_L) to total plant mass (W) (dimensionless). Thus,

$$\text{LAR} = \frac{A}{W_L}\frac{W_L}{W} = \text{SLA} \times \text{LWR} \qquad (6.9)$$

As an aside, average LAR over the growth interval t_1 to t_2 is

$$\text{LAR} = \frac{1}{2}\left(\frac{A_1}{W_1} + \frac{A_2}{W_2}\right) \qquad (6.10)$$

Expressed this way, LAR becomes a more meaningful growth index than A/W (Equation 6.8) and can help resolve sources of variation in RGR.

If both A and W are increasing exponentially so that W is proportional to A, it follows that

$$\frac{1}{W}\frac{dW}{dt} = \frac{1}{A}\frac{dW}{dt} \times \frac{A}{W} \qquad (6.11)$$

0r (substituting Equations 6.5, 6.6 and 6.8)

$$\text{RGR} = \text{NAR} \times \text{LAR} \qquad (6.12)$$

As LAR can be broken into SLA and LWR (Equation 6.9) then

$$\text{RGR} = \text{NAR} \times \text{LWR} \times \text{SLA} \qquad (6.13)$$

Sources of variation in RGR partitioned this way provide useful insights on driving variables in process physiology and ecology. For an expanded discussion on methodological issues associated with the determination of RGR in experimental populations see Poorter and Lewis (1986).

Increases in leaf area over time can be a more useful basis for measuring plant growth rates than biomass increases, particularly as non-destructive techniques for measuring leaf area are now available. Plant growth rate can be measured as the relative increase in leaf area over time, by substituting total plant leaf area for total biomass in the conventional RGR equation.

$$\text{RGR}_A = (\ln LA_2 - \ln LA_1) / (t_2 - t_1) \qquad (6.14)$$

where RGR_A is relative leaf area expansion rate, LA is total plant leaf area and t is time at two time intervals, t_1 and t_2, preferably 2-3 days apart.

Growth indices in summary

Five key indices are commonly derived as an aid to understanding growth responses. Mathematical and functional definitions of those terms are summarised below.

Growth index	**Mathematic-al definition**	**Units**	**Functional definition**
RGR Relative growth rate	$1/W\ \mathrm{d}W/\mathrm{d}t$	d^{-1}	Rate of mass increase per unit mass present (efficiency of growth with respect to biomass)
NAR Net assimilation rate	$1/A\ \mathrm{d}W/\mathrm{d}t$	$g\ m^{-2}\ d^{-1}$	Rate of mass increase per unit leaf area (efficiency of leaves in generating biomass)
LAR Leaf area ratio	A/W	$m^2\ g^{-1}$	Ratio of leaf area to total plant mass (a measure of 'leafiness' or photosynthetic area relative to respiratory mass)
SLA Specific leaf area	A/W_L	$m^2\ g^{-1}$	Ratio of leaf area to leaf mass (a measure of thickness of leaves relative to area)
LWR Leaf weight ratio	W_L/W	dimension-less	Ratio of leaf mass to total plant mass (a measure of biomass allocation to leaves)

6.2 - Environmental impacts on RGR

Light, CO_2, temperature, water and nutrients are key driving variables or limiting factors for growth responses in a wide range of species. Growth indices serve as an indicator of plant response, and of interactions between environmental factors where they occur. Variation in whole-plant RGR can be resolved into contributions from NAR (net assimilation rate) and LAR (ratio of leaf area to total plant mass). LAR in turn can be separated into SLA (ratio of leaf area to leaf mass) and LWR (ratio of leaf mass to total plant mass).

Ecological and agronomic implications for managed and natural communities are considered in this section in the context of growth responses to light, temperature and CO2 concentration. The same principles apply to the analysis of effects of nutrients on growth, and to interactions between environmental variables.

6.2.1 – Light

Light impacts both photosynthetic activity and morphology of individual leaves and of plant canopies. Leaves are larger at higher light. Leaf area increases because of more cells per leaf rather than by cells having a larger surface area. Cells volume, however, increases and gives rise to substantial increases in leaf thickness. This is usually achieved by a greater depth of palisade cells, either greater in depth or an extra layer of cells.

Table 6.1
Leaf size and cell volume in cucumber (*Cucumis sativus)* responds to irradiance. Plants were maintained in growth cabinets at low or high daily irradiance. The leaf measured was at node 3.

Leaf 3	Daily irradiance (MJ m^{-2})	
	0.5	3.2
Area of leaf (cm^2)	127	356
Thickness of leaf (µm)	88	211
Mean cell volume (10^4 $µm^3$)	1.46	3.11
Cell cross-section ($µm^2$)	131	138
Cell volume:area (µm)	111	222

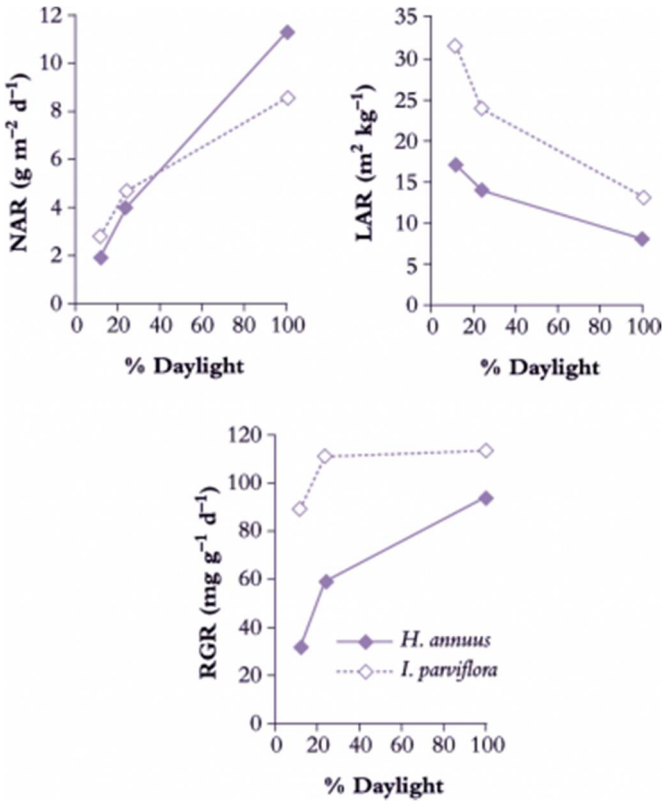
Based on Wilson (1966) J Exp Bot 17, 440-451

In the example shown for cucumber in Table 6.1, high light caused a three-fold increase in area, but the cell cross-section was the same, indicating that the leaves had three times the number of cells. The cell volume more than doubled under high light (3.11×10^{-5} mm^3 at 3.2 MJ m^{-2} s^{-1} cf. 1.46×10^{-5} mm^3 at 0.5 MJ m^{-2} d^{-1}), and because cross-sectional area was virtually unchanged, cell depth was responsible. This greater depth of palisade cells in strong light confers a greater photosynthetic capacity (per unit leaf area) and translates into larger values for NAR and a potentially higher RGR.

At lower irradiance (Table 6.1) leaves are thinner and SLA will thus increase with shading. Because LAR = SLA × LWR (Equation 6.9) a smaller leaf area at lower irradiance is offset to some extent by a higher SLA for maximum light capture with the most efficient use of resources.

The significance of LAR × NAR interaction for whole-plant growth was appreciated early by G.E. Blackman (Agriculture Dept, Oxford University), who in a series of papers analysed shade-driven growth responses for many species. RGR response to growing conditions in low light, and the degree to which upward adjustment in LAR could offset reduced NAR, was a recurring theme. In a series of 20 pot experiments, Blackman and Wilson (1951a) established a close relationship between NAR and daily irradiance where shade-dependent reduction in NAR was similar for 10 species. NAR was linearly related to log irradiance, and extrapolation to zero NAR corresponded to a light-compensation point of 6–9% full sun for eight species, and 14–18% full sun for two others. Significantly, neither slope nor intercept differentiated sun-adapted plants such as barley, tomato, peas and sunflower from two shade-adapted species (*Geum urbanum* and *Solanum dulcamara*). LAR proved especially responsive to light and accounted for contrasts between sun plants and shade plants in their growth response to daily irradiance.

Concentrating on sunflower seedlings, Blackman and Wilson (1951b) confirmed that NAR increased with daily irradiance (Figure 6.2) and that LAR was greatly decreased (Figure 6.2). Response in RGR reflected LAR and especially in young seedlings which also showed highest RGR and were most sensitive to shading. LAR appeared sensitive to both daily maxima as well as daily total irradiance.



New Figure 6.2 A sun-adapted plant such as *Helianthus annuus* adjusts LAR to some extent in response to lower daily irradiance but not enough to maintain RGR. By contrast, a shade-adapted plant such as *Impatiens parviflora* with somewhat higher LAR and RGR in full sun makes further adjustment in LAR so that RGR does not diminish to the same extent in moderate or deep shade as does that of *H. annuus* (Based on Blackman and Wilson 1951b; Evans and Hughes 1961)

A comparison between sunflower (Blackman and Wilson 1951b) and the woodland shade plant *Impatiens parviflora* (Evans and Hughes 1961) confirms this principle of LAR responsiveness to irradiance (Figure 6.2). Sunflower achieved noticeably higher NAR in full sun than did *I. parviflora*, but LAR was considerably lower, and translated into a somewhat slower RGR for sunflower. This species contrast was much stronger in deep shade (12% full sun) where RGR for *I. parviflora* had fallen to 0.090 d^{-1} whereas sunflower was only 0.033 d^{-1}. Clearly, *I. parviflora* is more shade tolerant, and retention of a faster RGR in deep shade is due both to greater plasticity in LAR as well as a more sustained NAR. Adjustments in both photosynthesis and respiration of leaves contribute to maintenance of higher NAR in shade-adapted plants growing at low irradiance.

6.2.2 – Temperature

Within a moderate temperature range readily tolerated by vascular plants (10–35°C, see Chapter 14) processes sustaining carbon gain show broad temperature optima. By contrast, developmental changes are rather more sensitive to temperature, and provided a plant's combined responses to environmental conditions do not exceed physiologically elastic limits, temperature effects on RGR are generally attributable to rate of canopy expansion rather than rate of carbon assimilation. In the early days of growth analysis, Blackman *et al*. (1955) inferred from a multi-factor analysis of growth response to environmental conditions that NAR was relatively insensitive to temperature, but whole plant growth was obviously affected, so that photosynthetic area (LAR) rather than performance per unit surface area (NAR) was responsible. Such inferences were subsequently validated.

Table 6.2
Relative rate of whole plant growth (RGR, d^{-1}) and rate of area expansion (RGR_A, d^{-1}) are both sensitive to temperature, but NAR is less so. Responses in RGR are therefore driven primarily by responses of area expansion. RGR and RGR_A wasere higher in C_4 than C_3 species, especially under warm conditions.

Species		21/10ºC		32/21ºC		38/27ºC	
		RGR	RGR_A	RGR	RGR_A	RGR	RGR_A
Cotton	C_3	0.086	0.073	0.206	0.197	0.188	0.172
Soybean	C_3	0.108	0.124	0.202	0.199	0.165	0.168
Cocklebur	C_3	0.165	0.151	0.269	0.263	0.204	0.176
Maize	C_4	0.096	0.133	0.255	0.354	0.178	0.189
Pigweed	C_4	0.262	0.239	0.482	0.436	0.393	0.328
Johnson grass	C_4	0.156	0.139	0.391	0.370	0.359	0.324

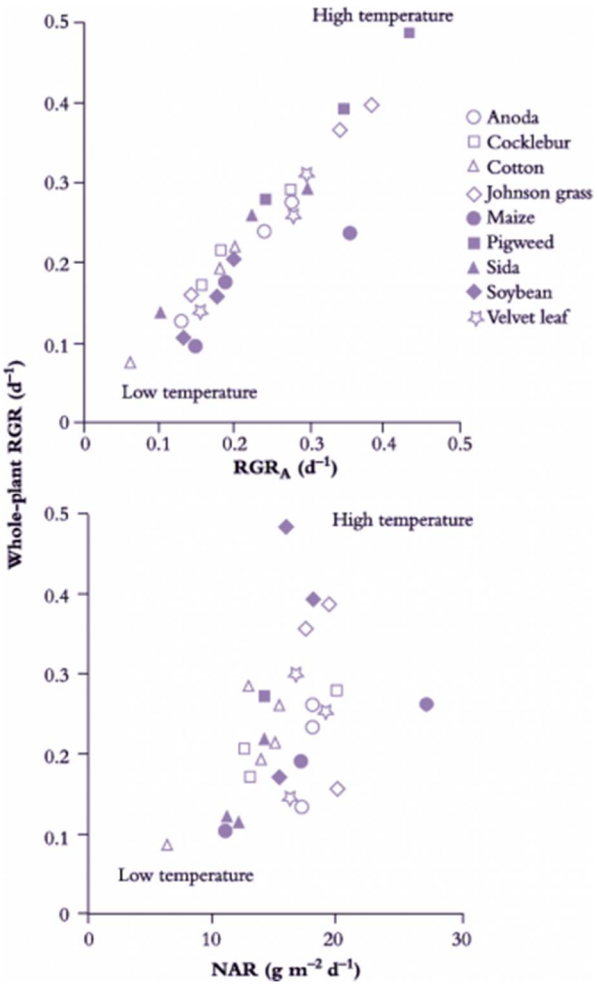
Based on Potter and Jones (1977). Species listed are *Gossypium hirsutum, Glycine max, Xanthium pensylvanicum, Zea mays, Amaranthus retroflexus, Sorghum halepense*.

Using day/night temperature as a driving variable, Potter and Jones (1977) provided a detailed analysis of response in key growth indices for a number of species (Table 6.2). Data for maize,

cotton, soybean, cocklebur, Johnson grass and pigweed confirmed that 32/21°C was optimum for whole-plant relative growth rate (RGR) as well as relative rate of canopy area increase (RGR_A). Both indices were lowest at 21/10°C. This was true for C4 as well as C3 species.

C4 species had a higher RGR and RGR_A than C3 species, especially under warm conditions (Table 6.2)

All populations described in Potter and Jones (1977) maintained strict exponential growth. NAR could then be derived validly and temperature effects on NAR could then be compared with temperature effects on RGR and RGR_A (Figure 6.3). With day/night temperature as a driving variable, most values for NAR fell between 10 and 20 g m^{-2} d^{-1}. Correlation between NAR and RGR was poor (Figure 6.3). By contrast, variation in both RGR and RGR_A was of a similar order and these two indices were closely correlated (Figure 6.3).



New Figure 6.3 Variation in whole-plant RGR is linked to relative rate of canopy expansion (RGR_A). Nine species (including C_3 and C_4 plants) grown under three temperature regimes (21/10 °C, 32/21 °C and 21/27 °C day/night) expressed wide variation in RGR that showed a strong correlation with RGR_A but was poorly correlated with variation in NAR. Extent rather than activity of leaves appears to be more important for RGR response to temperature. (Based on Potter and Jones 1977)

A later chapter in this book, Chapter 14, explains the effect of temperature on growth of different plant species, with particular focus on adaptation to very low and very high temperatures.

6.2.3 - Carbon dioxide

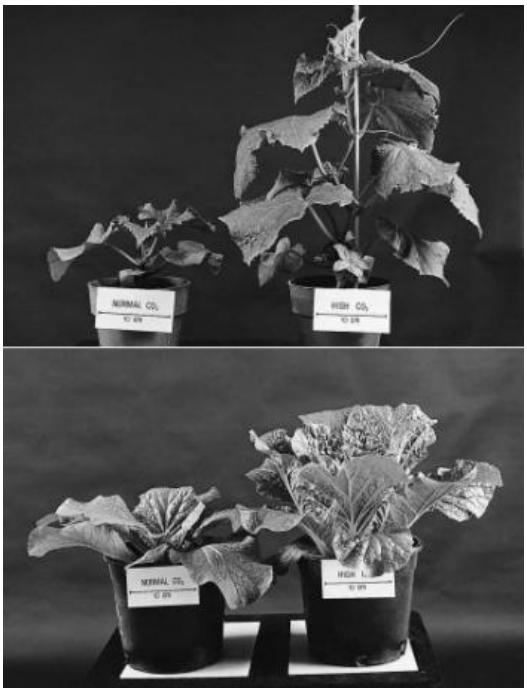


Figure 6.4 Early growth of cucumber (*Cucumis sativus, top panel*) and wong bok (*Brassica pekinensis, bottom panel*) is greatly enhanced in elevated CO_2 (1350 ppm) compared with ambient controls (330-350 ppm). As shown here, that initial effect is still apparent after 52 d of greenhouse culture in nutrient rich potting mix. Scale bar = 10 cm. (Further details in Kriedemann and Wong (1984) and Table 6.3) (Photographs courtesy Maureen Whittaker)

Growth responses to elevated CO_2 can be spectacular, especially during early exponential growth (Figure 6.4) and derive largely from direct effects of increased CO_2 partial pressure on photosynthesis. C_3 plants will be most affected, and especially at high temperature where photorespiratory loss of carbon has the greatest impact on biomass accumulation.

Global atmospheric CO_2 partial pressure is expected to reach 60–70 Pa (600–700 ppm) by about 2050 so that growth response to a CO_2 doubling compared with 1990s levels has received wide attention. Instantaneous rates of CO_2 assimilation by C_3 leaves can increase two- to three-fold in response to such elevated levels of CO_2, but the short-term response is rarely translated into biomass gain by whole plants where growth and reproductive development can be limited by low nutrients, low light, low temperature, physical restriction on root growth (especially pot experiments) or strength of sinks for photoassimilate. Given such constraints, photosynthetic acclimation commonly ensues. Rates of CO_2 assimilation (leaf area basis) by CO_2-enriched plants, grown and measured under high CO_2, will match rates measured on control plants at normal ambient levels.

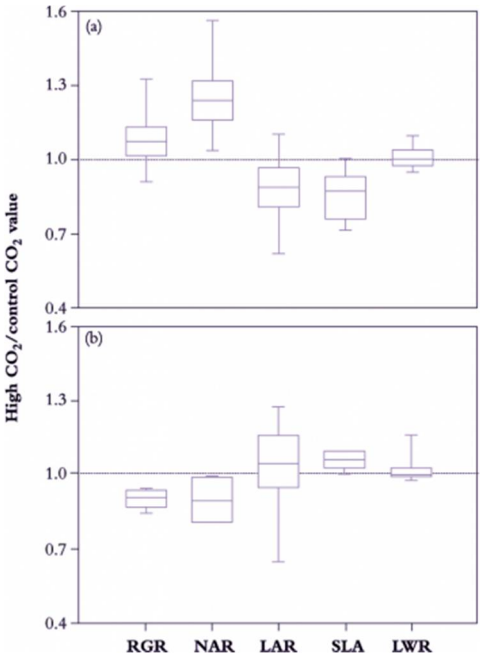


Figure 6.5 A survey of growth response to elevated CO_2 (ratio of growth indices in 600-800 cf. 300-400 ppm CO_2) in 63 different C_3 species (a) and eight C_4 species (b) reveals systematic differences in median values for growth indices that relate to photosynthetic mode. C_3 plants show a positive response in NAR that results in slightly faster RGR despite some reduction in LAR. C_4 plants reduce RGR under elevated CO_2 due to diminished NAR. SLA of C_3 plants is generally lower under elevated CO_2, but increased somewhat in C_4. LWR is essentially unchanged in either group (Based on Poorter *et al.* 1996)

Acclimation takes only days to set in, and because plant growth analysis commonly extends over a few weeks, CO_2-driven responses in growth indices tend to be more conservative compared with instantaneous responses during leaf gas exchange. C_4 plants will be less affected than C_3 plants (see Chapter 2) so that broad surveys need to distinguish between photosynthetic mode. For example, in Figure 6.5, average NAR for 63 different cases of C_3 plants increased by 25–30% under 600–800 ppm CO_2 compared with corresponding values under 300–400 ppm CO_2. However, NAR increase was not matched by a commensurate response in RGR, and decreased LAR appears responsible. CO_2-enriched plants were less leafy than controls (i.e. lower LAR), but not because less dry matter was allocated to foliage (LWR was on average unaltered). Rather, specific leaf area (SLA in Figure 6.5) decreased under high CO_2 so that a given mass of foliage was presenting a smaller assimilatory surface for light interception and gas exchange. Accumulation of non-structural carbohydrate (mainly starch; Wong 1990) is commonly responsible for lower SLA in these cases, and in addition generally correlates with down-regulation of leaf photosynthesis.

By contrast, in C_4 plants LWR was little affected by elevated CO_2, but in this case SLA did show slight increase with some positive response in LAR. However, photosynthetic acclimation may have been more telling because NAR eased and RGR even diminished somewhat under elevated CO_2.

Global change, with attendant increase in atmospheric CO_2 over coming decades, thus carries implications for growth and development in present-day genotypes and especially the comparative abundance of C_3 and C_4 plants. Elevated CO_2 also has immediate relevance to greenhouse cropping. In production horticulture, both absolute yield and duration of cropping cycles are factors in profitability. Accordingly, CO_2 effects on rate of growth as well as onset of subsequent development are of interest.

Table 6.3
Wong bok (*Brassica pekinensis*) and cucumber (*Cucumis sativus*) are strongly affected by elevated CO_2 (ambient x 3.85) during early growth, but the response in NAR (g m^{-2} d^{-1}) and RGR (d^{-1}) becomes muted as plants grow. Leaf area expansion (RGR_A) is especially sensitive to CO_2 enrichment, but only during early growth. RGR_A typically falls with age, and CO_2 enrichment appears to both hastens the process and expands the range.

Species	Age (d)	Ambient CO_2			Enriched CO_2		
		RGR	NAR	RGR_A	RGR	NAR	RGR_A
Wong bok	0-18	0.195	7.0	0.230	0.258	30.1	0.960
	18-24	0.307	9.8	0.297	0.291	11.8	0.222
	24-40	0.155	6.6	0.130	0.147	9.3	0.120
	40-52	0.114	8.1	0.061	0.066	6.6	0.020
Cucumber	0-21	0.107	6.9	0.164	0.173	13.3	0.215
	21-40	0.138	8.7	0.093	0.147	12.9	0.122
	40-52	0.036	3.3	0.061	0.051	5.8	0.035

Based on Kriedemann and Wong (1984) Acta Horticul 162, 113-120

Young seedlings in their early exponential growth phase are typically most responsive to elevated CO_2, so that production of leafy vegetables can be greatly enhanced. This response is widely exploited in northern hemisphere greenhouse culture. In commercial operations, ambient $CO_2$is often raised three- to four-fold so that growth responses can be spectacular (Figure 6.4) but they tend to be short lived (Table 6.3), as accelerated early growth gives way to lower RGR. During each cycle of growth and development, annual plants show a sigmoidal increase in biomass where an initial exponential phase gives way to a linear phase, eventually approaching an asymptote as reproductive structures mature. If CO_2 enrichment hastens this progression, a stage is soon reached where RGR is lower under elevated CO_2 due to accelerated ontogeny.

The fall in RGR with time of exposure to high CO2 is illustrated for wong bok (*Brassica pekinensis*) in Table 6.3. Wong bok is a highly productive autumn and winter vegetable that serves as 'spring greens' and is especially responsive to CO_2 during early growth. RGR_A at *c*. 330 ppm CO_2 was initially 0.230 d^{-1} compared with 0.960 d^{-1} at *c*. 1350 ppm CO_2, but by 40–52 d, RGR_A had fallen to 0.061 and 0.020 d^{-1} for control and CO_2 enriched, respectively (Table 6.3). CO_2-driven response in NAR and RGR also diminished with age, and especially where these larger individuals failed to sustain higher RGR past 18 d (Table 6.3). Nevertheless, a response in NAR was maintained for a further two intervals so that a CO_2 effect on plant size was maintained (Figure 6.4).

Component analyses of RGR as exemplified above are also useful for analysing whole plant responses to the supply of various nutrients and to interactions between nutrient supply and light, temperature or CO2. There are also strong interactions between these ambient conditions and abiotic stresses such as drought and salinity that can be quantitatively analysed.

The following two sections consider the developmental stages of leaf, shoot and reproductive organ formation, and how this information contributes to different types of quantitative growth analyses.

6.3 - Vegetative growth and development

Growth is an irreversible increase in plant size accompanied by a *quantitative* change in biomass. Development is more subtle and implies an additional *qualitative* change in plant form or function. Development thus lends 'direction' to growth and can apply equally well to a progressive change in gross morphology as to a subtle change in organ function, or to a major phase change from vegetative to reproductive development.

Increases in leaf area over time can be a useful basis for measuring plant growth rates than biomass increases, particularly as non-destructive and automated techniques for measuring leaf area are now available. Plant growth rate can be assessed as the relative increase in leaf area over time, by substituting total plant leaf area for total biomass in the conventional RGR equation.

$$RGR_A = (\ln LA_2 - \ln LA_1) / (t_2 - t_1) \qquad (6.14)$$

where RGR_A is relative leaf expansion rate, LA is total leaf area and t is time at two time intervals, t_1 and t_2, preferably 2-3 days apart. This can be done by image analysis. This information can be extrapolated to whole plant growth rates as leaves, stems and roots generally maintain a balance in biomass that can be described by an allometric relationship.

In the first part of this section, growth of individual leaves is described at the cellular level of organisation, how this is influenced by light, and how much the photosynthetic activity of leaves changes with development. The second part shows how root:shoot ratios change with availability of resources and the third part how these change with ontogeny (allometry).

6.3.1 - Patterns of leaf growth

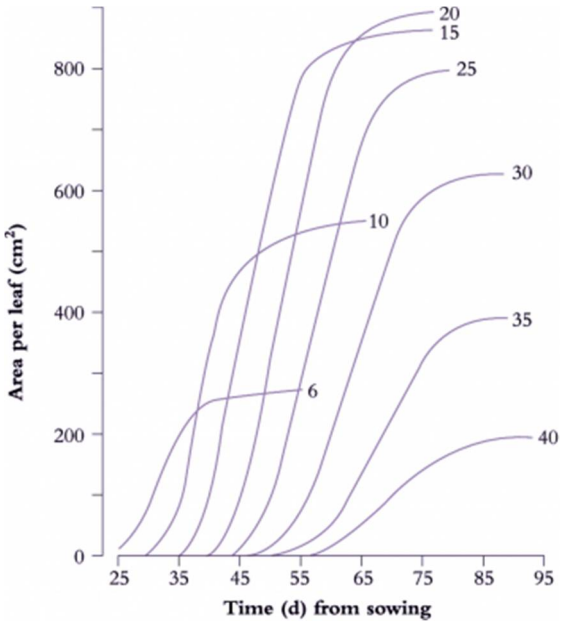


Figure 6.6 Leaf expansion in sunflower shows a sigmoidal increase in lamina area with time where rate of area increase and final size both vary with nodal position, reaching a maximum around node 20. The curves were drawn by hand through all data points (two measurements of leaf length (L) and leaf breadth (B) per week with area A estimated from the relationship $A = 0.73\ (L \times B)$. Based on Rawson and Turner (1982) Aust J Plant Physiol 9, 449-460

Growth rate of individual leaves provides much useful information on plant growth, especially in response to changes in environment, as leaf growth can be measured over hours or even minutes. Rates of leaf elongation or individual leaf area expansion cannot be used to calculate whole plant relative growth rates, but they can be used to assess current rates of individual leaf growth and effects of a treatment on the rate of leaf emergence ("phyllocron"). Leaf elongation (increase in length of a given leaf per hour or per day) is a sensitive measure of leaf growth and can be accomplished electronically with a transducer, over minutes, manually with a ruler over 4-24 hours, or automatically with a digital photographic technique over intervals of days. Linear measurements with a transducer or ruler are particularly sensitive for monocots whose growth is largely one-dimensional.

(a) Measurement of leaf expansion

Differences in canopy development result from the frequency of new leaf initiation and the time-course of lamina expansion. These can be inferred from comprehensive measurement of lamina expansion on successive leaves. Lamina expansion in both monocotyledons and dicotyledons is approximately sigmoidal in time and asymmetric about a point of inflexion which coincides with maximum rate of area increase. However there is a period of several days over which expansion rates are constant.

A determinate plant with large leaves such as sunflower (Figure 6.6) provides a typical example. Leaf area is shown as a function of time for eight nodes selected between node 6 and node 40. Final leaf area was greatest at node 20, but daily rates of expansion were uniform for leaves between nodes 10 and 25. Thus at any time between days 35 to 65, the daily rate of expansion of any leaf was the same. Slowest growth and smallest final size was recorded for node 40, adjacent to the terminal inflorescence.

Growth curves for monocots leaves are very similar, in that there is a period of several days during which the leaf has a constant rate of area expansion. Increases in leaf areas of cereals and other monocots are easier to measure than dicots as they grow only in length and not width, for the reason explained below.

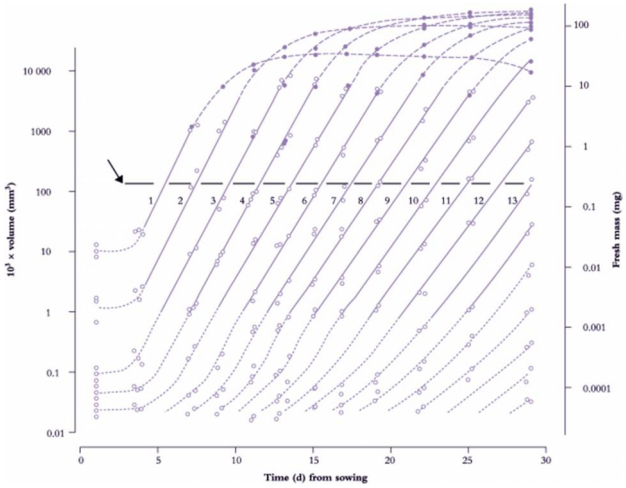


Figure 6.7. Leaves of subterranean clover achieve a 10-million-fold increase in size from primordium to final area (volume of primordia shown as dotted lines; leaf fresh mass shown as solid lines). Successive leaves are initiated and enlarge in a beautifully coordinated fashion revealed here as a family of straight lines on a semi-log plot. Intervals along an arbitrary abscissa (arrow at 100×10^{-3} mm^3) that intersects theses lines represent time elapsed (about 1.8 d) between attainment of a given development status by successive leaves (phyllochron). Full-sized leaves exceed about 100 mm^3 in volume. Based on Williams (1975) J Aust Inst Agric Sci 41, 18-26

Frequency of leaf initiation can be inferred from a more comprehensive family of such curves where early exponential growth in area for each successive leaf is recorded and plotted as $\log_{10}$ area versus time. This results in a near-parallel set of lines which intersect an arbitrary abscissa (Figure 6.7). Each time interval between successive points of intersection on this abscissa is a 'phyllochron' and denotes the time interval between comparable stages in the development of successive leaves. This index is easily inferred from the time elapsed between successive lines on a semi-log plot (Figure 6.7). Cumulative phyllochrons serve as an indicator of a plant's physiological age in the same way as days after germination represent chronological age.

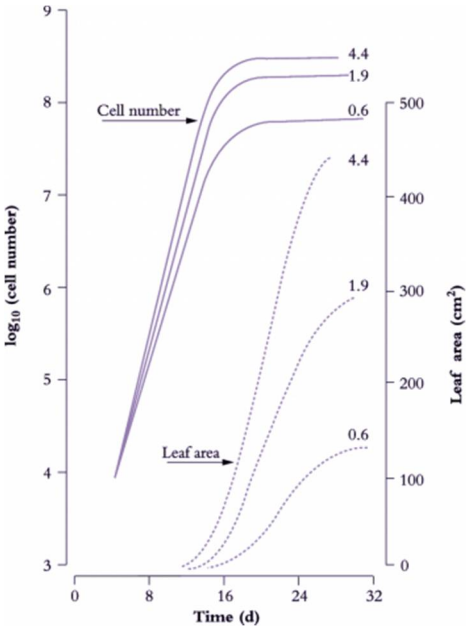


Figure 6.8. Leaves of cucumber (node 2 on plants in growth cabinets) show an approximately sigmoidal increase in area with time (broken lines) where final size and cell number vary with daily irradiance (0.6, 1.9 or 4.4 MJ m^{-2} d^{-1}). During an initial exponential phase in area growth, cell number per leaf (solid lines) also increases exponentially. The slope of a semi-log plot (hence relative rate of cell division) is higher under stronger irradiance. Cell number per leaf approaches asymptote as the rate of leaf area increase becomes linear. Based on Milthorpe and Newton (1963) J Exp Bot 14, 483-495

(b) Developmental stages of leaf expansion

Leaves are first discernible as tiny primordia which are initiated by meristems in accord with a genetically programmed developmental morphology. They undergo extensive cycles of cell division (peak doubling time about 0.5 d). Leaf growth is anatomically different in grasses (monocotyledonous species) and broad-leafed (dicotyledonous) plants.

Primordia of broad-leafed plants undergo extensive cycles of cell division and enlargement to form recognisable leaves with petioles that elongate and lamina that unfold and expand. Lamina expansion follows a coordinated pattern of further cell division and cell enlargement that is under genetic control but modified by the environment, particularly light. Early growth of the leaf is driven primarily by cell division, and cell number per leaf increases exponentially prior to unfolding. Cell division can continue well into the expansion phase of leaf growth, so that up to 90% of cells in a mature dicot leaf can have originated after unfolding. Cell division finishes about the time the leaf enters its period of linear rate of area expansion, so this period of maximum leaf expansion rate is due to expansion of pre-formed cells.

Primordia of grasses and other monocotyledonous species are hidden from view. All phases of cell growth occur at the base of the leaves which are usually not exposed to the environment. Cell division is confined to basal meristems which give rise to files of cells and a linear zone of cell expansion and differentiation. The emerging blade therefore is composed of cells that are fully expanded, and the elongation of that leaf takes place by addition of fully expanded cells from below.

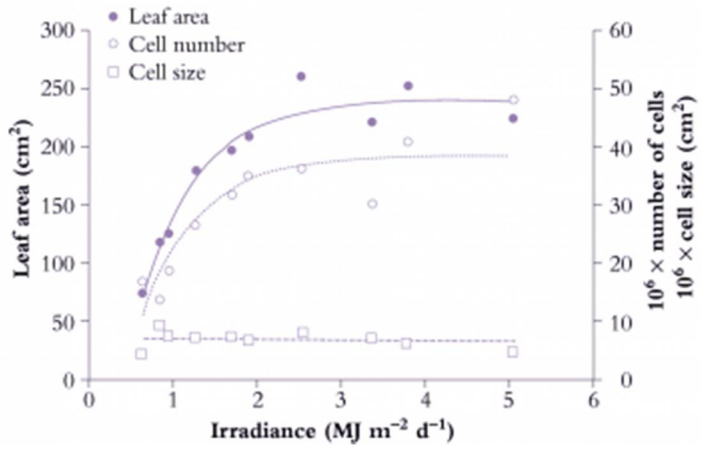


Figure 6.9. Area of individual leaves on cucumber (*Cucumis sativus*) responds to daily irradiance and reaches a maximum above about 2.5 MJ m^{-2} d^{-1}. Area increase (node 2 in this example) is due to greater cell number under stronger irradiance. Mean size of mesophyll cells is little affected and has no influence on area of individual leaves. Based on Newton (1963) J Exp Bot 14, 458-482

(c) Effects of light on leaf development

Light is the main variable affecting leaf growth rate, both the rate of leaf area expansion, final size, as well as cell shape as mentioned in the previous section.

Figure 6.8 shows the effect of light level on the rate of leaf area expansion in a cucumber leaf. As in all dicot leaves, the rate of lamina expansion is determined largely by the number of cells produced, with final cell area being unaffected (Figure 6.9). Rate of cell division during this early phase is increased by irradiance, so that potential size of these cucumber leaves at maturity is also enhanced. The upper curves in Figure 6.8 (highest irradiance), cell number per lamina reaches a plateau around 20 d, but area continues to increase to at least 30 d. Expansion of existing cells is largely responsible for lamina expansion between 20 and 30 d after sowing.

Figure 6.9 shows the effect of a range of light levels on final leaf area, and shows that area is strongly dependent on light level up to 2 MJ m^{-2} d^{-1}, and that the increased area has been achieved by more cells rather than larger cells.

A similar light response curve would be shown by monocot leaves, and with similar contributions from cell number versus cell size. The difference between monocots and dicots is that the cell number is determined in the basal meristematic zone, before the lamina emerges. This zone is not exposed to the light environment, so cell division activity in monocots is controlled by substrates or signals arising in the older expanded leaves.

(d) Leaf development and photosynthesis

When dicotyledonous leaves are very young and first unfold they have low rates of net photosynthesis (expressed per unit area) so have to import carbon from other leaves to support their growth. But as they expand their rates increase rapidly such that within a few days they can assimilate all their own carbon requirements and export excess (Figure 6.10).

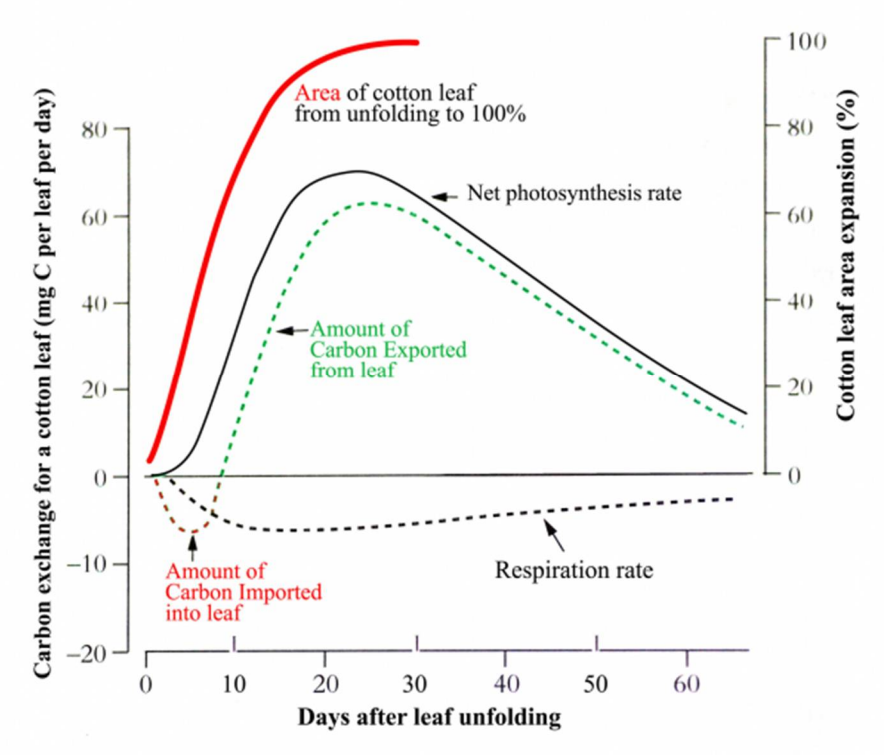


Figure 6.10 Change in net photosynthesis rate as a cotton leaf unfolds, expands, reaches maximum area and ages. An initial phase of carbon import helps sustain early expansion but by the time the leaf is 70% of its final area it is self sufficient for carbon and exporting excess. From Constable and Rawson (1980) Aust J Plant Physiol 7, 89-100 and 539-553

In the example for cotton in the figure, this self-sufficiency occurs when the leaf is about 70% of its final area. Typically, net photosynthesis rate will reach a maximum before the leaf has fully expanded though this can range from 25 to 100% of final area across species. Photosynthesis rate will then remain at that maximum or start to decline with further leaf expansion before leaf aging, lessening requirement for the carbon produced, and environmental factors accelerate the decline. Because the amount of carbon produced by a leaf is the product of two largely independent variables, its photosynthesis rate x its area, leaf carbon production can continue to increase while photosynthesis rate is stable or even declining.

Monocotyledonous leaves grow from their base where the very young expanding parts of the leaf are fully enclosed inside a sheath created by the surrounding leaf bases. The emerged parts of the leaf blade are already approaching full expansion as they emerge from the sheath and unroll. Photosynthesis rates of those exposed parts are already close to their maximum. Once the whole blade is exposed, photosynthesis rate and leaf carbon production follow plateau and declining patterns similar to those described for dicots though magnitude and duration differ amongst species and environments.

When doing experiments that investigate the effects of environmental treatments on photosynthesis, it is important bear in mind the continuous progression in photosynthesis rate between growing, recently fully expanded and aging leaves. Leaves should be compared that are of equivalent age and stage of development, particularly if single leaves are being measured to represent a whole plant or a breeding line. If the eventual aim of the experiment is to compare or select for carbon production, the area of the leaf must also be known since photosynthesis rate and fully expanded area of a leaf are not linked. Leaves of some dicotyledonous species take a few days to reach full expansion while others take weeks.

6.3.2 - Root:shoot ratios

Roots, stems and leaves are functionally interdependent and these three systems maintain a dynamic balance in biomass which reflects relative abundance of above-ground resources (light and CO_2) compared with root-zone resources (water and nutrients) (Poorter et al. 2012). Whole-plant growth rate and summary measures such as root:shoot ratio are thus an outcome of developmental stage and of environmental influences.

Change in root:shoot ratio during a plant's life cycle is part of an intrinsic ontogeny, but growth rates of roots and shoots continually adjust to resource availability with photoassimilate (hence biomass). In herbaceous plants, root:shoot ratios typically decrease with age (size) due to sustained investment of carbon in above-ground structures (root crops would be a notable exception). Developmental morphology is inherent, but expression of a given genotype will vary in response to growing conditions (hence phenotypic plasticity).

Irradiance is a case in point where shoot growth takes priority in low light, whereas root growth can be favoured under strong light. For example, Evans and Hughes (1961) grew *Impatiens parviflora* at five light levels and demonstrated a steady increase in root mass relative to whole-plant mass (root mass ratio) from 7% to 100% full sun. Stem mass ratio showed the opposite sequence. Leaf mass ratio increased somewhat at low light, but increased SLA was far more important for maintenance of whole-plant RGR in this shade-adapted species.

If light effects on root:shoot ratio are translated via photosynthesis, then CO_2 should interact with irradiance on root:shoot ratio because carbon assimilation would be maintained by a more modest investment in shoots exposed to elevated CO_2. *Chrysanthemum morifolium* behaved this way for Hughes and Cockshull (1971), returning a higher NAR due to CO_2 enrichment under growth cabinet conditions despite lower LAR which was in turn due to smaller leaf weight ratio. Adjustment in SLA exceeded that of leaf weight ratio, and so carried more significance for growth responses to irradiance × CO_2.

Consistent with shoot response to above-ground conditions, root biomass is influenced by below-ground conditions where low availability of either water or nutrients commonly leads to greater root:shoot ratio. For example, white clover (*Trifolium repens*) growing on a phosphorus-rich medium increased root:shoot ratio from 0.39 to 0.47 in response to moisture stress; and from 0.31 to 0.52 when moisture stress was imposed in combination with lower phosphorus (see Table 1 in Davidson 1969b). A positive interaction between low phosphorus and low water on root:shoot ratio was also evident in perennial ryegrass (*Lolium perenne*) grown on high nitrogen. In that case, root:shoot ratio

increased from 0.82 to 3.44 in response to moisture stress when plants were grown on low phosphorus in combination with high nitrogen.

Adding to this nutrient × drought interaction, a genotype × phosphorus effect on root:shoot ratio has been demonstrated by Chapin *et al*. (1989) for wild and cultivated species of *Hordeum*. Weedy barleygrass (*H. leporinum* and *H. glaucum*) was especially responsive, root : shoot ratio increasing from about 0.75 to 1.5 over 21 d on low phosphorus. By contrast, cultivated barley (*H. vulgare*) remained between 0.5 and 0.75 over this same period. Held on high phosphorus, all species expressed comparable root:shoot ratios which declined from around 0.55 to about 0.35 over 21 d. High root:shoot ratios on low phosphorus in weedy accessions would have conferred a selective advantage for whole-plant growth under those conditions, thus contributing to their success as weeds.

Even stronger responses to phosphorus nutrition have been reported for soybean (Fredeen *et al*. 1989) where plants on low phosphorus (10 µM KH_2PO_4) invested biomass almost equally between roots and shoots, whereas plants on high phosphorus (200 µM KH_2PO_4) invested almost five times more biomass in shoots than in roots (daily irradiance was about 30 mol quanta m^{-2} d^{-1} and would have been conducive to rapid growth).

Root:shoot ratios are thus indicative of plant response to growing conditions, but ratios are not a definitive measure because values change as plants grow. Trees in a plantation forest would show a progressive reduction in root:shoot ratio, and especially after canopy closure where a steady increase in stem biomass contrasts with biomass turnover of canopy and roots and thus predominates in determining root:shoot ratio.

Broad generalisations are that root:shoot ratio increases with nutrient deficiency and moisture stress or under elevated CO_2, but decreases in strong light. Too often, however, reports of treatment effects on root:shoot ratio have can overlooked differences in developmental ontogeny or size, and real responses may be obscured. Allometry then becomes a preferred alternative where repeated measurements of size or mass provide an unambiguous picture of carbon allocation.

6.3.3 - Allometry

During whole-plant growth in a stable environment, roots and shoots maintain a dynamic balance such that

$$y = bx^k \qquad (6.17)$$

Where *y* is root biomass and *x* is shoot biomass. More generally, *x* and *y* can be any two parts of the same organism that are growing differentially with respect to each other, but root–shoot relations are the most common candidate in such analyses of plant growth.

The allometric equation (Equation 6.17) was formalised by Huxley (1924) and can be ln transformed to become

$$\ln y = \ln b + k \ln x \qquad (6.18)$$

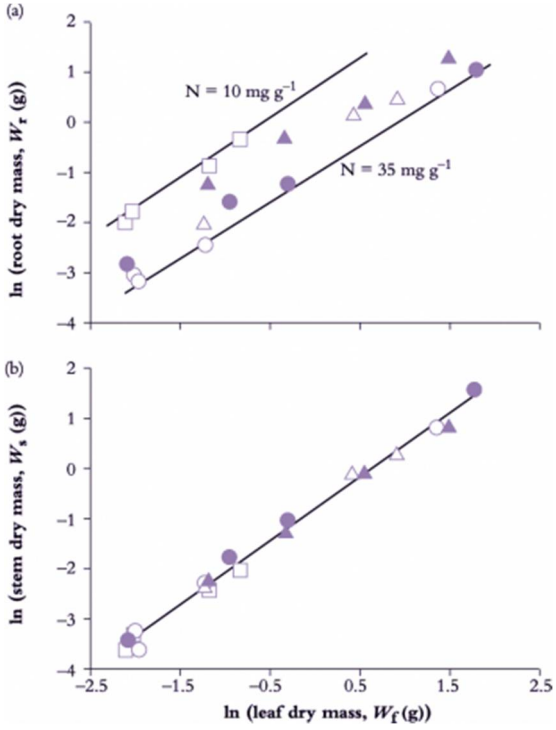


Figure 6.11 Seedlings of *Eucalyptus grandis* growing in aeroponic culture on five different nitrogen treatments show a strict allometry between root (W_r) and leaf growth (W_f) (a) as well as between stem (W_s) and leaf growth (b). With all other nutrient elements non-limiting, nitrogen was supplied at five relative addition rates (d^{-1}), namely 0.12 (open circles), 0.10 (solid circles), 0.08 (open triangles), 0.06 (solid triangles) and 0.04 (open square). Root:leaf allometry in seedlings on the lowest relative addition rate (plant [N] 10 mg g^{-1}) shows a similar slope but a higher intercept compared with plants maintained continuously on the highest rate (plant [N] 35.5 mg g^{-1}). Stem:leaf allometry (b) was highly conserved regardless of N addition rate with a slope (*k*) of 1.261 reflecting a steady commitment to stem growth over leaf growth in these tree seedlings. Based on Cromer and Jarvis (1990) Aust J Plant Physiol 20, 83-98

This formulation enables a straight-line plot of ln *y* as a function of ln *x* with slope *k* (i.e. the allometric coefficient) and intercept ln *b*. This empirical model does not explain the nature of growth controls between roots and shoots but does offer a simple description which is not confounded by plant size. Moreover, any departure from a particular root : shoot relationship is immediately

obvious, and sources of variation in root : shoot ratio can be resolved into starting conditions (differences in intercept, ln *b*) versus biomass partitioning during growth (differences in slope, *k*).

Leaf, stem and root growth under controlled conditions in *Eucalyptus grandis* seedlings demonstrate such application (Figure 6.11). Nitrogen input in nutrient spray chambers was used as a driving variable for growth where five relative addition rates generated a wide range in whole-plant RGR (from 0.039 d^{-1} 0n lowest to 0.111 d^{-1} on highest rate).

Data from all treatments and harvests were pooled to reveal a strict allometric relationship between root and leaf growth (Figure 6.11) with a nitrogen effect on intercept but not slope. Nitrogen nutrition had influenced biomass allocation to the extent that low addition rate had initially promoted root growth relative to leaves (hence higher intercept), but subsequent to this early adjustment, and once growth had stabilised, biomass allocation to roots and leaves maintained a constant relationship irrespective of addition rate. In this case $k = 0.982$, indicating a net bias towards leaf growth over root growth — a 'net bias' because carbon loss via excretion, root renewal and respiration was not measured so that more photoassimilate would have been allocated to roots than was fixed in biomass.

Stem and leaf biomass also maintained a strict allometric relationship (Figure 6.11) where $k = 1.261$. A value for *k* greater than unity implies a consistent bias towards stem growth relative to canopy growth, as would be expected in a eucalypt with a high rate of stem growth (and favoured in plantation forestry). Significantly, nitrogen treatment was without effect on either intercept or slope (Figure 6.11) and emphasises the highly conserved relationship between leaves and stem in these seedlings.

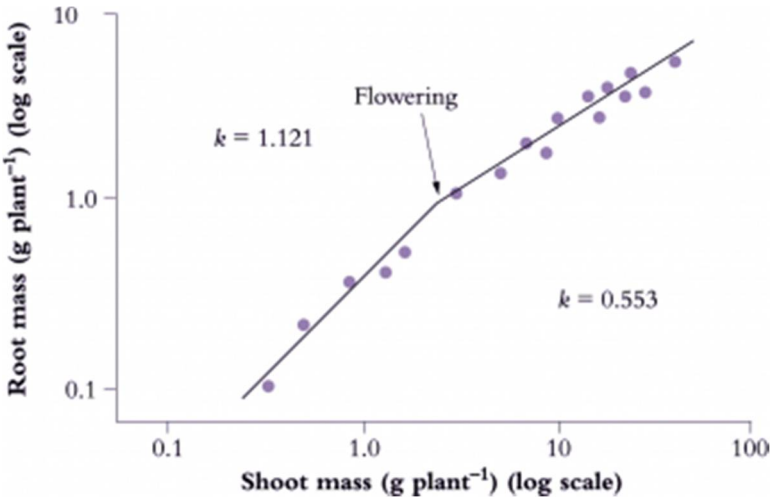


Figure 6.12 Root:shoot allometry in Italian reygrass (*Lolium multiflorum)* shows an abrupt change with flowering (log-log plot). A change in allometric coefficient (*k*) for this species from 1.121 to 0.553 indicates a shift in biomass allocation from root growth towards shoot growth following emergence of inflorescences. Mean values for *k* during vegetative cf. Reproductive phase from several accompanying species were 1.145 and 0.627 respectively. Based on Troughton (1956) J Brit Grassland Soc 11, 56-65

Developmental events also influence allometry and Italian ryegrass (*Lolium multiflorum*) provides a nice example (Figure 6.12) where a log–log plot of root mass as a function of shoot mass showed an abrupt change in slope when flowering occurred. In that case, *k* decreased from 1.121 to 0.553, and although shoot dry mass was about 10 times root biomass, a change in allometry was clearly evident.

6.4 - Reproductive development

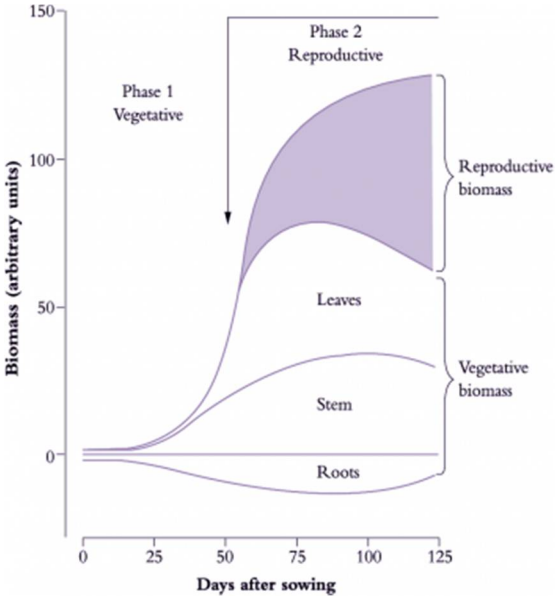


Figure 6.13 A notional distribution of biomass during the vegetative growth and reproductive development in an idealised annual plant such as a cereal or grain legume over *c.* 125 d. Whole-plant biomass follows a sigmoidal pattern with a near-exponential increase during vegetative growth and an asymptotic increase during subsequent maturation. Reproductive structures have by then become dominants sinks for photoassimilate, drawing 90-95% of their carbon from current photosynthesis but also mobilising stored assimilate from leaves, stems and roots, which lose biomass during that process (Original drawing P.E. Kriedemann; based on various sources)

Annual plants show a sigmoidal increase in total biomass during each life cycle (Figure 6.13) where a near-exponential vegetative phase (Phase 1) gives way to a reproductive phase (Phase 2) starting with flower initiation. In effect, Phase 1 sets a potential for reproductive yield whereas events during Phase 2 determine realisation of that potential because nearly all of the photoassimilate stored in reproductive structures (90–95% in cereal grains, for example) comes from carbon fixed subsequent to initiation. Reproductive organs then become dominant sinks for current photoassimilate as well as carbon-based resources previously stored in leaves and stems.

The carbon content of shoot components changes dramatically following onset of reproductive development. As shown for lupin in Figure 6.14, the dynamic balance between leaves and stem that had been previously maintained during vegetative growth is now replaced by an accelerated senescence of leaves and loss of non-structural carbohydrates from leaves plus stems to provide assimilates for the developing pods. At full maturity, reproductive structures in lupin account for about 50% of above-ground biomass, with seeds accounting for about two-thirds of that investment (Figure 6.14). In most grain or seed crops, the mature reproductive structure accounts for 50% of the above-ground biomass (Table 6.4).

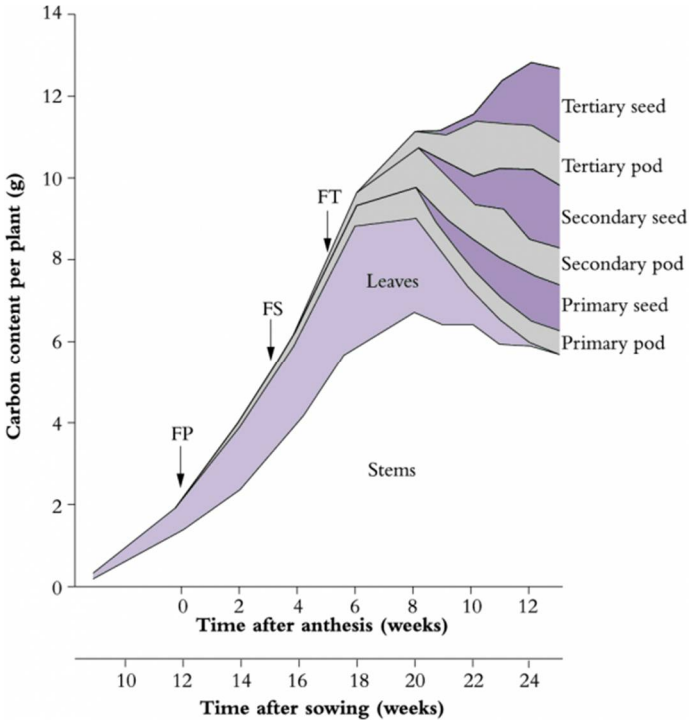


Figure 6.14 An unirrigated crop of lupin (*Lupinus angustifolius* cv. Unicrop) shows major redistribution of plant carbon from vegetative to reproductive structures during grain filling. This cultivar is indeterminate with successive cycles of reproductive development. FP, FS and FT indicate commencement of flowering on primary, secondary and tertiary shoots respectively. Seed carbon increased exponentially over the period 8-12 weeks after anthesis coinciding with leaf loss and some reduction in stem carbon. Nearby irrigated lupins retained leaves much longer. Based on Pate et al. (1980) Aust J Plant Physiol 7, 283-297

In wheat, also, assimilates are redistributed from stems to grains, more so when photosynthesis is limited (Rawson and Evans 1971). Remobilisation of stem reserves into grain is particularly important in a terminal drought. In wheat, stem reserves might contribute a high proportion to grain weight, and account for 80% of the carbon source rather than 10% as in well-watered conditions. But because grains are much smaller after drought, the absolute amount of carbon transported from the stem may be similar to that moved in good conditions. Percentages can be misleading.

In nature, a combination of ecological factors and life cycle options has led to wide variation in reproductive effort by vascular plants so that dry matter invested in reproductive structures relative to vegetative biomass will vary accordingly. For example, late successional rainforest species which combine shade adaptation with longevity are characterised by large propagules where massive seed reserves buffer young seedlings against shortfalls in carbon supply due to deep shade or dry spells. By contrast, early successional (pioneer) species on disturbed sites benefit by producing a large number of widely disseminated seeds. Their reproductive effort is best invested in number rather than size, and carries an added advantage that at least some viable seed will be produced even under stressful conditions. Weedy barleygrass is a case in point where Chapin *et al*. (1989) report that these species produce 4.5-fold more grains, but they are only one-sixth the size of cultivated barley. Ripening patterns also differed where grains matured synchronously in cultivated barley, but matured and dehisced progressively from tip to base in ears of barleygrass.

6.4.1 - Harvest index

The term “harvest index” is used in agriculture to quantify the yield of a crop species versus the total amount of biomass that has been produced. The commercial yield can be grain, tuber or fruit. Harvest index can apply equally well to the ratio of yield to total plant biomass (shoots plus roots) but above-ground biomass is more common because root mass is so difficult to obtain.

Table 6.4
Harvest index (dry mass of harvested component / total shoot dry mass) varies with crop species. Plant breeders have selected for high HI as their part of crop improvement strategies and have achieved some substantial gains. Their higher values are listed here.

Crop species	Harvested component	Harvest index (HI)
Wheat, barley	Grain	0.55
Rice	Grain	0.50
Maize	Grain	0.52
Sunflower	Seeds	0.50
Bean (Phaseolus)	Pods	0.25
Peanut	Pods	0.50
Cotton	Bolls	0.33
Sugar beet	Root	0.50
Potato	Tuber	0.82
Sweet potato	Tuber	0.65
Chrysanthemum	Flowers	0.46
Tulip	Flowers	0.20

Composite data drawn from a variety of sources including Evans 1993; Gifford 1986; Warren Wilson 1969

The harvest index of the lupin plants shown in Figure 6.14 was about 0.33. Potential values for the harvest index of various crop and horticultural species are shown in Table 6.4.

Domesticated plants have been subjected to sustained selection pressures on reproductive development by humans (Table 6.4) and now reflect wide variation from tuber-forming species such as potato, where over 80% of plant biomass is harvested as storage organs, to high-value flower crops such as tulip where blooms might represent only 20% of the final biomass of whole plants. Mid-range are legumes, cereals and other grain crops where human selection for yield has led to a notable increase in HI. Wheat, for example (Figure 6.15), increased from between 0.30 and 0.35 to almost 0.55 over a century, while barley and rice have shown similar trends.

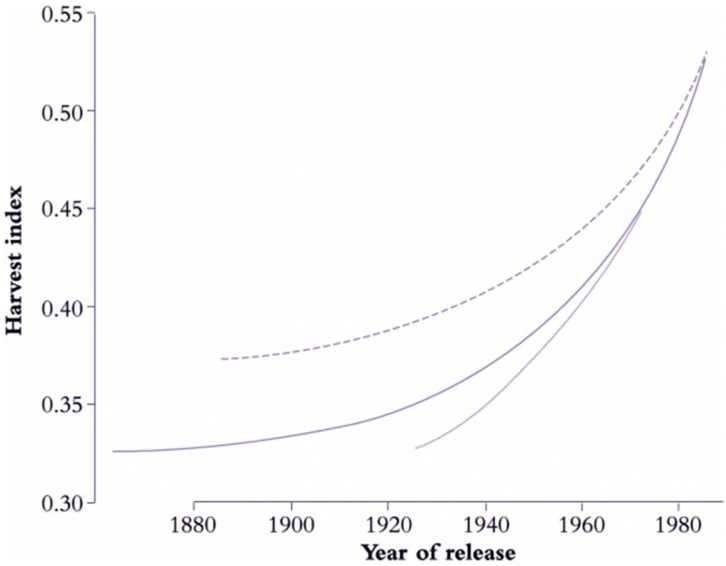


Figure 6.15 A century of breeding and selection has produced some solid gains in harvest index (HI) (ratio of grain to whole shoot biomass) for crop species including barley (dashed line), wheat (solid line) and rice (dotted line) as shown here. Introduction of dwarfing genes to reduce lodging under high-nutrient cultivation was a major factor in this achievement. Cereal architecture necessitates some trade off between stout stems to support heavy ears and a retention of leaf area to generate photoassimilate. HI will eventually reach a ceiling set by those constraints. Based on Evans (1993)

Yield improvement in cereals, cotton, peanuts and soybean which is similarly due to substantial increase in HI, emphasising (Gifford *et al*. 1984) that partitioning of photoassimilate rather than generation of whole-plant biomass was responsible for such yield improvement.

6.4.2 - Yield components

Yield of a cereal crop such as wheat or rice depends on the numbers of seeds that mature on a plant, and their size. Carbon partitioning during vegetative development and before flowering influences the number of flowers that are formed on a plant, as the reproductive sink competes with growing tissue in leaves, stems and roots for carbon supply. Carbon partitioning after flowering influences the rate of seed growth and the final size of the seed.

Major sources of variation in yield can be identified via a simple yield component model. Taking cereals as an example, final grain yield (g m^{-2}) is a product of grains per square metre and mass per grain.

Planting density and fertilizer can further influence yield components, as shown in the example in Table 6.5. In cereals, lateral shoots are called “tillers”, and the mature inflorescence that forms on a mature tiller an “ear”. Ears m^{-2} is in turn an outcome of planting density (plants m^{-2}), tillers per plant and ears per tiller. Not all tillers produce an ear, especially if the density is high and the plants then limited by light as well as possibly by fertilizer or water.

Some yield components such as mass per grain are especially stable, others such as ears m^{-2} and grains per ear vary widely with seasonal conditions or according to original planting density (Table 6.5). In that case (*Insignia* wheat at Glen Osmond, South Australia), mass per grain was highly conserved (33–35 mg) whereas tillers per plant varied from 41 at lowest planting density to only three at highest density. Significantly, yield variation was buffered by compensatory responses in yield components. For example, effects of low planting density were offset by production of more

tillers per plant and more ears per tiller. Grains per ear then determine potential yield so that growing conditions would have become crucial for realising such potential via grain retention and filling.

Table 6.5
Yield components of wheat vary according to planting density. A commercial crop of wheat is sown at 100 – 300 plants m^{-2}, according to water availability. Mass per grain is highly conserved, but plant mortality plus compensatory response between tiller numbers per plant, ears per tiller (not all tillers mature to produce a reproductive structure) and grain number per ear buffers yield against variation in seedling density.

Yield component	Original density at planting (plants m^{-2})				
	1.4	7.0	35	184	1078
Density at harvest (m^{-2})	1.4	7.0	35	154	446
Tillers per plant	41	30	14	7	3
Ears per tiller	0.7	0.6	0.5	0.3	0.2
Ears per m^2	41	130	252	323	303
Grains per ear	33	38	30	22	19
Mass per grain (mg)	34	35	33	33	33
Grain mass per plant (g)	33.2	24.7	7.05	1.52	0.42
Grain yield (g m^{-2})	46	173	247	234	183

Based on Puckridge and Donald (1967) Aust J Agric Res 18, 193-211

Genotype × environment interactions lead to huge variation in cereal grain yield and have been exploited for yield improvement. Universally, high grain number per square metre is a prerequisite for high yield and can be achieved via more ears per square metre and/or more grains per ear. In wheat and barley, grain number per ear has been primarily responsible for gains in yield; ears m^{-2} and mass per grain have not shown consistent increase (see Evans 1993 and literature cited).

For a commercial crop, mass per grain is the most important single component, and determines its use. The size (and sometimes shape) of the harvested product determines the value of the crop to the grower. A small or “pinched” wheat grain is of little value as it cannot be milled for flour and is fed to animals.

6.4.3 - Increasing harvest index

A major impetus to improve HI in cereals came from the introduction of dwarfing genes. In primitive wheats, and tall plants generally, reproductive structures have to compete with rapidly extending stems for photoassimilate, but dwarf cultivars alleviate such competition and enable a shift in carbon partitioning to ears. Early growth of ears and stems in two lines of a Mexican spring wheat (Figure 6.16) illustrate this principle. A steeper slope in the dwarf line (designated *Rht 1+2*) compared with the tall line (*rht*) implies greater allocation of photoassimilate to ear growth relative to stem growth. The two dominant dwarfing genes (*Rht 1* plus *Rht 2*) which are insensitive to gibberellic acid result in short stems and enhanced yield. Such genotypes formed the basis of the Green Revolution.

Tall wheat commonly “lodges” (falls over) in nitrogen-rich conditions, and dwarf wheats were originally developed to overcome this problem. Crop physiologists and breeders subsequently

recognised the yield advantage from improved partitioning of photoassimilate. Continuing selection for yield within the semidwarf background, which became common after the 1970s in both spring and winter wheats, has seen further yield progress with little change in plant height. Yield has improved further in spring wheats (Sayre et al 1997; Sadras and Lawson 2011) and in winter wheats (Shearman et al 2005) but yield progress in more recent varieties is associated with notable increases in total biomass. This has occurred in both spring wheats (Sadras and Lawson 2011) and winter wheats (Shearman et al 2005; Zheng et al 2011). Also whereas past yield progress in wheat has always been associated with more grains m^{-2} and unchanged or smaller grains, yield gain in recent varieties in some cases has been linked to heavier grains (e.g. Zheng et al 2011). The switch from higher harvest index to greater biomass may reflect limits to harvest index, now around 0.5 for the best varieties about 80-100 cm in stature, while the appearance of newer varieties with heavier grains may reflect pressure from grain processors. Either way the changes point to the power of empirical selection.

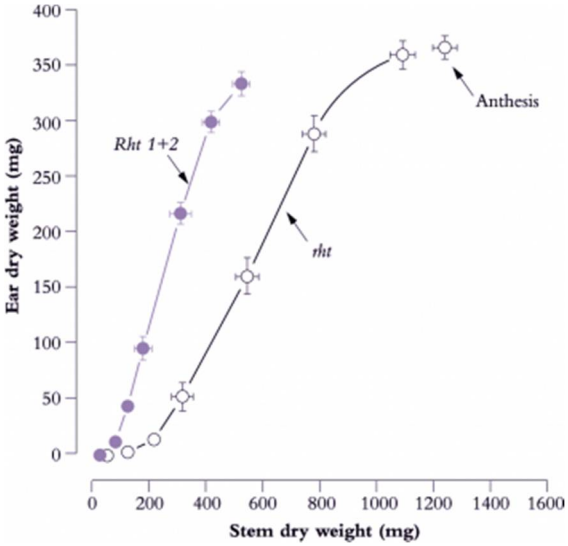


Figure 6.16 Early growth of reproductive tissues relative to stem mass in dwarf genotypes foreshadows faster ear development and higher HI. The tall and productive Mexican spring wheat (Yaqui 50, designated *rht*) eventually produces heavier ears, but returns a lower HI at maturity. Introduction of two major dwarfing genes (*Rht* 1 + *Rht* 2) resulted in shorter stems. Consequently developing ears were subject to less competition for photoassimilate during early differentiation and for grain filling subsequent to anthesis. Bars represent standard errors. Based on Bush and Evans (1988) Field Crops Res 18, 243-270

Some room still exists for further improvement in shoot HI compared with 1980s values (Figure 6.15) but there is a corollary. If shoot biomass remains unchanged, further improvement in HI implies further reduction in leaf and stem mass. Considering leaves, specific leaf area (area:mass ratio or SLA) will have a finite limit for structural reasons so that the area of CO_2-assimilating tissue servicing those enlarged sinks must also reduce as mass is reduced. Net assimilation per unit area (NAR) will therefore need to increase even further if potentially higher yields are to be realised. This could be achieved by either increases in photosynthetic potential or in more efficiency use of the energy produced.

The following section deals with respiratory efficiency and plant growth.

6.5 - Respiratory efficiency and plant growth

A significant amount of the CO2 fixed by photosynthesis is respired to produce the energy needed for production of new organs and maintenance of old ones. This is often termed a “cost”.

Costs associated with growth and maintenance of vascular plants can be represented as biomass equivalents. Calculations for dry matter utilisation during growth and development (Table 6.6) show that respiratory loss is substantial and can range from about 20-40% of the dry matter produced.

Table 6.6

Table 6.6 Typical rates of utilization of photosynthate by three types of sink relative to total dry weight (g g^{-1} d^{-1}) in an annual crop plant at the three major stages of plant development. The maturing plant has a sizable storage organ: fruit, seed or tuber. New photosynthate generated each day is allocated to structural growth, storage and respiration.

Stage of development	Structural growth (d^{-1})	Storage (d^{-1})	Respiration (d^{-1})
Seedling	0.20	0.05	0.10
Vegetative	0.15	0.05	0.08
Maturing	0.05	0.10	0.04

Based on Warren Wilson 1969.

During growth and development (Table 6.6) a fall in structural growth rate has been accompanied by a fall in whole-plant respiration, while the amount of photosynthate allocated to storage has risen. Overall, respiration accounts for a significant fraction of photoassimilate. Commonly one-third and, under stressful conditions as much as two-thirds, of a plant’s daily fixed CO_2 can be respired.

According to the estimates in Table 6.6, a germinating seedling with starting biomass of 1 g has in one day gained a further 0.2 g in structural growth plus 0.05 g in storage, with respiratory costs equivalent to 0.10 g g^{-1} d^{-1}, or 40% of the dry matter formed. Using similar logic, the young vegetative plant has produced structural growth and storage at a respiratory cost equivalent to 0.08 g g^{-1} d^{-1}, also 40% of the dry matter formed. In a maturing plant with less structural growth and with storage organs that are importing photoassimilate, the respiratory cost has fallen to 0.04 g g^{-1} d^{-1} or 27%, as the production of storage compounds requires less energy than does structural growth.

The physiological and biochemical processes involved in energy production, respiration, and utilization of energy have been described in detail in Chapter 2, but for convenience a summary is presented in the next section.

6.5.1 - Processes of energy generation and utilisation

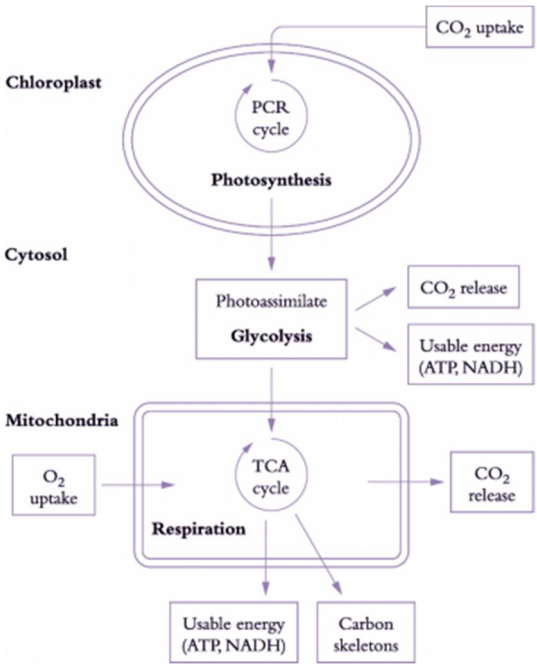


Figure 6.17. Simplified view of processes involved in carbon gain and generation of respiratory energy. The figure represents a mesophyll cell in a leaf. CO_2 assimilated by chloroplasts produces carbon-rich compounds (photoassimilates) that are exported to the cytosol and mitochondria. CO_2 is then produced during breakdown of these carbon-rich compounds by glycolysis and by mitochondrial respiration. Release of CO_2 and uptake of O_2 by mitochondria are coupled to production of usable energy (ATP, NADH). Carbon skeletons (necessary for protein synthesis) are also produced during mitochondrial respiration (Original drawing courtesy Owen Atkin)

(a) Photosynthesis and energy production

Photoassimilate is used to generate respiratory products needed for plant growth (Figure 6.17). Carbohydrate compounds produced from photosynthesis are exported from chloroplasts to the cytosol and mitochondria, and used to generate ATP, redox equivalents (in particular NADH) and carbon skeletons via glycolysis, mitochondrial tricarboxylic acid (TCA) activity and mitochondrial electron transport. Generation of these respiratory products results in CO_2 loss during glycolysis and passage of metabolites around the TCA cycle.

(b) Respiration and energy utilisation

Energy (ATP and NADH) and carbon skeletons produced by mitochondrial respiration are used for various processes essential to growth, maintenance, nutrient uptake and transport within the plant.

Maintenance respiration represents the portion of respiratory CO_2 release that is coupled to production of energy (ATP and reducing power) necessary for maintenance of chemical and electrochemical gradients across membranes, turnover of cellular constituents such as proteins, and

processes involved in physiological acclimation to changing or harsh environments (Penning de Vries 1975). Energy needed for maintenance is determined by the specific costs of processes taking place and is generally regarded as proportional to tissue mass.

Protein turnover is an energy-intensive process accounting for 60–80% of maintenance respiration (Penning de Vries 1975). Demand for respiratory energy associated with protein turnover will depend on turnover rate, respiratory costs associated with turnover, as well as the total amount of proteins undergoing turnover. Enzymes such as nitrate reductase (a key enzyme involved in nitrogen assimilation) have a very high turnover rate (Amthor 1984). As a result, plants assimilating nitrate have higher maintenance requirements than ammonium-grown plants (Hansen 1979).

Translocation of photoassimilate is also a potentially expensive process that accounts for approximately 30% of total dark respiration in several starch-storing plant species and would represent a substantial drain on photo-assimilate that could otherwise go into storage organs (Table 6.6). Phloem loading and unloading is largely responsible for this high cost because transport of sugars between symplasm and apoplasm depends on cotransport of H^+. Movement of H^+ is in turn dependent on ATP being consumed in the symplasm (Chapter 5). Traffic in photoassimilate thus increases demand for maintenance respiration

Energy costs associated with nutrient aquisition are often very high because ions have to be transported across root cell membranes using active transport systems that require substantial amounts of ATP. Energy requirement for ion uptake will depend on several factors, including the degree to which absorbed nutrients are released back to the soil and the degree to which protons and anions are cotransported into roots.

Table 6.7
Construction costs of synthesis of compounds in plant tissues (g glucose needed per g of organic compound) in plant tissues. Non-structural carbohydrate includes sucrose and starch.

Compound	Glucose needed (g per g)
Lipids	3.03
Lignin	2.12
Protein (using NO_3^-)	2.45
Protein using NH_4^+	1.62
Cellulose	1.22
Non-structural carbohydrate	1.09
Organic acids	0.91

Based on Poorter 1994; Penning de Vries et al. 1974

Growth respiration covers synthesis of new biomass from photosynthate and mineral nutrients and is regarded as proportional to the rate at which new material is being formed. Specific respiratory costs associated with growth (i.e. construction cost) will depend to a large extent on the chemical composition of plant material and by implication the amount of energy embedded in these molecules (Table 6.7). Compounds with a high carbon concentration require more ATP and reducing power for

their synthesis (Lambers and Poorter 1992). For example, biomass stored as lipid represents an investment of almost three times as much energy as would be required for storage of the same mass of non-structural carbohydrate. Plant growth analysis based on dry mass accumulation takes no account of such differences in chemical composition of end-products, so that comparisons of growth efficiencies based solely on RGR of biomass must be viewed circumspectly.

Construction cost, and thus growth respiration, also varies according to the chemical form of available nitrogen (e.g. N_2, NO_3^- and/or NH_4^+) *and* sites of assimilation. Nitrogen reduction is an energetically expensive process, requiring considerable input of respiratory energy (e.g. ATP + reductant) and TCA cycle intermediates. Plants fixing atmospheric N_2 in their roots demand much ATP, namely 12.5–26.5 mol ATP per mol of NH_4^+ produced, and a further 2.5–3.0 mol ATP for subsequent assimilation into nitrogen-based metabolites such as amino acids and proteins. NO_3^- reduction to NH_4^+ is cheaper, costing around 12 mol ATP per mol NH_4^+ produced.

Respiratory costs associated with NO_3^- assimilation can be substantially reduced if reduction of NO_3^- to NH_4^+ and subsequent assimilation of NH_4^+ into amino acids takes place in leaves. Reduction and assimilation of NO_3^- can then used excess photosynthetic reductant and ATP. Growth respiration associated with synthesis of nitrogen-based resources is thus greatly reduced by shoot assimilation of NO_3^-.

6.5.2 - Fast-growing versus slow-growing plants

Plants vary in their intrinsic growth rate, and may under the same environment differ three-fold in the relative growth rate. Some species are inherently fast-growing, and some inherently slow-growing. This section investigates the reason for this, and in particular the energy efficiency of the various species.

Fast-growing species tend to have higher rates of photosynthesis, but also use respiratory energy more efficiently for maintenance, growth and ion uptake. Variations in efficiency of energy use reflect differences in the proportion of whole-plant respiration that is allocated to these three processes and/or the specific costs of each process.

Fast-growing species achieve a higher RGR under optimum conditions than do slow-growing species under similar conditions. Carbon loss via respiration is considerable with genetic differences in generation and utilisation of respiratory energy contributing to these differences in RGR. Fast-growing species achieve a higher RGR than slow-growing species because their **net** rate of CO_2 uptake per unit of shoot and whole-plant mass is greater (Figure 6.18). By definition, net carbon fixed per day must depend to some extent on the proportion of fixed CO_2 that is subsequently lost by respiration, so that differences in respiratory CO_2 loss have an important impact on net carbon gain, and can be linked quantitatively to RGR.

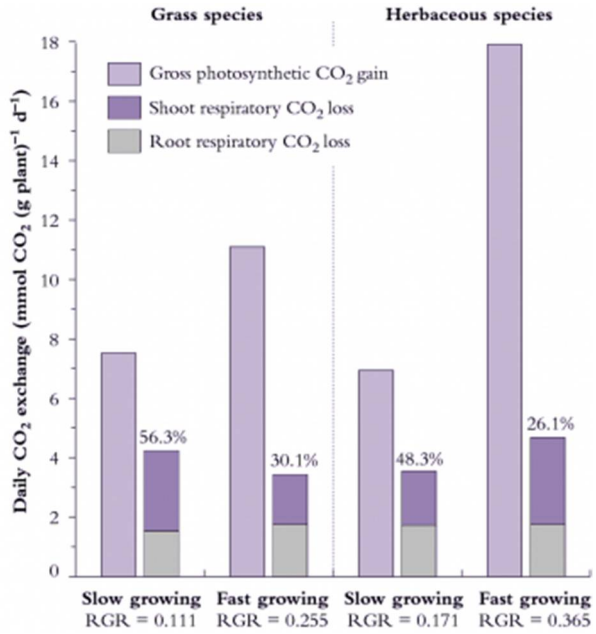


Figure 6.18 Daily carbon economy of plant species that differ with respect to inherent maximum RGR (g g^{-1} d^{-1}). The fast-growing grass and fast growing herb both exhibit higher rates of gross photosynthetic CO_2 uptake per unit mass (i.e. net photosynthesis plus shoot dark respiration) than their slow-growing counterparts. Fast-growing species lose a smaller percentage of daily fixed carbon via respiration. Based on data in Atkin *et al.* (1996) Funct Ecol 10, 698-707 for slow-growing Australian alpine and fast-growing lowland *Poa* species, and Poorter *et al.* (1990) Plant Physiol 94, 621-627 for the slow-growing herb *Pimpinella saxifrage* versus the fast-growing herb *Galinsoga parviflora*).

Data shown in Figure 6.18 can be used to calculate RGR for each species from photosynthesis and respiration measurements if the plant's carbon concentration is known.

Processes supporting a net gain in new biomass (d*W*, g) per unit time (d*t*, d) can be represented as:

$$\frac{dW}{dt} = A - R \qquad (6.25)$$

where *A* is daily carbon assimilation and *R* is whole-plant respiratory loss, so that net gain per unit existing plant biomass per unit time (or RGR, g g^{-1} d^{-1}) becomes

$$\mathrm{RGR} = \frac{1}{W}\frac{dW}{dt} = \frac{A}{W} - \frac{R}{W} \qquad (6.26)$$

If *A* and *R* are expressed as mmol carbon g^{-1} dry matter per day, then Equation 6.26 becomes

$$\mathrm{RGR} = (A - R)/C_{wp} \qquad (6.27)$$

where C_{wp} is plant carbon concentration in mmol carbon g^{-1} dry matter. *R* can be separated into R_{shoot} and R_{root}.

Whole-plant RGR can now be linked to gas exchange data for shoot assimilation (*A*), shoot respiration (R_{shoot}) and root respiration (R_{root}) according to the expression

$$\mathrm{RGR} = (A - (R_{shoot} + R_{root})/C_{wp} \qquad (6.28)$$

A and *R* can be determined from direct measurement of whole-plant gas exchange. The example below uses a value for C_{wp} of 34.8 mmol C g^{-1} dry matter.

Taking the fast-growing grass in Figure 6.18, where A is 11.1 mmol C g^{-1} plant d^{-1}, and R for shoots and roots is 1.75 and 1.68 mmol C g^{-1} d^{-1} , then RGR = 0.22 g g^{-1} d^{-1} .

This prediction of 0.22 d^{-1} for RGR represents an instantaneous value derived from whole-plant gas exchange measurements, whereas 0.255 d^{-1} in Figure 6.18 represents an average RGR from growth analysis over several days. Gas exchange values are generally within 10% of RGR values from sequential harvests.

Herbs and grasses can differ in the degree to which respiratory losses account for differences in RGR. Considering grasses (Figure 6.18, left side), 56% of daily fixed CO_2 is lost by respiration in the slow-growing alpine species whereas only 30% of daily fixed CO_2 is respired by the fast-growing lowland grass species. Over half of the carbon loss is attributable to roots in both species and, overall, respiration rate per unit plant mass is slightly higher in the slow-growing grass species.

Herbs in Figure 6.18 (right side) differ from grasses because the fast-growing herb respires faster than the slow-growing herb (on a mass basis) so that differences in percentage loss of carbon between these species cannot be due to differences in respiration rates *per se*. Significantly, however, the fast-growing herb still loses a smaller percentage of daily fixed carbon due to whole-plant respiration because daily CO_2 assimilation (mass basis) is especially high. A notably higher SLA in this fast-growing herb contributes to faster photo-synthesis on a mass basis (Figure 6.18).

A lower percentage loss of daily fixed carbon due to respiration in fast-growing grasses and fast-growing herbs does imply that carbon metabolism is more effective in these species than in their slow-growing counterparts, and serves as a model for generalisations. Such fast-growing plants may be more efficient in how they *generate* and/or *use* respiratory energy.

It is likely that an inherent capacity for fast growth confers a selective advantage for plants in favourable environments such as warm moist lowlands, but would be selectively neutral in restrictive environments such as nutritionally poor sites or alpine regions.

6.5.3 - Maintenance versus growth respiration

Growth respiration can be distinguished from maintenance respiration by relating variation in respiration rate to variation in RGR over short time intervals (Figure 6.19; Penning de Vries 1975). This approach assumes a model for respiration where:

Total respiration = Maintenance respiration + (Specific costs of growth x RGR) (6.31)

where respiration is expressed in mmol CO_2 g^{-1} d^{-1}, and specific costs of growth in mmol CO_2 g^{-1}.

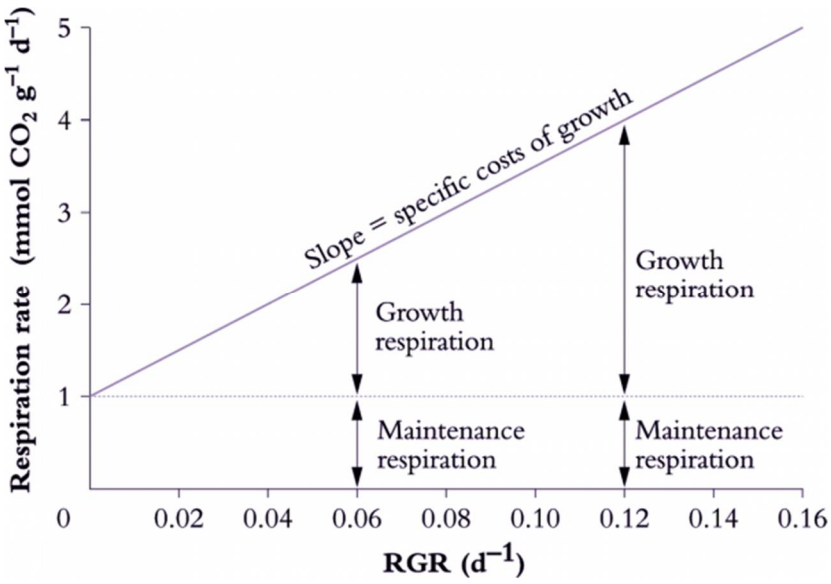


Figure 6.19 Determination of growth and maintenance respiration in whole plants, roots or shoots. Respiration rates are plotted as a function of RGR and maintenance respiration is taken as the rate of respiration when RGR is extrapolated to zero. The slope of this plot (25 mmol CO_2 g^{-1}) provides an estimate of the specific costs of growth which are assumed to remain constant for a given plant regardless of RGR. Variation in both RGR and respiration rate can be generated in several ways, including growing plants under different irradiances, or by measuring respiration and growth rates during development (RGR and respiration rate commonly decrease with age) (Original drawing courtesy Owen Atkin)

Decreases in RGR (e.g. due to growth under different irradiance or during ageing) are assumed to decrease demand for growth respiration, whereas demand for maintenance respiration is assumed to remain constant at different RGR values. Based on these assumptions, the maintenance component can be estimated by extrapolating the respiration rate back to a point where no growth occurs (1 mmol CO_2 g^{-1} d^{-1} in Figure 6.19). Specific respiratory costs associated with growth can be estimated from the slope of the respiration–RGR plot (25 mmol CO_2 g^{-1} in Figure 6.19).

An alternative approach to maintenance and growth components of respiration involves holding plants in extended darkness. Most annual plants use up their readily available energy sources after about 2 d and shoot growth will cease. Rate of CO_2 release would then reflect the maintenance component of dark respiration. The difference in dark respiration rates before and after 2 d darkness would be the growth component.

Such methods incorporate specific costs of ion uptake into estimates of growth respiration, but do not isolate the ion uptake component of root respiration. Ion uptake respiration can be separated from growth by partitioning root respiration into growth, maintenance and ion uptake components. The approach adopted by Veen (1980) assumes a model where:

Root respiration = Maintenance respiration + (Specific costs of growth x RGR) + (Specific costs of ion uptake x Ion uptake rate) (6.32)

A multiple regression analysis approach can be used to separate these components (Figure 6.20). Root respiration is taken as a dependent variable; while RGR and ion uptake rate are independent variables (van der Werf *et al*. 1994). The maintenance component of root respiration is taken as the rate of respiration when growth and ion uptake are extrapolated back to zero. Specific costs of growth and ion uptake are taken as the slope of the respiration versus growth and ion uptake regressions, respectively.

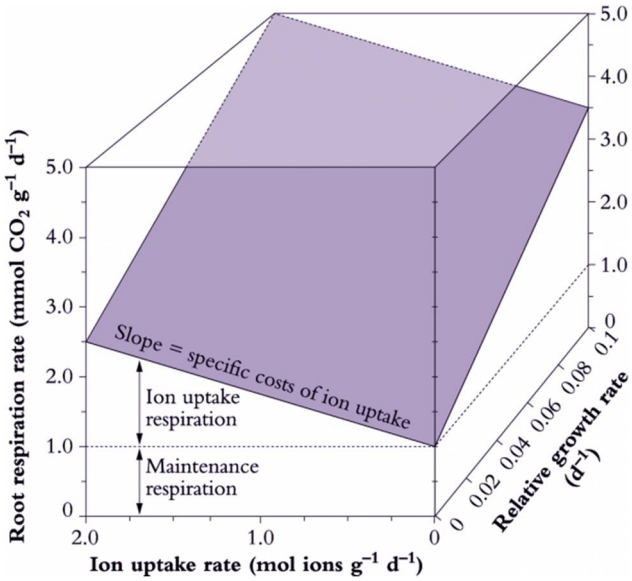


Figure 6.20. Determination of growth, maintenance and ion uptake components of root respiration. Maintenance respiration is taken as the rate of respiration when ion uptake rate and relative growth rate (RGR) are extrapolated to zero. Specific costs of ion uptake are estimated from the slope of the respiration versus ion uptake rate plot, while the actual amount of respiration allocated to ion uptake is shown. The slope of respiration versus RGR represents the specific costs of growth. Growth respiration varies with RGR, but specific costs of growth, ion uptake and maintenance are assumed to remain constant irrespective of variation in RGR or ion uptake (Original drawing courtesy Owen Atkin)

Most respiratory energy is allocated to nutrient acquisition in both fast- and slow-growing species (Figure 6.21) and this proportion increases even further under suboptimal conditions as maintenance costs rise. However, fast-growing species are distinguished by allocating less respiratory energy to nutrient acquisition, and more to growth. Presumably, a lower allocation to ion uptake in fast-growing species arises from lower specific costs. Loss of absorbed nutrients could also be lower in fast-growing species, while cotransport of protons and anions into roots might conserve energy. Maintenance costs also appear to be slightly lower in fast-growing plants (Figure 6.21) but any difference between these two plant categories in allocation to maintenance processes is small and is unlikely to matter overall. Nevertheless, differences in maintenance respiration will become more important when a plant is exposed to unfavourable conditions which invariably increase allocation of respiratory energy to fine-root turnover and maintenance of those structures.

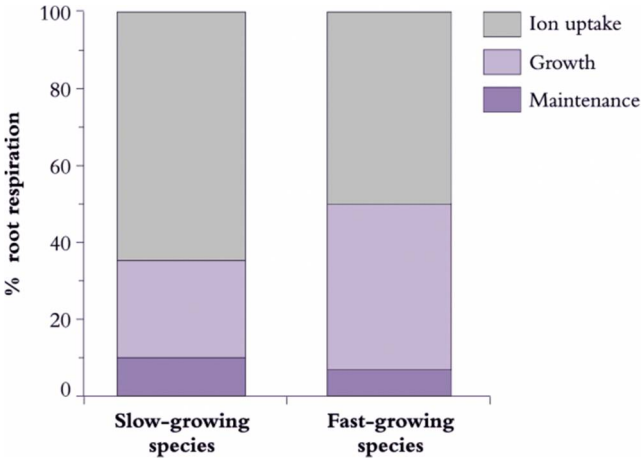


Figure 6.21 Root respiration is largely devoted to ion uptake and maintenance in slow-growing species (left-side) compared with a predominant allocation to growth in fast-growing species (right-side). (Generalised values comparable to Figure 6.18) (Based on Poorter *et al.* 1991)

6.5.4 - Suboptimal environments

Nitrogen limitation decreases absolute rates of shoot and root respiration in both fast- and slow-growing species (Figure 6.22) but the decrease in gross photosynthesis is much greater. Thus, the percentage of daily fixed CO_2 lost during respiration increases under nitrogen limitation. This mainly results from a greater allocation of photoassimilate to roots. Slower growth of whole plants on low nitrogen is therefore due to both slower photosynthesis due to less Rubisco coupled with more costly nitrogen acquisition.

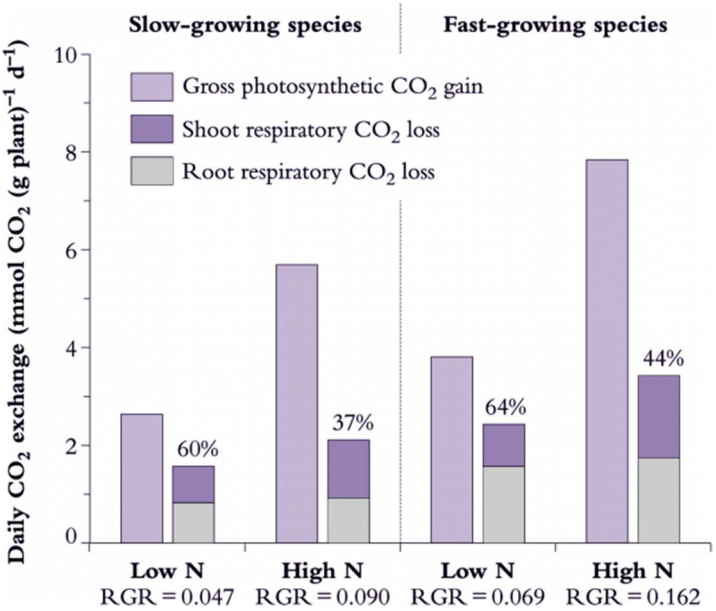


Figure 6.22 Low nitrogen (supplied as nitrate) reduces RGR in both fast-growing and slow-growing grass species. Photosynthesis and respiration (mass basis) also decrease, but the percentage of daily fixed carbon that is lost via respiration is higher on low nitrogen due to a greater investment of photoassimilate in roots. Photosynthetic CO_2 gain is expressed as net photosynthesis plus shoot respiration (assuming shoots respire in daytime at the same rate as that measured in darkness). Values for CO_2 exchange per unit plant mass were calculated from whole-plant measurements and proportions of plant biomass allocated to shoots and root, respectively. Based on Poorter *et al.* (1995) Plant Soil 171, 217-227

The proportion of daily fixed CO_2 that is respired may also increase under other stressful conditions such as drought, high temperature and ion toxicity. Challenged by such stresses, a greater proportion of respiratory energy is being used to support cellular maintenance in place of growth.

In conclusion, this chapter has shown that respiratory costs are high, for both formation of new tissues and maintenance of old ones. Plants profit from shedding old leaves and roots, where the costs of maintenance outweigh the benefits of their function. Future research into ways to minimise costs while maximising functions may produce more efficient plant forms. Quantitative growth analyses will be essential in developing new plants or improving management practises for higher yields in both optimal and suboptimal environments.

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