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PLANT ECOLOGY

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Science

1: Photosynthesis

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1.1 Introduction

The growth of plants depends upon their capacity to incorporate atmospheric carbon into organic compounds through the use of light energy absorbed during photosynthesis. This is a two-step process: (i) an initial photochemical reaction traps light energy in absorbing pigments (chlorophyll and accessory pigments), producing a reductant (NADPH) plus ATP; (ii) subsequently, atmospheric CO₂ is reduced and biochemically incorporated into carbohydrates (Fig. 1.1). The CO₂ to fuel this reaction diffuses from the atmosphere to the site of fixation within the chloroplast. Limitations to the overall rate of photosynthesis may occur through restrictions at either of these steps; the nature of these limitations is discussed in detail in the following sections.

1.2 Background

1.2.1 Photochemical reactions

A portion of the light energy impinging on a leaf is absorbed by chlorophyll pigments and then transferred to specialized reaction centres where electrons are moved along an energy gradient (Fig. 1.2). The free energy released in a series of subsequent electron transfers (known as the 'light reactions' of photosynthesis) is utilized to phosphorylate ADP and to reduce NADP (Barber & Baker 1985). Both molecules are

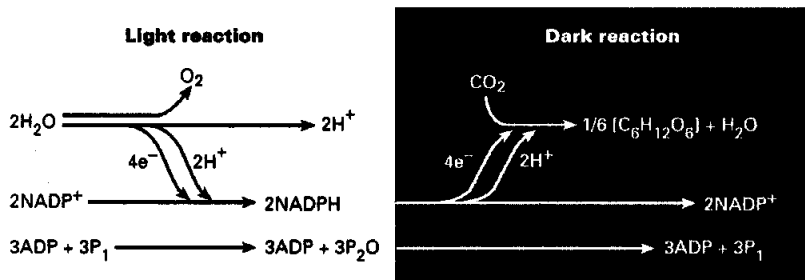
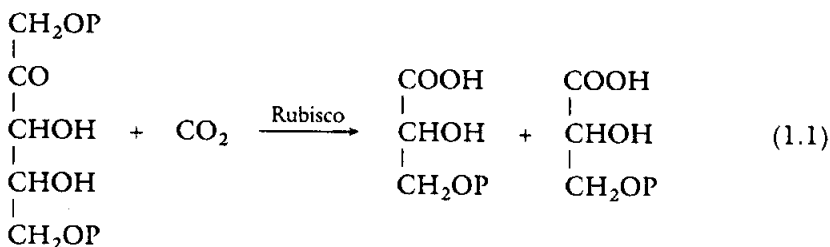


Fig. 1.1 Coupling of photochemical and biochemical reactions in photosynthesis. Since the biochemical reactions are not dependent on light they are termed 'dark reactions'. (From Miller 1979.)

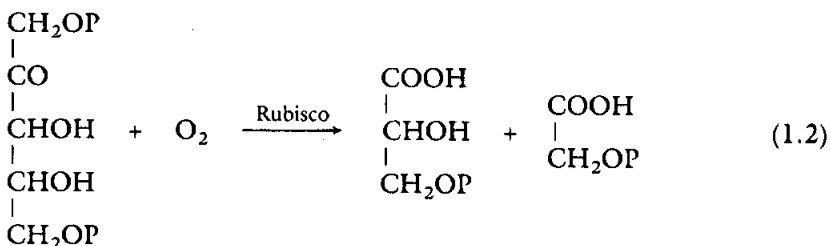
essential in the biochemical reduction cycle (the 'dark reactions') described below.

1.2.2 Biochemical reactions

In most plants, the initial reduction of CO₂ in photosynthesis depends upon the activity of a single enzyme, ribulose biphosphate carboxylase oxygenase (Rubisco). A fundamental feature of this enzyme is that both CO₂ and O₂ are competitive substrates for the active site. In the carboxylation reaction, atmospheric CO₂ is coupled with the five-carbon acceptor molecule, ribulose biphosphate (RuP₂), to form two molecules of a three-carbon product, 3-phosphoglycerate (3-PGA).



In the oxygenation reaction, O₂ and RuP₂ combine to form a two-carbon molecule, phosphoglycolate, and PGA.



The glycolate is broken down in a series of reactions (called photorespiration) that involve the generation of CO₂. Photosynthesis and photorespiration are linked as shown in Fig. 1.3. The photorespiratory cycle serves no known function, except to salvage as much of the carbon fixed as glycolate as possible; photorespiration appears to be an inevitable consequence of Rubisco activity in an aerobic environment.

The balance between the oxygenase and carboxylase reactions shifts according to atmospheric composition. Under today's atmospheric conditions (~350 ppm CO₂ and 21% O₂), about seven molecules of CO₂ react with RuP₂ for every two molecules of O₂. One CO₂ molecule is subsequently lost during photorespiration to give a net fixation of six molecules of CO₂. At an increased atmospheric CO₂ concentration, the CO₂ reaction predominates, resulting in (i) an increased rate of net photosynthesis, and (ii) a decrease in the compensation point (the concentration at which net CO₂ uptake balances O₂ evolution). Certain kinds of plants, the so-called C₄ species, possess mechanisms for main-

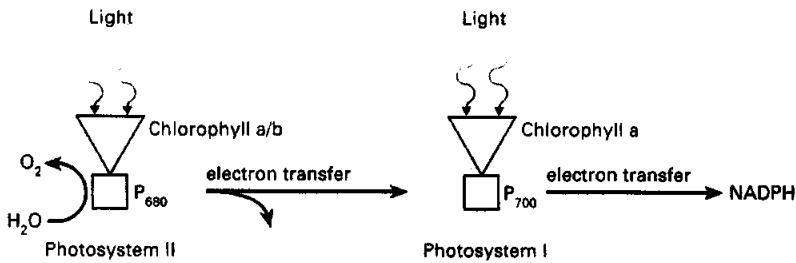


Fig. 1.2 Light reactions involved in the production of NADPH and ATP. Light is absorbed by 'antennae' chlorophyll pigments and transferred to specialized reaction centres and then to photosystems I and II. The photosystems are responsive to different wavelengths, with photosystem I absorbing light of 680 nm and photosystem II absorbing wavelengths longer than this. The electrons removed from the splitting of water are moved along this pathway obtaining reducing potential through the light reactions and eventually producing stored energy as ATP and the strong reductant NADPH. These, in turn, are utilized to reduce CO_2 to carbohydrate during non-light-requiring reactions. Plants from sun and shade habitats have leaves with different proportions of pigments, electron transfer chains and reaction centres.

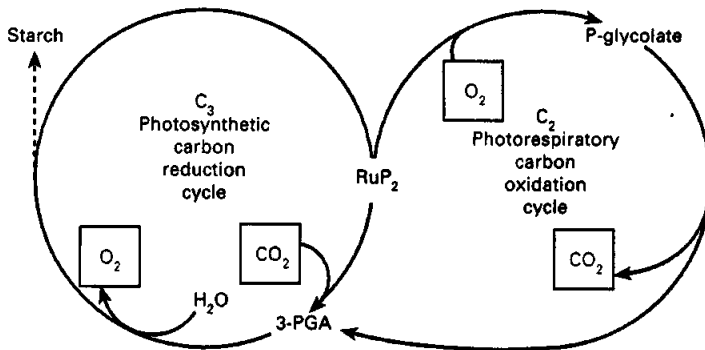


Fig. 1.3 Linkage of photosynthesis and photorespiration. (Modified from Osmond *et al.* 1981.)

taining the site of carboxylation at high CO_2 concentrations, so that carbon is not lost in photorespiration (see section 1.6).

1.3 Environmental influences on photosynthetic capacity

With this brief sketch of the process of photosynthesis as background, we are in a position to examine the influences of the physical environment on photosynthetic rates. We begin by considering the bulk of the world's plant species, which utilize RuP_2 as the primary carbon acceptor in photosynthesis. These are called C_3 plants because the initial product of photosynthesis is a three-carbon compound, PGA.

1.3.1 Light

Of the total solar and terrestrial radiation impinging on a leaf, it is only the fraction lying within the band between 400 and 700 nm that is photosynthetically active (Fig. 1.4). This is referred to as photosynthetically active radiation (PAR). Photosynthetic rates of leaves increase with increasing PAR because the supply rate of reducing power increases through photochemical reactions. The rate levels off as limitations of carboxylating capacity and diffusion begin to predominate. The stomatal conductance to CO_2 greatly influences the maximum photosynthetic rates achieved at high light intensities. At very low intensities, there is no net uptake of CO_2 since the rate of CO_2 uptake through photosynthesis is less than the rate of CO_2 evolution from mitochondrial respiration.

The photosynthetic light response may differ considerably between species and among leaves on the same individual plant (Fig. 1.5). The nature of these differences has been studied most thoroughly in leaves of

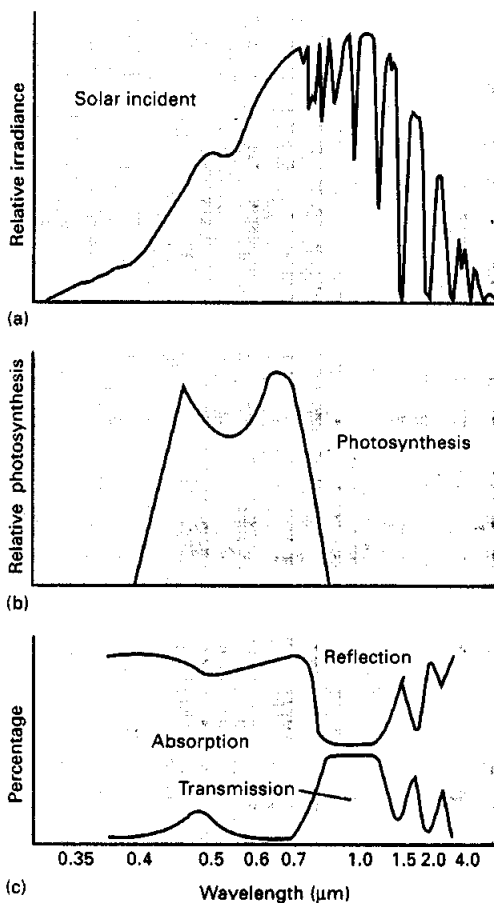


Fig. 1.4 Incoming solar radiation (a), photosynthetically active radiation, PAR (b), and leaf spectral characteristics (c). Note that the leaf has a high absorbance to PAR and a low absorbance to longer solar radiation wavelengths.

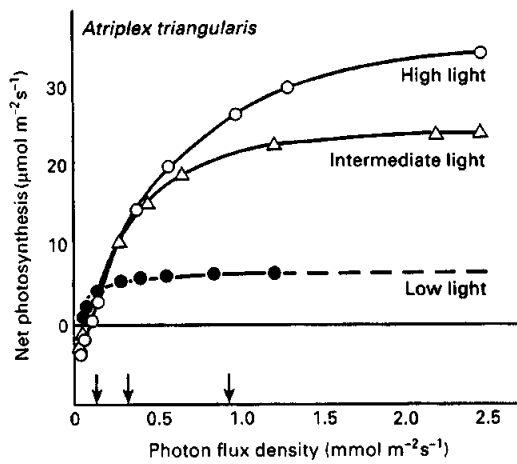


Fig. 1.5 Photosynthetic response to light intensity of leaves grown at three irradiance levels (indicated by arrows on *x*-axis). The high-light grown plants have high respiration and photosynthetic rates. (From Björkman *et al.* 1972.)

the same plant that have been produced under either low or high light intensities ('shade leaves' or 'sun leaves'). Under these contrasting conditions, the sun leaves almost always have higher saturated photosynthetic rates and higher light compensation points (Boardman 1977). The mechanisms underlying these differences are complex, and involve both morphological and biochemical components. Sun leaves generally have a greater density of stomata and hence a greater conductance to gas transfer. Further, they have a greater capacity for photochemical electron transport, higher mitochondrial respiration rates, and a higher content (and activity) of carboxylating enzymes than occurs in shade leaves.

Moving a shade leaf directly into the sun can cause damage to the photosynthetic system (photoinhibition), because the light energy trapped cannot be used fully in photosynthesis and these leaves do not have the capacity to dissipate this excess energy through the xanthophyll cycle (Demming-Adams & Adams 1992). In this case, there is inactivation of the photosystem II reaction centres. Over the course of several days, however, a shade leaf may be able to adjust (acclimate) to sun conditions, by increasing its photosynthetic enzyme content (dark reactions) and light reaction components, thereby enhancing its capacity to utilize light energy.

1.3.2 Carbon dioxide

Carbon dioxide is a primary substrate for photosynthesis and Rubisco activity is often the rate-limiting step in photosynthesis. Rates of photosynthesis increase linearly with increasing intercellular CO₂ concentrations (*c_i*) at low intercellular CO₂ levels, because RuP₂ levels are not limiting (Fig. 1.6). At higher intercellular CO₂ concentrations, the photosynthetic rate begins to level off as the capacity to regenerate RuP₂ fails to keep pace with the increased CO₂ supply. The regeneration of

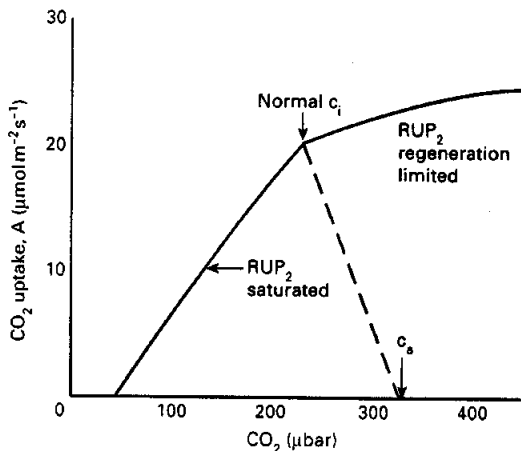


Fig. 1.6 The solid line represents the response of an intact leaf to differing intercellular CO₂ concentrations. This is the overall capacity of a leaf to take up CO₂ at high light levels for a given intercellular CO₂ concentration. The arrow on the curve indicates the transition between Rubisco-limited and RuP₂ regeneration limitations on overall CO₂ uptake rates. The arrow on the x-axis indicates the atmospheric CO₂ concentration. The dashed line emerging from this point has a slope equal to that of the leaf conductance (but negative in sign). The intersection of the solid and dashed lines is the operational intercellular CO₂ concentration. Under non-limiting light and water conditions, leaves often operate at the break-point (indicated by the arrow at the intersection) (Adapted from Farquhar & Sharkey 1982.)

RuP₂ is dependent on photochemical activity (electron transport and photophosphorylation), which means that photosynthetic limitations at low light intensities and high CO₂ concentrations are due to similar causes. Most leaves appear to operate at a stomatal conductance that maintains the c_i value in the vicinity of the break-point between Rubisco limitation and RuP₂ regeneration limitation (Farquhar & Sharkey 1982). This means that carboxylating capacity and electron transport capacity are co-limiting, and results in an economical investment by the leaf in the biochemical components of these processes.

Analyses of the carbon isotope discrimination (Δ) that continuously occurs during photosynthesis provides a long-term estimate of the intercellular CO₂ concentration in C₃ plants (Farquhar *et al.* 1989). There are two stable isotopes of carbon, ¹²C and ¹³C. While ¹³C constitutes only about 1% of the total pool of these two isotopes, small changes in the isotopic composition of leaves can be determined through mass spectroscopy. Discrimination occurs whenever the isotopic composition of the source carbon (R_{air}) is different from that of the product (R_{plant}). We express this discrimination in parts per thousand (‰) as

$$\Delta = \left(\frac{R_{\text{air}}}{R_{\text{plant}}} - 1 \right) \times 1000\text{‰} \quad (1.3)$$

Where $R = {}^{13}\text{C}/{}^{12}\text{C}$. Because of mass differences, the two CO₂ mole-

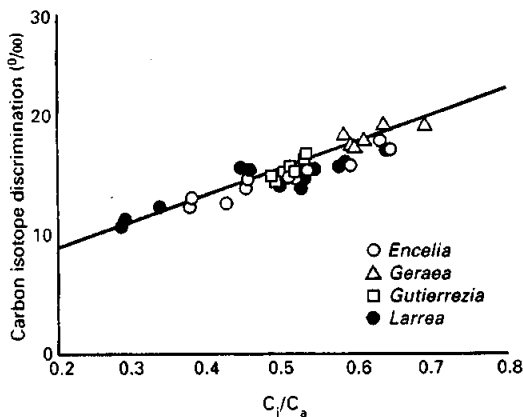


Fig. 1.7 Changes in carbon isotope discrimination of four desert species as a function of the c_i/c_a ratio. Line through the data is equation 1.2. (Adapted from Ehleringer *et al.* 1992.)

cules will have different diffusivities in air, with a , the discrimination associated with slower diffusivity of $^{13}\text{CO}_2$, equal to 4.4‰. A second discrimination step (b) of 27‰ occurs during photosynthesis because Rubisco favours $^{12}\text{CO}_2$ over $^{13}\text{CO}_2$. However, the overall discrimination during photosynthesis depends on c_i as

$$\Delta = a + (b - a) \frac{c_i}{c_a} \quad (1.4)$$

where c_a is the atmospheric CO_2 concentration. The result of this discrimination provides valuable information on plant–environment relationships. For example, as stomata regulate inward CO_2 diffusion during drought or other stress conditions, c_i values will change and this is faithfully recorded in the organic material produced as shown in Fig. 1.7.

Water stress will induce a stomatal closure, impeding the inward CO_2 diffusion and therefore reducing c_i values; as a consequence photosynthesis is also decreased (Fig. 1.6). Water stress can develop slowly as a soil dries out or may exist as steep gradients along a transect (Fig. 1.8). In either situation, the closure of stomata reduces photosynthesis first by decreasing c_i values; secondarily, there may be a downward regulation of photosynthetic capacity (Farquhar & Sharkey 1982).

1.3.3 Temperature

Photosynthesis increases with temperature because an increase in enzymatic activity leads to an enhanced capacity to bind CO_2 . At high temperatures, diffusion of CO_2 and photorespiration become limiting and the temperature response levels off. Finally, at extreme temperatures, the integrity of the photosynthetic system begins to break down and rates begin to decrease. At the highest temperatures, the decline may be irreversible. The nature of the decline depends on the structure of the membrane lipids, and the composition of these lipids varies from species to species (Berry & Björkman 1980).

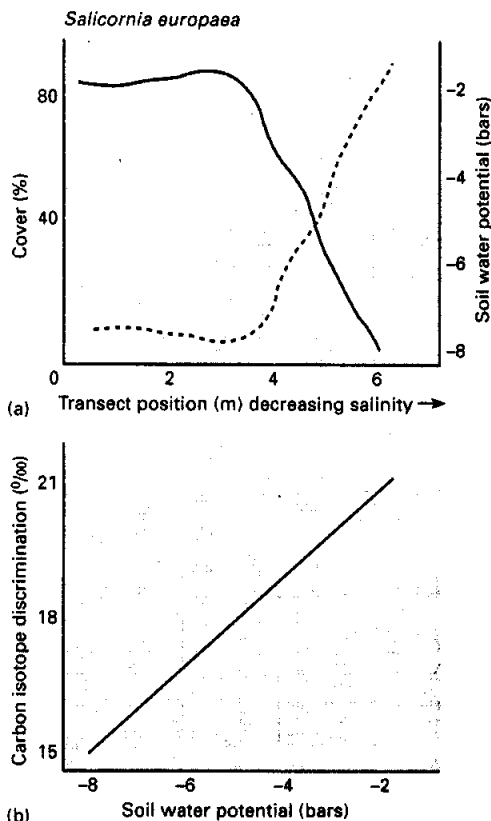


Fig. 1.8 (a) Abundance of *Salicornia europaea* (Chenopodiaceae) (a halophyte) (solid line) and soil water potential (dashed line) along a salinity gradient. (b) The relationship between carbon isotope discrimination of *S. europaea* and soil water potential along this gradient. (Adapted from Guy *et al.* 1980.)

Plants vary greatly in their photosynthetic response to temperature, depending on the kind of conditions they experience in their natural environments (Fig. 1.9). For example, some desert perennials have thermal optima of more than 40 °C, whereas Antarctic lichens have their optima close to freezing point. Plants that occur in the same

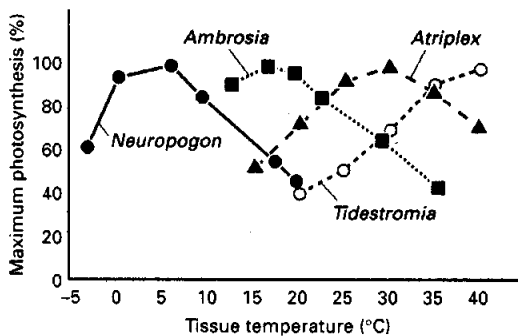


Fig. 1.9 Temperature photosynthetic response curves of plants from dissimilar habitats. Curves from left to right are for *Neuropogon acromelanus*, an Antarctic lichen (Lange & Kappen 1972); *Ambrosia chamissonis* (Asteraceae), a cool coastal dune plant (Mooney *et al.* 1983); *Atriplex hymenolytra* (Chenopodiaceae), an evergreen desert shrub and *Tidestromia oblongifolia* (Amaranthaceae), a summer active desert perennial (Mooney *et al.* 1976).

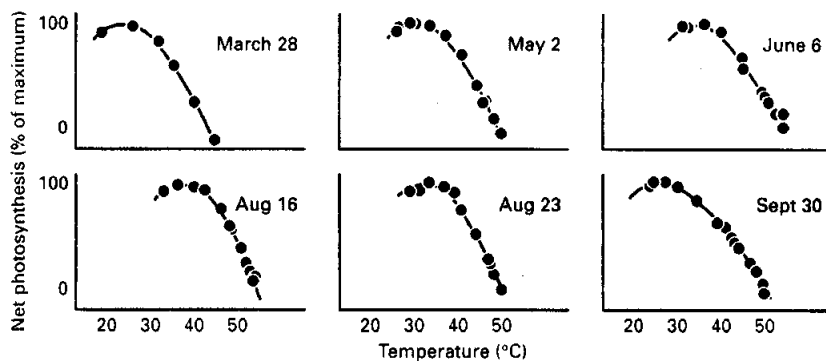


Fig. 1.10 Changes in the photosynthetic temperature optima of irrigated apricot *Prunus armeniaca* (Rosaceae) with seasons. (Adapted from Lange *et al.* 1974.)

habitat may also have different seasonal growth patterns which are associated with differences in temperature-related photosynthesis (Kemp & Williams 1980).

Many plants have been shown to have leaves that adjust their photosynthetic capacity with the changing seasons in an apparently adaptive manner (acclimation). A good example of this is the changing optimum temperature of photosynthesis in leaves of a Negev Desert plant, which experiences temperatures that fluctuate widely throughout the year (Fig. 1.10). Those species that show the most complete acclimation are those which have no reduction in photosynthetic capacity through the year (although their thermal optimum may shift).

1.3.4 Photosynthesis with respect to water use

An inevitable consequence of the expansion of plants onto land was the trade-off between controlling water loss while enhancing CO_2 uptake. In order to fix carbon, plants must lose water, simply because water vapour and CO_2 diffuse through the same stomatal-pore pathway. While stomata are open and CO_2 is diffusing inward to the sites of fixation, water vapour is diffusing outward into the drier atmosphere. This loss of water is directly proportional to the water vapour concentration gradient between the leaf and the atmosphere expressed as a water vapour mole fraction gradient (V), multiplied by the stomatal (g) and boundary layer (g_b) conductances (just as CO_2 uptake is proportional to the CO_2 concentration gradient across the stomata multiplied by similar conductances; see below). The water vapour gradient across the stomata is about 200-fold greater than the CO_2 gradient and usually changes during the course of the day, due largely to changing temperature and the associated effects on vapour pressure. The CO_2 gradient also changes during the day as stomata open at sunrise, partially closed during the driest midday periods, and then completely closed at sunset.

Water loss from stomata is regulated in the short term in response to

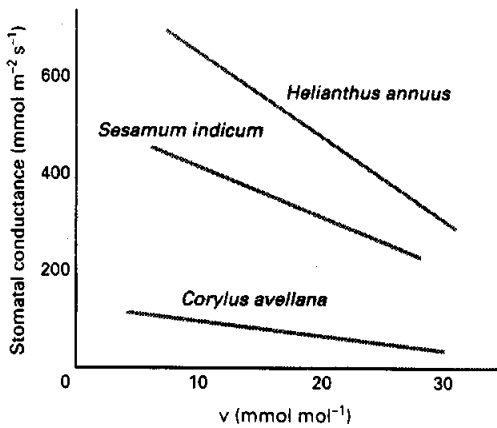


Fig. 1.11 Short-term responses of stomata to changes in the evaporative gradient between the leaf and air by three species, representing a range of life forms. *Helianthus* (Asteraceae) is an annual herb, *Sesamum* (Pedaliaceae) is a herbaceous oil-seed plant and *Corylus* (Betulaceae) is a small deciduous tree. (Adapted from Schulze & Hall 1982.)

diurnal changes in the water vapour gradient between the leaf and the atmosphere (Fig. 1.11), and in the long term in response to changes in available soil moisture levels (Fig. 1.12). These changes in stomatal conductance appear related to the loss of bulk leaf water (reduced leaf water potential) and to hormonal signals received from the roots (Davies & Zhang 1991). As a result of these combined responses, plants appear to be able to regulate the rates of water loss during dry or stressful periods; this has led to the notion of water-use efficiency, which is defined as the ratio of photosynthesis to transpiration rates.

There are times of the day, especially mornings, when the amount of water lost per unit of carbon fixed is rather low (i.e. water-use efficiency is high). It has been proposed that plants 'manage' stomatal conductance in such a way as to optimize this relationship (Cowan 1977), and, particularly during periods of drought, plants may close their stomata during the midday period when the water loss to carbon gain would be most unfavourable (Tenhunen *et al.* 1981).

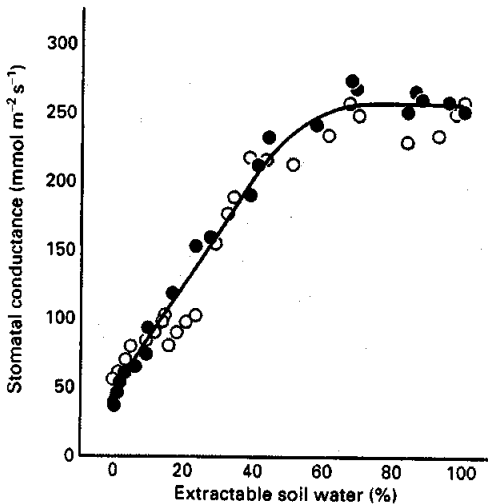


Fig. 1.12 Long-term changes in the maximum stomatal conductance in response to changes in the available soil moisture. (Adapted from Schulze 1986.)

Water-use efficiency can be measured at any given moment by determining photosynthesis (A) and transpiration (E) simultaneously. A more important ecological measure, however, may be the lifetime amount of carbon gained versus water lost. Such measures are difficult to make, but there is an indirect way of evaluating water-use efficiency based on carbon isotope analysis. This arises because

$$A = (c_a - c_i)g/1.6 \quad (1.5)$$

and

$$E = vg \quad (1.6)$$

with water-use efficiency (A/E) then equal to

$$A/E = \frac{c_a \left(1 - \frac{c_i}{c_a}\right)}{1.6v} \quad (1.7)$$

If we assume equivalent leaf temperatures among the plants under comparison, any denominator differences disappear and all differences in water-use efficiency are based on differences in c_i/c_a , which is measured by Δ as previously shown in Fig. 1.7.

When variations in carbon isotope discrimination among species in a habitat are examined, there are distinct patterns associated with life history. Longer-lived plants exhibit lower discrimination values than shorter-lived plants (Ehleringer & Cooper 1988). Within a semi-arid grassland community, annual plants discriminate more than do perennials; among the perennials, forbs discriminate more than do grasses (Fig. 1.13). These patterns of carbon isotope discrimination may relate to overall differences among the different life forms with respect to water stress tolerance and the nature of xylem architecture (especially susceptibility to cavitation; see Chapter 2).

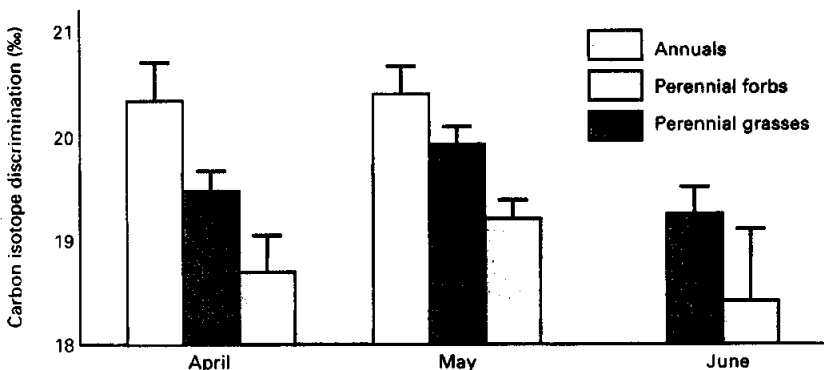


Fig. 1.13 Differences in the carbon isotope discrimination by annual plants, perennial grasses and perennial forbs in a semi-arid grassland community in three different months. The annuals had died by June. (Adapted from Smedley *et al.* 1991.)

1.3.5 Energy balance considerations

Transpirational cooling is an important mechanism for reducing leaf temperatures. As noted in section 1.3.1, leaves generally absorb a high fraction of the usable radiation between 400 and 700 nm, and reflect a high fraction of the non-photosynthetic radiation of wavelengths greater than 700 nm (Fig. 1.4). Under these conditions, a high transpiration rate will cool the leaves by offsetting the high solar radiation load on the leaf. In environments where radiation is abundant but water is limited, leaf reflectance may also be high in the visible wavebands especially as water stress develops (Fig. 1.14). This change in leaf absorptance is an advantage since stomatal closure under drought conditions can lead to detrimentally high leaf temperatures. In such arid environments, the loss of potential absorbed radiation is of little consequence to carbon gain, because photosynthesis is generally water-limited rather than light-limited.

There are alternative mechanisms for reducing leaf temperature under periods of water deficit other than through the use of a reduced leaf absorptance. Increased vertical leaf orientation occurs in many species under long-term drought periods and midday 'leaf wilting' occurs in many plants such as cassava and sunflower. Active leaf movements, whereby leaf lamina are oriented parallel to the sun's rays through the day, is called paraheliotropism and commonly occurs among legume species. All three mechanisms serve to reduce the heat load on the leaf by reducing the incident solar radiation. To reduce the leaf boundary and increase convective heat exchange, leaves produced under periods of water deficit or in high solar radiation environments often are smaller and/or deeply lobed.

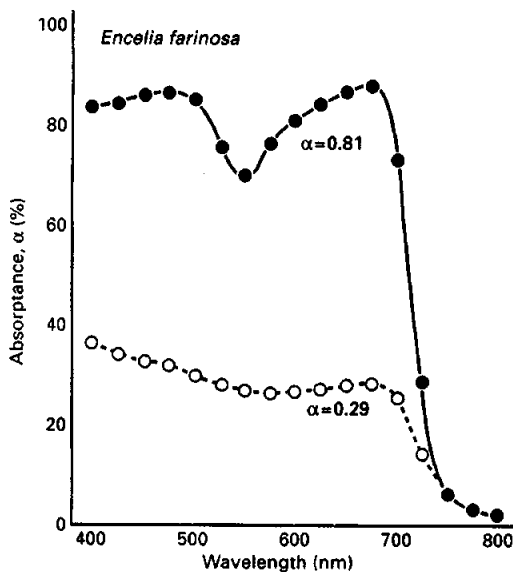
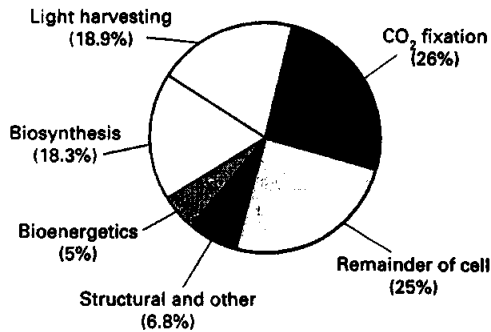


Fig. 1.14 Leaf absorptances of *Encelia farinosa* (Asteraceae), a desert shrub, collected early (high absorptance) and late (low absorptance) in the growing season. (Adapted from Ehleringer & Björkman 1978.)

Fig. 1.15 Nitrogen apportionment in leaves. Note that about 50% of the nitrogen is devoted directly to the photochemical and biochemical machinery involved in photosynthesis. (Adapted from Evans 1983.)



1.3.6 Nutrients

Nutrients can affect photosynthetic performance in a relatively direct fashion, since nitrogen and phosphorus are both involved in the photosynthetic reactions. Alternatively, nutrients may act indirectly through their effects on the overall metabolic environment. Direct effects are most conspicuous for nitrogen. Of the nitrogen found in a leaf, a large fraction is contained in the carbon-fixing enzyme Rubisco (Fig. 1.15). It is not surprising, therefore, that there is generally a strong positive correlation between photosynthetic capacity and leaf nitrogen content (Fig. 1.16). This relationship only holds, however, if other factors such as solar radiation are not limiting. As nitrogen content is reduced, so the amount of carbon fixed per molecule of nitrogen present in the leaf is reduced, since a fraction of the nitrogen is involved in processes other than carbon fixation (Fig. 1.17).

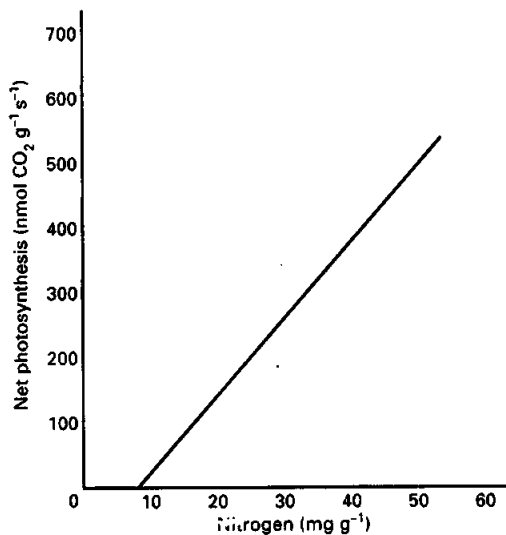


Fig. 1.16 Light-saturated photosynthetic rates as a function of leaf nitrogen content for leaves of plants from a variety of habitats. (From Field & Mooney 1983.)

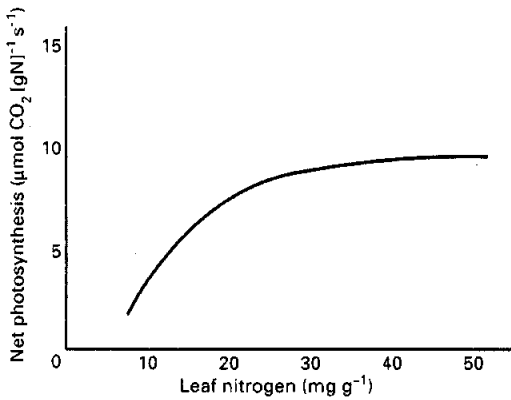


Fig. 1.17 Nitrogen-use efficiency (carbon gained/unit nitrogen) versus leaf nitrogen content for a variety of plant types. At low nitrogen contents, the efficiency is low. (From Field & Mooney 1986.)

1.3.7 Atmospheric pollutants

Many atmospheric pollutants affect the photosynthetic rate of leaves because they enter directly into the leaf mesophyll by the very same pathway as CO₂. The nature of their effects may be complex, and can differ from one pollutant to another. Often, as in the case of SO₂, the effect of the pollutant is to reduce photosynthesis through its effect on reducing leaf conductance. Photosynthesis is reduced because of a reduced c_i value and the impacts of varying pollutant concentrations can be measured over extended time periods through either leaf or tree-ring analyses (see Chapter 17).

1.4 Seasonality of photosynthesis

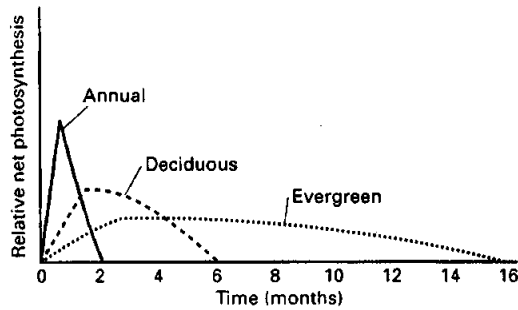
1.4.1 Individual leaves

The amount of photosynthesis that a leaf performs during its lifetime depends on: (i) its intrinsic photosynthetic capacity; (ii) the amount of limiting resources available; and (iii) how long the leaf stays on the plant. The longer the leaf remains productive, the greater its return (in terms of carbon fixed) on the resources invested to build and maintain it. Plants will generally maintain leaves as long as they are providing a positive carbon input.

In addition to the direct relationship between leaf duration and photosynthetic gain, there is an inverse relationship between leaf longevity and photosynthetic capacity (Fig. 1.18). Leaves of plants with fast growth rates do not live long, but they have a high photosynthetic capacity and a low water-use efficiency as discussed earlier in section 1.3.4. Thus, plants with different leaf-durations (e.g. an evergreen tree and a deciduous tree) could have similar integrated carbon gains.

The photosynthetic capacity of a leaf changes with age as well as with the seasons. The leaves of most plants go through a predictable change in their photosynthetic capacity as they age. The highest rates are

Fig. 1.18 Generalized relationship between leaf duration and photosynthetic capacity. (From Mooney & Gulmon 1982.)



attained prior to, or near, the period of maximal leaf expansion, after which time fixation capacity begins to decline. It is interesting that leaves with basal growth, such as grasses, do not appear to show this decline (Sestak 1985).

In slower growing plants, the life of individual leaves is prolonged, and leaves may remain active throughout different seasons or over several years. Such leaves have a changing photosynthetic capacity through time, and exhibit reduced (or no) capacity during winter or in periods of drought (Fig. 1.19). Evergreen leaves in severely cold climates, for example, may completely lose their capacity for photosynthesis in the winter, even under temporally favourable conditions (Larcher & Bauer 1981). Evergreen leaves of plants in less severe environments, however, maintain their competence, and thus have the potential to fix carbon throughout the year.

1.4.2 Whole plants

The productive potential of a plant through the seasons depends on the behaviour of its entire population of leaves. There is remarkably little information available on the seasonal pattern of change in leaf number on plants of different life histories. In certain perennial plants, one crop of leaves is produced per year, and all leaves appear and are lost more or less synchronously. In other species, leaves may be produced and lost throughout the growing season, with mean leaf longevity changing from one season to another. In the case of evergreen plants whose leaves last several years, leaf production may occur continuously or in simultaneous bursts. The net result of these diverse patterns in the birth and death rates of leaves, and of their changing photosynthetic capacity, is that whole plant photosynthesis shows pronounced seasonal changes (Constable & Rawson 1980).

The net photosynthesis of entire leaf canopies can be conveniently described in terms of the leaf area index (LAI); this is the area of photosynthetic surface per unit area of ground. Early in the growing season of an annual crop, for example, LAI will be much less than 1 and there is substantial bare ground. Later in the season LAI may reach

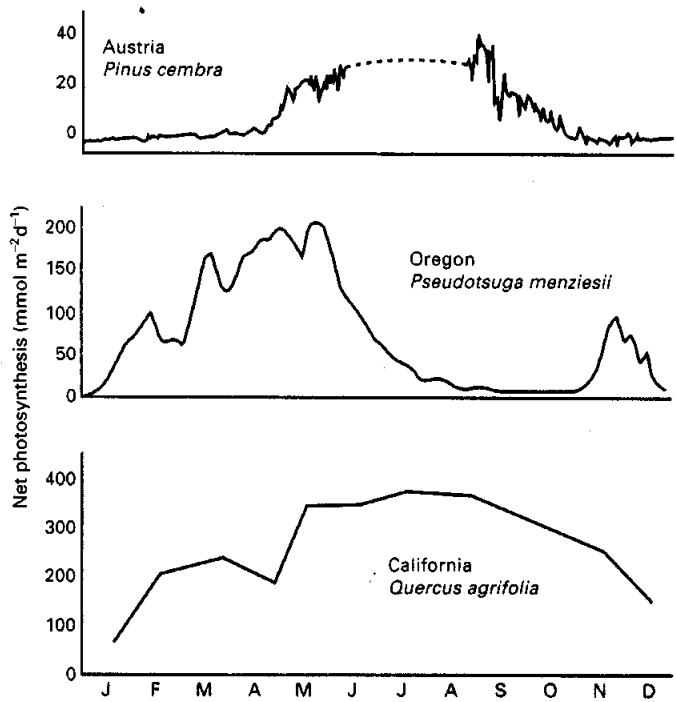


Fig. 1.19 Seasonal course of photosynthesis of evergreen trees from three different climatic regions. Top, A timberline tree, *Pinus cembra*, growing at 1980 m in the Swiss Alps. The needles have no photosynthetic capacity during the winter months. (From Hassler, unpublished data.) Centre, Simulated net photosynthesis of *Pseudotsuga menziesii* (Pinaceae) in Oregon. Summer drought limits photosynthesis. (From Emmingham 1982.) Bottom, Simulated photosynthesis of the evergreen oak *Quercus agrifolia* (Fagaceae) in central California. These plants have adequate water even during the summer drought because of a deep root system. (From Hollinger 1983.) Simulations are based on site climatic features in combination with plant physiological responses to environmental parameters.

values of 6 or more. In both agronomic and natural canopies, the distribution of LAI is not random, but rather leaves are distributed in the upper portions of the canopy with those leaves at the top having the steepest leaf angles (Fig. 1.20). This allows more of the lower leaves to remain above their light-compensation points. Leaves lower in the canopy are in a decreased light environment and nitrogen is allocated in leaves through the canopy in such a way as to maximize canopy productivity (Fig. 1.20). Of course, water can play a significant role in determining canopy development and the amount of water available for transpiration places an upper limit on the realized maximum LAI for any canopy (Fig. 1.21).

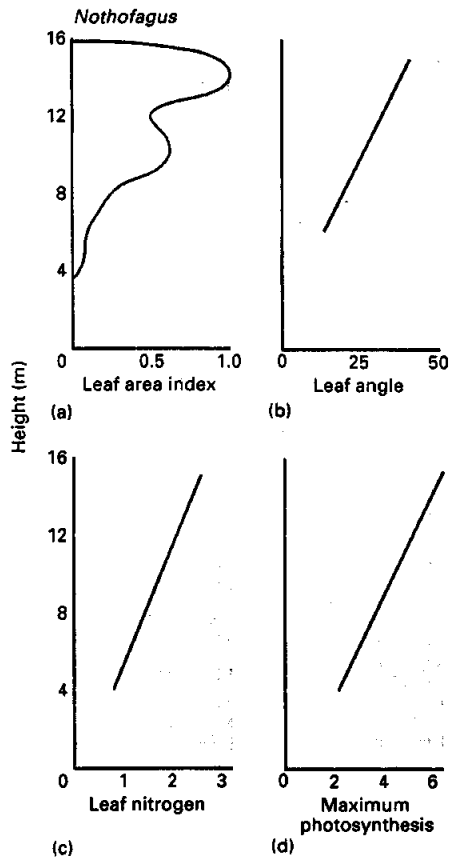


Fig. 1.20 Integration of canopy architecture to maximize canopy-level photosynthesis in *Nothofagus solandri* (Fagaceae) forests of New Zealand. (a) The distribution of leaf area index by layer. (b) Distribution of leaf angle from the horizontal (degrees). (c) Distribution of leaf nitrogen (% dry weight). (d) Maximum photosynthesis by layer ($\mu\text{mol m}^{-2}\text{s}^{-1}$). (Based on data from Hollinger 1989.)

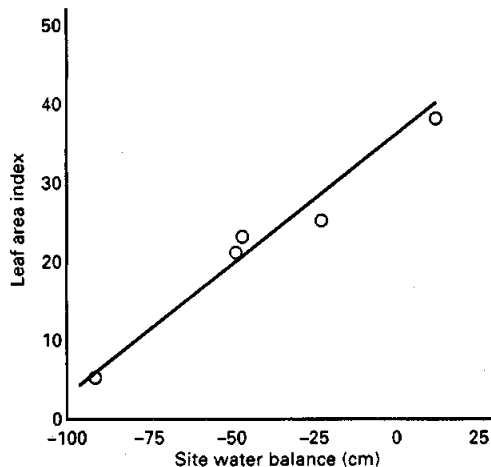


Fig. 1.21 Relationship between site water balance and leaf area index for five forest zones in western Oregon. (Adapted from Gholz 1982.)

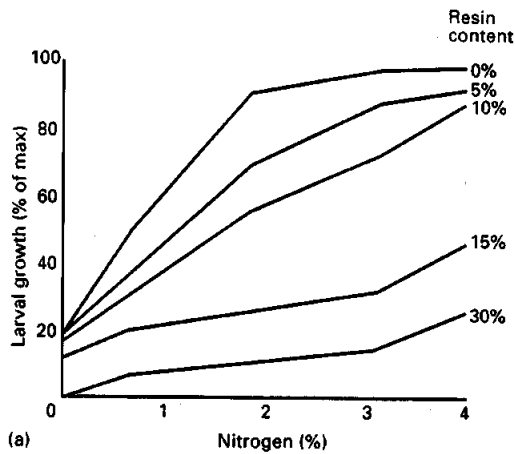
There is a reallocation of nitrogen resources among leaves within a canopy as leaves get progressively more shaded at the bottom. The rate of decline of photosynthesis in individual leaves is correlated with many factors, but is most clearly related to the growth rate of the plant. Leaves at the top of a fast-growing plant rapidly overtop the older leaves. The older leaves thus become light-limited and the repayment in carbon gain per unit of nitrogen invested declines. Limiting nitrogen may then be reallocated to the newer leaves at the apex. Photosynthetic capacity of the older leaves is reduced by exporting nitrogen and their maintenance respiratory losses are decreased by having reduced leaf protein levels. Eventually, the older, shaded leaves form an abscission layer and fall from the canopy. The consequence of this reallocation of nitrogen is an increase in the overall canopy net photosynthetic rate.

1.5 Photosynthetic capacity and defence against herbivores

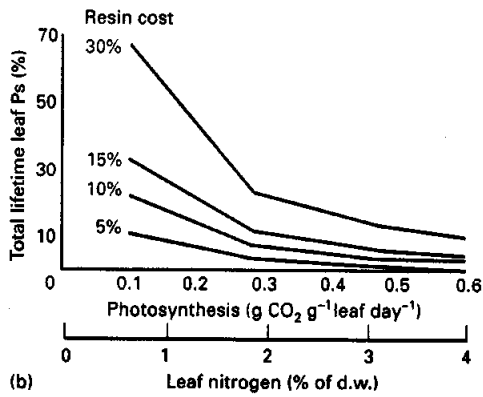
The photosynthetic capacity of leaf and the probability of it being subject to herbivory are related through the strong positive correlations between leaf nitrogen content and photosynthetic capacity on the one hand, and leaf nitrogen content and food quality for herbivores on the other (see Chapter 10). A specific illustration of this relationship is provided by the shrub *Diplacus aurantiacus* (Scrophulariaceae) and its principal herbivore, the butterfly *Euphydryas chalcedona*. Because the photosynthetic capacity of sun leaves is directly related to their nitrogen content (Fig. 1.16), we can employ a common axis to describe both these variables, as shown in Fig. 1.22.

On an artificial medium (and, presumably, in nature) larval growth is positively related to nitrogen content. Leaves of *Diplacus*, however, contain a phenolic resin called diplacol that can constitute as much as 30% of leaf dry weight, and this resin effectively inhibits larval growth. Thus one can readily see that leaves could discourage herbivores in two different ways: by reducing nitrogen content, or by increasing the content of resin. The economics of these two options can be assessed from a knowledge of the amount of photosynthate (or other limiting resources) needed to produce the resin. If a plant maintains a low nitrogen content it will suffer a reduced photosynthetic capacity and it will take a substantial fraction of its lifetime carbon gain in order to produce the resin in high quantities. In contrast, with high leaf nitrogen levels, the payback time is relatively short. From this kind of analysis one might conclude that the optimum leaf would have high leaf nitrogen and resin levels, since both photosynthetic capacity and herbivore protection would be greatest under these conditions.

The interrelationships between photosynthetic capacity and the direct and indirect costs of defence can be evaluated in more general terms



(a)



(b)

Fig. 1.22 (a) Nitrogen-resin interaction in relation to the growth of the larvae of *Euphydryas chalcedona*, the principal herbivore of the shrub *Diplacus aurantiacus*. (From Lincoln *et al.* 1982.)
(b) The fractional cost of leaf lifetime-acquired carbon. (From Mooney & Gulmon 1982.)

by calculating the direct costs (in carbon units) of making a particular defensive compound, and the indirect costs in terms of loss of future carbon gain (the opportunity cost of investing in that compound). The increase in dry weight of a leaf is determined by: (i) its CO_2 fixation rate (A); (ii) the conversion efficiency of making dry matter from CO_2 (k) (iii) the allocation of acquired assimilate to new leaf material (L); and (iv) the initial amount of leaf material present (W_1) as

$$\frac{dW_1}{dt} = W_1 \cdot A \cdot L \cdot k \quad (1.8)$$

The direct cost of making a defensive compound (C) can be subtracted directly from the photosynthesis term to indicate the impact of defence cost on future carbon gain as

$$\frac{dW_1}{dt} = W_1 \cdot (A - C) \cdot L \cdot k \quad (1.9)$$

The direct costs are then calculated as

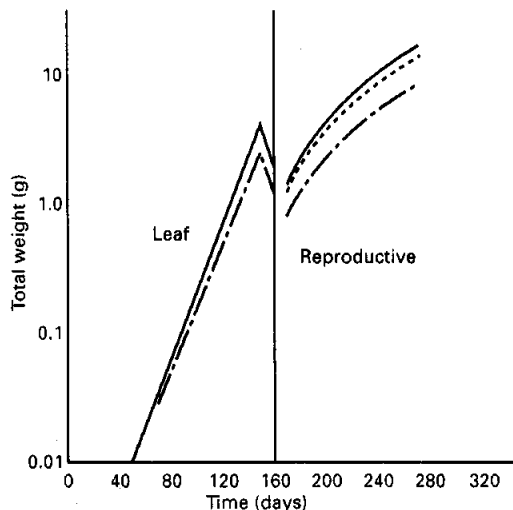


Fig. 1.23 Growth simulations for leafy tissue of the California annual *Hemizonia luzulaefolia* (Asteraceae) assuming no production of resin (solid line), production throughout the life of the plant (dash/dot), or production during reproduction only (dashed). The reduction in dry weight at initial reproduction is due to basal mesophytic leaf loss associated with the annual drought. (From Gulmon & Mooney 1986.)

$$C(t) = SC \left(\frac{d \frac{S(t)}{W(t)}}{dt} \right) \quad (1.10)$$

Where SC is the specific cost of the compound expressed as weight of the compound per weight of CO_2 required to produce it, and $S(t)$ is the amount of the compound in the leaf at time t . Specific costs appear to vary considerably for different types of leaves (Table 1.1).

Growth simulations of the indirect costs of defence have been carried out using information from the herbaceous annual *Hemizonia luzulaefolia* (Asteraceae) (Fig. 1.23). This plant produces a resinous compound on cauline leaves at the beginning of reproduction, at which time the basal leaves are lost with the onset of the dry season. During the annual drought *Hemizonia* is one of the few plants with green tissue, and it suffers enhanced herbivory in consequence. The production of

Table 1.1 Costs of construction of leaves and various leaf constituents presumed effective in herbivore defence. (From Gulmon & Mooney 1986.) See text for definitions.

Type	Species example	Compound	Formula	Specific cost (SC) ($\text{g CO}_2 \text{g}^{-1}$)	Content (% leaf d.w.) $\left(\frac{S}{W} \right) \times 100$
Phenolic resin	<i>Diplacus aurantiacus</i>	Diplacol	$\text{C}_{22}\text{H}_5\text{O}_7$	2.58	29
Cyanogenic glucoside	<i>Heteromeles arbutifolia</i>	Prunasin	$\text{C}_{14}\text{H}_{17}\text{NO}_6$	2.79	6
Alkaloid	<i>Nicotiana tabacum</i>	Nicotine	$\text{C}_{10}\text{H}_{14}\text{N}_2$	5.00	0.2–0.5
Long-chain hydrocarbon	<i>Lycopersicon hirsutum</i>	2-Tridecanone	$\text{CH}_3(\text{CH}_2)_{10}$	4.78	0.9–1.7
Terpene array	<i>Salvia mellifera</i>	Camphor (50%) + others	$\text{C}_{10}\text{H}_{16}\text{O}$ + others	4.65	1.3
Whole leaves	Various shrub species			1.93–2.69	

resin has a different impact on biomass accumulation depending on whether it is produced throughout the life of the plant, or only during the reproductive period (as happens in nature). Clearly, if the probability of herbivory is low during the early growth stages, the plant might increase its fitness by delaying the elaboration of the defensive resins.

1.6 Variations on the basic photosynthetic pathway

So far, we have considered the basic mode of carbon fixation via C_3 photosynthesis. Several important variations on this basic metabolic theme allow improvements in photosynthetic efficiency in certain kinds of habitats. The most common variant is C_4 photosynthesis, so called because the initial products of CO_2 fixation are four-carbon organic acids, rather than the usual three-carbon PGA (Fig. 1.24). The carboxylating enzyme in C_4 photosynthesis is phosphoenolpyruvate carboxylase (PEP carboxylase). C_4 plants possess specialized cells that surround their vascular bundles, known as bundle sheaths, where chloroplasts operate in normal C_3 mode (Kranz anatomy). Four-carbon products of the initial CO_2 fixation are transported from the surrounding mesophyll cells to the bundle sheath cells where the CO_2 is released and then refixed by the C_3 pathway. The refixation of CO_2 in isolation in the bundle sheath acts as a CO_2 'pump', and overcomes the oxygenation reaction of Rubisco.

Another photosynthetic pathway, termed crassulacean acid metabolism (CAM), occurs in certain desert plants and tropical epiphytes. It is similar to C_4 photosynthesis, except that separate carboxylations take place within the same cells, displaced in time rather than in space as in C_4 photosynthesis. In typical CAM plants, the stomata open at night rather than during the heat of the day. CO_2 diffusing into the leaf at night is fixed in four-carbon organic acids through the use of stored energy (Fig. 1.24). During the day, while the stomata are closed, the stored CO_2 is refixed via the C_3 pathway using light energy. An essential

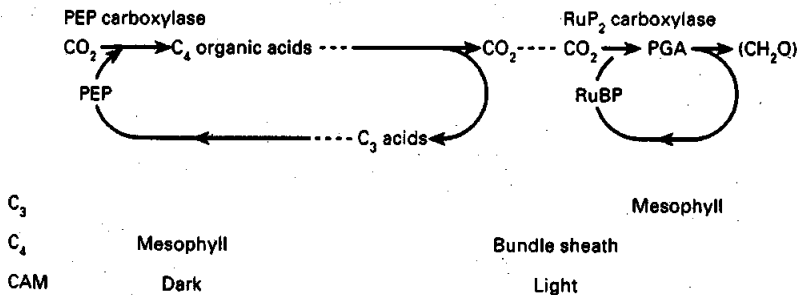


Fig. 1.24 Comparative features of C_3 , C_4 and CAM photosynthesis. (Modified from Jones 1983.)

feature of this pathway is succulence or the possession of large vacuoles in which the organic acids can be temporarily stored. Large, columnar cacti in the deserts and orchids in the tropics are typical of the kind of plants that employ CAM photosynthesis.

Other CAM plants, particularly leafy succulents of the family Crassulaceae, exhibit flexibility in their mode of photosynthesis. During wet periods they fix carbon directly through the C_3 mode during the day, and at night they use the CAM mode. As drought sets in, they shift entirely to the CAM mode. This adjustment has become highly evolved in some South African plants such as *Frerea indica* (Asclepiadiaceae), which has deciduous C_3 leaves and an evergreen succulent CAM stem.

1.7 Ecological consequences of different photosynthetic pathways

1.7.1 Water-use efficiency

The biochemical dissimilarity of C_3 , C_4 and CAM plants results in dissimilar physiological behaviour and this, in turn, leads to different ecological performance (Table 1.2). Because they possess an effective CO_2 pumping mechanism, C_4 plants are able to saturate net photosynthesis at lower internal CO_2 concentrations than C_3 plants. This means that stress-induced stomatal closure tends to have a much greater effect on photosynthesis in C_3 compared with C_4 plants. While photosynthesis of C_3 and C_4 plants is differentially affected by stomatal closure, transpiration rate is not. This simple relationship has a profound influ-

Table 1.2 Comparative characteristics of the different photosynthetic pathways. (Modified from Jones 1983.)

	Pathway		
	C_3	C_4	CAM
Initial carboxylating enzyme	RuP ₂	PEP	PEP, RuP ₂
Tissue isotope range ($\delta^{13}C$, ‰)	- 20 to - 35	- 10 to - 20	Spans C_3 - C_4 range depending on fraction of daytime versus night-time fixation
Anatomy	Normal	Kranz	Succulent
Water-use efficiency	Low	Medium	High
Photosynthetic capacity	Medium	High	Low
Oxygen inhibition of photosynthesis	Yes	No	Yes in day, no at night
Growth form occurrence	All	Shrubs and herbs	Succulents
Principal geographic range	Everywhere	Open tropical areas or arid habitats	Arid regions or habitats

PEP, phosphoenolpyruvate; RuP₂, ribulose bisphosphate.

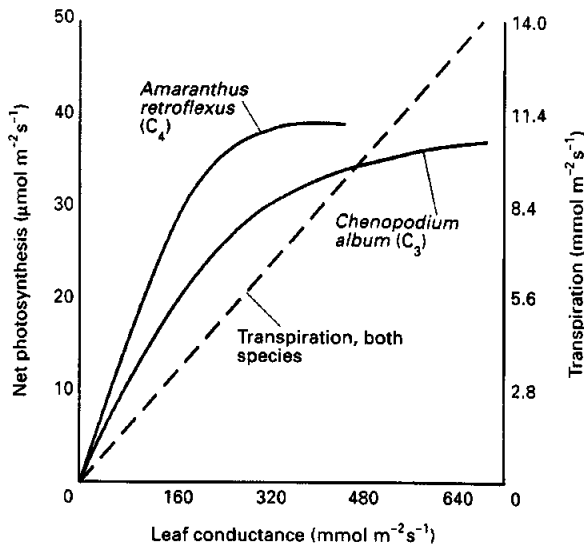


Fig. 1.25 Photosynthesis and transpiration of a C_3 and a C_4 species at different leaf conductances. (From Pearcy & Ehleringer 1984.)

ence on the instantaneous water-use efficiency (i.e. on the amount of carbon fixed per unit water lost). At an equivalent stomatal conductance, C_3 and C_4 plants will lose identical amounts of water but the C_4 plant will fix more carbon and so will have higher water-use efficiency (Fig. 1.25). One consequence of this is that C_4 species tend to become more common in saline habitats, where conservative water use may be of significant selective advantage.

CAM plants have an even higher water-use efficiency than C_4 plants because they only open their stomata at night, when evaporative water loss is minimal. CAM plants are typically found in the driest environments, such as coastal and interior deserts or as rootless epiphytes in mesic environments.

1.7.2 Significance of temperature

Another important physiological difference between C_3 and C_4 plants is their differential efficiency of fixing carbon at different temperatures when light intensities are low. As we saw in section 1.3.1, at low light intensities photosynthetic rate is directly proportional to the amount of light absorbed by the leaf (the quantum yield). C_4 plants have an intrinsically lower quantum yield because of the extra costs associated with this pathway (they require two additional molecules of ATP in order to regenerate PEP). At low temperatures (10–20 °C), the quantum yield of C_3 plants is as much as 30% greater than that of C_4 plants. However, this difference is offset in favour of C_4 plants at high temperatures, because C_4 plants lack photorespiration which reduces the quantum yield of C_3 plants at high temperatures. The result is a reduction of net photosynthesis in C_3 plants at higher temperatures because previously fixed CO_2 is lost.

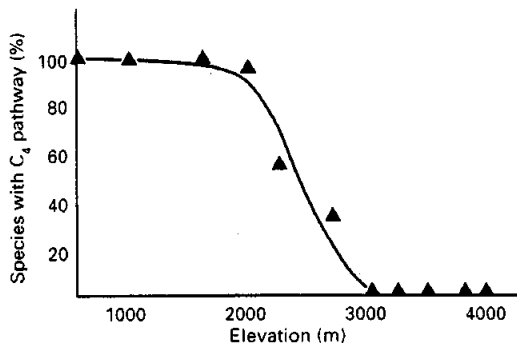


Fig. 1.26 Relative distribution of C_3 and C_4 grasses in relation to elevation on an African tropical mountain. The vegetation at the lowest elevations has all C_4 grass species and at the high elevations all C_3 . (From Tieszen *et al.* 1979.) Similar distribution patterns along temperature gradients have been described in other parts of the world.

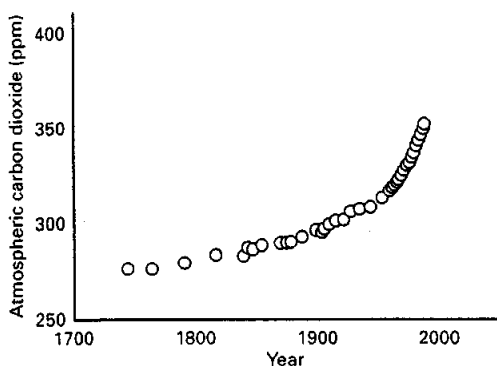
Although individual leaves on a plant may not be light-limited, whole plants in natural environments generally *are* light-limited because of carbon losses through respiration of non-photosynthetic tissues such as stems and roots. Thus, differences in quantum yields take on considerable significance in overall plant performance. From the quantum yield considerations just described, we would predict that C_4 plants would be most abundant in habitats where summer temperatures are high and moisture is available to support growth. This would include regions such as tropical and subtropical grasslands and summer-monsoon deserts. Similarly, we would predict that along elevational transects C_4 plants would be more frequent at lower elevation grasslands and C_3 plants more common at higher elevations (Fig. 1.26).

1.8 Climate change and photosynthesis

1.8.1 Photosynthesis in the recent past and near-future CO_2 environments

Atmospheric CO_2 concentrations have been measured continuously since the late 1950s (Fig. 1.27). These data show a clear trend of increasing CO_2 concentration in response to fossil fuels burned by humans. There is an annual oscillation in these data, reflecting natural ecosystem shifts between photosynthesis (reducing c_a) and decomposition (increasing c_a) in the summer and winter periods. In 1960, the mean atmospheric CO_2 concentration was 316 ppm. By 1990, it had reached 354 ppm, and by 2020 the atmospheric CO_2 concentration is expected to be approximately 600 ppm. From the air bubbles trapped during snow deposition in Arctic regions, we can examine the ice layers and reconstruct the history of atmospheric CO_2 concentration over a period of 160 000 years. This record shows fluctuations between 180 and 260 ppm, depending on whether it was a glacial or interglacial

Fig. 1.27 Changes in atmospheric CO_2 concentrations over the past several hundred years. The recent data since 1958 are from observations at Mona Loa in Hawaii (from Keeling *et al.* 1989), whereas the earlier data are from atmospheric air trapped in ice (from Friedli *et al.* 1986).



period, but the concentration was always lower than present-day levels. In recent times, it is only since the Industrial Revolution that the earth has seen an increase in atmospheric CO_2 (Fig. 1.27).

There is geological evidence, however, which indicates that atmospheric CO_2 concentrations were much higher in previous geological periods, and that it is only since the Miocene that atmospheric CO_2 concentrations reached levels as low as they are today (Berner 1991). Indications are that atmospheric CO_2 concentrations may have been as high as 1200–2800 ppm during the Cretaceous. By comparison, the CO_2 levels during the Pliocene and Pleistocene were so much lower (180–280 ppm) that we may consider that plants today are relatively CO_2 starved.

What happens to photosynthesis under these different ambient CO_2 levels and what ecological changes are likely to occur in the future? Several common patterns are observed when plants are grown under elevated CO_2 conditions. First, plants invest significantly less nitrogen in leaves, which results in a CO_2 dependence curve (Fig. 1.6) that has a lower slope under elevated CO_2 conditions (Stitt 1991). However, since CO_2 concentrations are much higher, the photosynthetic rate is increased. Second, there is an increase in water-use efficiency. Since nutrient levels are not expected to increase under elevated CO_2 conditions, it is not clear how much overall canopy growth rates will increase (Norby *et al.* 1992). One consequence of a reduced nitrogen allocation to leaves is that they become less palatable to insect herbivores. Therefore animals would need to eat more leaf tissues to acquire the equivalent amount of nitrogen they obtain under present atmospheric conditions (Lincoln *et al.* 1993).

1.8.2 Climate change and the evolution of photosynthetic pathways

The C_3 pathway is ancestral, with the CAM and C_4 pathways having evolved after plants invaded land (Ehleringer & Monson 1993). CAM

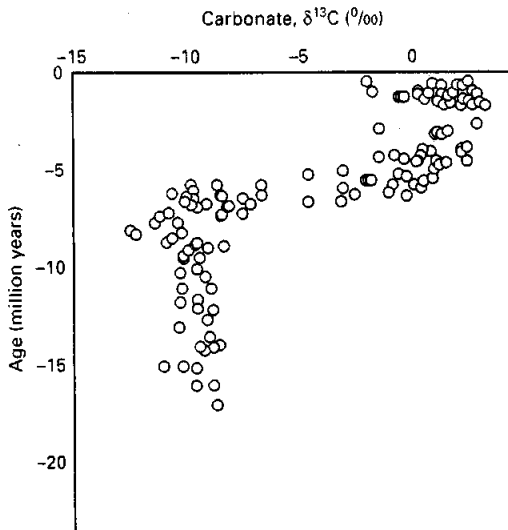


Fig. 1.28 The carbon isotope composition of carbonate nodules are enriched approximately 14–16‰ above that of the carbon isotope composition of plants growing in the soil at the time that carbonate was formed. The negative δ¹³C values prior to 7.5 million years ago indicate a C₃-dominated vegetation. The positive δ¹³C values after 7.5 million years ago indicate a switch to a C₄-dominated flora. (From Cerling *et al.* 1989.)

photosynthesis is found in diverse taxa in all the major extant groups and appears to have evolved in response to water-limited habitats, a condition that has existed since plants invaded land (Monson 1989).

The taxonomic and geographic distribution of C₄ plants suggests that this pathway evolved independently numerous times and over a short time period. This pathway is found in nearly two dozen diverse families, and intermediates on the evolutionary road to becoming C₄ are known from numerous other families. It has been suggested that C₄ photosynthesis evolved in response to the greatly reduced atmospheric CO₂ conditions that prevailed from the Miocene onwards (Ehleringer *et al.* 1991). At low CO₂ levels, reduced diffusion rates and increased photorespiration rates would have greatly decreased the carbon-gaining capacity of C₃ plants. The C₄ pathway has what amounts to a PEP carboxylase-driven CO₂ pump, and this would help to overcome the growth-limiting effects of a reduced CO₂ environment. Soil carbonate evidence indicates that C₄ plants first appeared about 7 million years ago, when atmospheric CO₂ levels were low, and that C₄ plants have persisted since that time (Fig. 1.28). As global atmospheric CO₂ increases in response to anthropogenic activity, CO₂ levels will soon reach a level where the C₄ pathway is no longer of advantage.

1.9 Conclusions

Photosynthesis is a central process in the functioning of all green plants. It provides the carbon skeletons and energy required to build biomass and to synthesize the wide variety of products utilized by plants in their metabolism. The basic chemistry of photosynthesis does not vary greatly among plant species, although there are three fundamentally different biochemical pathways for the process, each with different ecological consequences. The vast majority of the world's plants operate with the

C_3 pathway, where CO_2 is incorporated initially into the three-carbon product, phosphoglycerate. Plants utilizing a second pathway, CAM, are able to fix CO_2 into organic acids during the night, refixing it during the day into carbohydrate, and utilizing light energy even though their stomata are closed. CAM results in a high ratio of carbon gained to water lost, and is found typically in water-limited regions such as deserts and epiphytic habitats. A third pathway, C_4 photosynthesis, also results in efficient water use and may have evolved in response to a global reduction in atmospheric CO_2 levels beginning in the Miocene. In C_4 plants, high photosynthetic rate is gained through both anatomical and biochemical features that result in the maintenance of high photosynthetic capacity even whilst the stomata are partially closed. The C_4 pathway is found commonly in tropical and subtropical grasses and in plants of saline regions.

Photosynthesis is very sensitive to variations in the supply rates of light and CO_2 , the principal resources utilized in the process. Photosynthesis is further influenced by a wide array of environmental factors including temperature, nutrients, tissue water status, and atmospheric pollutants. These factors have influences on different time scales because of their different rates of change in natural environments. For example, leaf temperature and the quantity of radiation absorbed by a leaf change greatly during the course of a single day, whereas tissue water and nutrient status change over longer time spans.

Although plants do not differ greatly in the basic machinery utilized in photosynthesis, they do differ radically in the ways they acquire the resources needed for the process. Dissimilarities exist among plants in the amounts, display and duration of their leaves, and these affect the total amount of light intercepted and hence photosynthate accumulated. They further differ in their photosynthetic responses to various environmental factors both in the short and long term. For example, species may differ in the amount of photosynthesis they perform at a given light level, as well as in the way they respond (acclimate) to a long-term change in the light environment. These differences are often the result (and may be the cause in some cases) of dissimilar patterns of resource acquisition by plants. Such differences between species presumably play a role in permitting their coexistence.

The photosynthetic capacity of plants is directly linked to their ability to acquire water, light and nutrients, and the process itself serves as an integrator of 'success' in a given habitat. Photosynthetic capacity, however, may also be related directly to potential rates of herbivory, since leaves that have high photosynthetic rates generally have high leaf protein contents, and this makes them additionally attractive to herbivores.