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12.1?Photosynthesis in sun and shade

Plants have adapted to an extraordinarily wide range of light environments, from the deep shade of rainforest understoreys and underwater habitats to the high-radiation environments of deserts and mountain tops. Exploitation of such a wide diversity of habitats is possible because plants have evolved various mechanisms to optimise their use of sunlight. Many plants also exhibit great plasticity in their response to changes in light availability within a particular habitat. This potential for acclimation enables them to exploit more variable environments than plants with a narrower range of responses to light. This section will cover some features that make a plant suited to either a high or low light environment.

In low light, plants obviously need to absorb sufficient light for photosynthesis if they are to survive. To do this they need to maximise light absorption. In a high light environment however, the problem is reversed, with plants needing to maximise their capacity for utilising abundant light energy, while at the same time dealing with excess sunlight when photosynthetic capacity is exceeded. As a consequence of such unrelenting selection pressures, plants have evolved with a variety of features that optimise light interception, absorption and processing, according to the nature of the light environment to which they have adapted (Figure 12.2). Adaptation implies a genetically determined capability to acclimate to either sun or shade. Such acclimation calls for adjustment in one or a number of attributes concerned with interception and utilisation of sunlight. Common features of either sun or shade plants are outlined below, and their advantage to plants growing in different light environments is discussed. Field applications are illustrated via sun/shade acclimation and sunfleck utilisation in rainforest plants.

12.1.1?Light interception and utilisation

Initial steps of photosynthesis involve interception and absorption of photons by photosynthetic organs; subsequent steps are involved with utilisation or dissipation of quantum energy so derived. Interception of light varies according to size, angle, orientation and surface features of the photosynthetic organ(s) and is also influenced by changes in the arrangement of photosynthetic tissue within those organs.

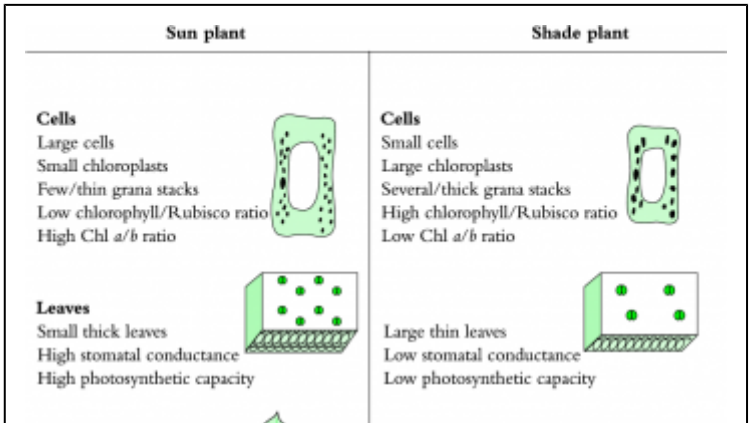


Figure 12.2 A comparison of photosynthetic structure and function in sun and shade plants. Major characteristics are described for cells, leaves and whole plants (Original drawing courtesy S.A. Robinson)



[2]

Figure 12.3 *Alocasia macrorrhiza* growing in a shaded understory of a North Queensland rainforest. Large leaves are oriented to maximise light interception. A sunfleck is crossing the forest floor

(Photograph courtesy S.A. Robinson)

Shade plants can increase their interception of light by producing larger leaves. Some of the largest leaves are produced by plants found in rainforest understoreys (Figure 12.3). Leaf size can even change within an individual plant, smaller leaves being produced near the top where irradiance is highest, and larger leaves towards the interior and base where light levels are lower. Another way to change light interception is by changing leaf angle and/or orientation. Vertical arrangements enhance interception of light at low sun angles during early morning or late afternoon, and reduce interception at solar noon when radiation levels are highest. Leaves that are displayed horizontally will intercept light all day long, but especially around midday. Accordingly, leaves in a rainforest tend to be vertical in emergent crowns and horizontal in the understorey. Similarly, pendulant leaves of many Australian trees such as eucalypts that typically occur in high light environments represent an adaptation that helps avoid excess midday radiation.

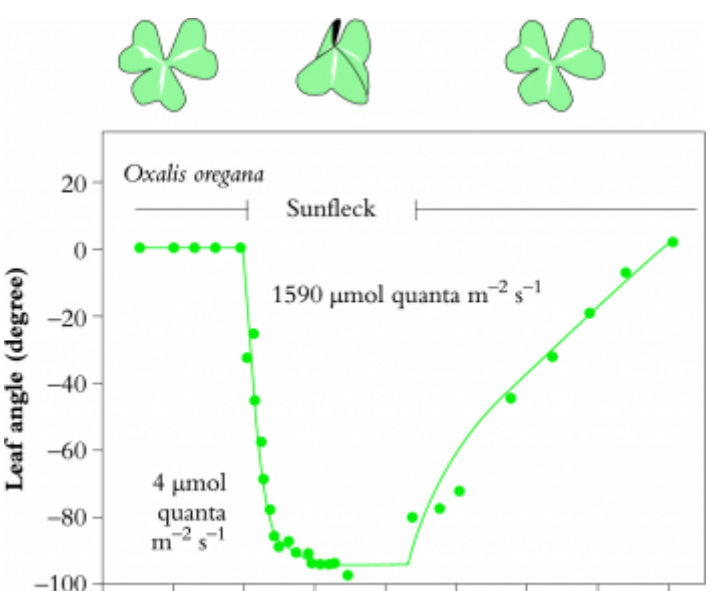


Figure 12.4 Time-course of leaf unfolding in *Oxalis oregana*, an understory herb of Redwood forests in western USA, in response to arrival and departure of an intense sunfleck. Photon irradiance before and after the sunfleck was 4 µmol quanta m^{-2} s^{-1} compared with 1590 µmol quanta m^{-2} s^{-1} during direct illumination. Leaf folding avoids photoinhibition

(Based on Björkman and Powles 1981)

Many plants can change their leaf angles and orientation in response to a change in light. Some do this to increase interception while others do it to avoid high light. A good example of optimising light interception through leaf move-ment is given by *Oxalis oregana*, an understorey herb of red-wood forests in western USA (Figure 12.4). This plant is able to track sunlight on dull days, but can change leaf angle from horizontal to vertical in only 6 min if exposed to full sunlight (Björkman and Powles 1981). In this way, leaves can maintain maximum photosynthetic rates under a variety of light conditions. *Omalanthus novo-guinensis*, an Australian rainforest plant, can also change leaf angles in response to full sunlight within about 20 min (Watling *et al*. 1997b).



[4]

Figure 12.5 *Cotyledon orbiculata* grown for 20 weeks under high light (1300 µmol quanta m^{-2} s^{-1}, left) or low light (350 µmol quanta m^{-2} s^{-1}, right) in controlled growth chambers. Plants grown at high light produce copious amounts of white wax which reflects over 50% of incident light whereas plants grown at low light produce very little wax and have much lower leaf reflectance.

Scale bar = 10 cm

(Based on Robinson *et al.* 1993; photograph courtesy S.A. Robinson)

Another way of regulating light capture is to change leaf-surface properties. Many plants in high light environments increase the reflectance of their leaves by coating them in hairs or wax or even salt crystals. *Cotyledon orbiculata*, a crassulacean acid metabolism (CAM) plant from southern Africa, produces a wax coating which reflects 60% of incident light. If *C. orbiculata* is grown in low light, wax production stops and leaf reflectance drops to 9% (Figure 12.5; Robinson *et al*. 1993). Young eucalypt leaves also produce wax, while leaves of *Celmisia longifolia*, a plant of the Australian alps, are covered

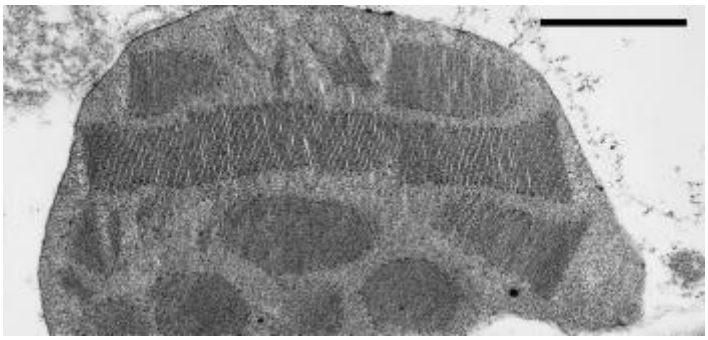
in a thick layer of silvery ?bres. In these instances plants are avoiding high light by creating their own shade, but does leaf anatomy adjust to environments where light is limiting?

Epidermal cells in some rainforest shade specialists are shaped to enhance light capture by acting as a lens. The optical properties of such cells focus incident sunlight into the layer of photosynthetic tissue just below the epidermis, reducing light lost due to reflectance and transmittance.

Light interception can also be regulated at a tissue and organelle level. Photosynthetic tissue can be concentrated equally on both sides of a leaf (isobilateral) to maximise use of light absorbed from either side, or preferentially on one side (dorsiventral) as is common in species where leaves are predominantly horizontal.

Chloroplast density and location within leaves is also sensitive to light climate, and energy capture varies accordingly. Alignment along vertical cell walls will reduce overall absorption of incident light (recall Figures 1.4 and 1.5), and in *Oxalis* leaves absorbance can be reduced 20% when chloroplasts move from the horizontal to the vertical walls of mesophyll cells (Brugnoli and Björkman 1992; Park *et al*. 1996).

Once sunlight has been intercepted by an assimilatory organ, photon absorption then depends on the extent and nature of light-absorbing pigments in photosynthetic tissues. In terrestrial plants the major light-absorbing pigments are chlorophylls *a* and *b* plus a range of carotenoids which can act as accessory pigments (see Section 1.2 for more detail). Compared with high-light plants, plants grown in low light tend to allocate relatively more resources to these light-harvesting pigments and their associated proteins than to Rubisco and other soluble proteins involved in CO_2 ?xation. This shift in allocation of nitrogen-based resources can be accompanied by marked changes in leaf anatomy, especially depth of mesophyll tissue (see Case study 12.1) and reflects a need for increased ef?ciency of light absorption when sunlight is limited.



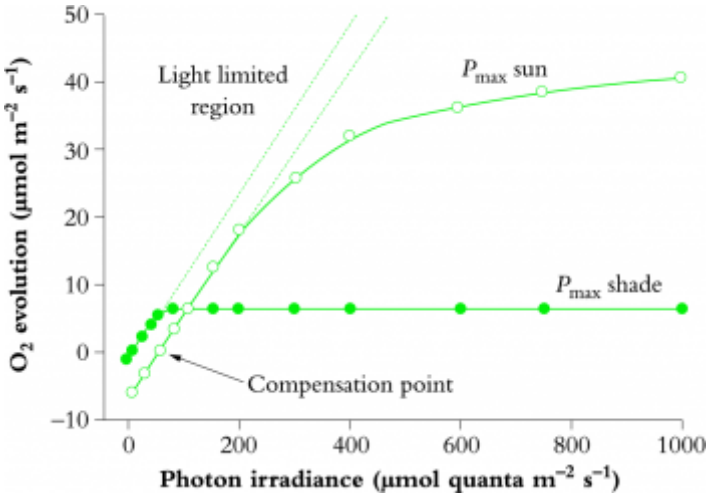
[5]

Figure 12.6 Electron micrograph of a chloroplast from a shade-grown *Alocasia macrorrhiza* (photon irradiance 10 µmol quanta m^{-2} s^{-1}, from incandescent lamps). An extensive development of randomly arranged granal stacks is a feature of photosynthetic acclimation to deep shade in this species. Scale bar = 1 µm

(Reproduced from Chow *et al.* 1988)

There are also differences in chloroplast structure between low- and high-light plants. Shade chloroplasts tend to be larger than those found in sun plants. They also contain more thylakoid membranes which show higher levels of stacking into appressed regions (see extreme development of grana in Figure 12.6). The higher proportion of appressed to non-appressed membranes found in shade

chloroplasts is the result of increased photosynthetic system II (PSII) antenna (LHCII) content. LHCII is thought to be involved in thylakoid appression and formation of granal stacks. Plants grown in low light also tend to have lower Chl *a*/*b* ratios. Chlorophylls *a* and *b* are both associated with the light-harvesting antennae, while only Chl *a* is found in the reaction centres. A lower *a*/*b* ratio reflects an increase in LHCII complexes relative to reaction centres (Anderson *et al*. 1988; Section 1.2).



[6]

Figure 12.7 Photosynthesis-light response curve for typical shade and sun plants, showing relationships between photosynthetic rate (measured as O_2 evolution) and absorbed light (expressed as a photon irradiance). Dashed lines are extrapolations of initial linear slopes where photosynthesis is light limited, and represent quantum yield (moles of O_2 evolved per mole quanta absorbed). Quantum yield (based on absorbed energy) is the same in both sun and shade plants, although the light-compensation point is highter in the sun plant (photon irradiance required to offset respiration; net exchange of CO_2 is then zero) due to faster dark respiration. The sun plant also achieves a highter rate of light-saturated photosynthesis (P_{max}) than the shade plant

(Representative original data courtesy of S.A. Robinson)

On top of striking differences in leaf anatomy and chloroplast ?ne structure, energy derived from absorbed sunlight is then processed in ways that differ subtly between shade-grown and sun-grown plants. In high light there is a requirement for greater capacity in both light and dark reactions of photosynthesis. Photosynthesis–light response curves for shade and sun plants (Figure 12.7) illustrate such differences. The initial slope of each light response curve represents the quantum ef?ciency of photosynthesis. This is the same for sun and shade plants. The reason it does not change is that the ef?ciency of the light reactions is the same no matter how much light has been received during growth (i.e. eight photons are required for the evolution of one molecule of O_2 and ?xation of one molecule of CO_2). However, sun plants tend to have a greater capacity for photosynthetic electron transport (greater abundance of components such as Cyt b_{559}, Cyt b_{563}, Cyt *f* and plastoquinone). They also have a greater capacity for ATP synthesis per unit of chlorophyll compared with shade plants. Taken together, those capacities allow them to process more sunlight into ATP and NADPH for use in CO_2 assimilation and other synthetic events. Such capacity is matched by a greater investment in biochemical machinery for CO_2 ?xation, resulting in a higher light-saturation point and a higher maximum rate of photosynthesis (P_{max}) for sun plants (Figure 12.7). In particular, this greater capacity for CO_2 ?xation is achieved via greater investment in enzymes of the photo-synthetic carbon reduction (PCR) cycle

relative to shade plants. As a further distinction, sun leaves tend to be thicker and have more cell layers (see Case study 12.1). They also have higher stomatal conductances to facilitate rapid uptake of CO_2.

A higher photosynthetic capacity in sun plants does, however, incur some costs. Their leaves tend to have higher respiration rates which increase light-compensation point relative to shade plants (Figure 12.7). Higher respiration rates probably result from (1) increased carbohydrate processing in high light, (2) increased costs of constructing sun leaves and (3) a higher cost of maintaining sun leaves (further details on maintenance costs are given in Section 6.5).

Greater transpiration is a further cost of higher photosynthetic capacity due to higher stomatal conductance. Sun plants often respond to this by increasing their root : shoot ratios. Under conditions where water is limiting, however, stomatal conductance may be reduced, sacri?cing photosynthesis in favour of slower transpiration.

12.1.2?Photoinhibition and photoprotection

In light-response curves for photosynthesis (Figure 12.7), photosynthesis is light limited, as implied by the initial linear region of the curve. However, once a light-saturation point has been reached, further light exceeds the energy-utilising capacity of that photosynthesising leaf. Dashed lines in Figure 12.7 represent a continuation of the initial rate of light processing (quantum yield of photosynthesis) and show actual light absorption. The extent to which this absorbed light is not ‘gainfully employed’ for photosynthesis is set by P_{max} (light-saturated rate of photosynthesis in normal air). At low light (< 100µmol quanta m^{-2} s^{-1}), both sun and shade leaves use more than 80% of absorbed light for photosynthesis. Once P_{max} has been reached, all additional light is in excess, and since shade plants have a lower P_{max} than sun plants, they experience more excess light at a given photon irradiance above saturation. Additional stresses such as drought, nutrient limitation or temperature extremes can lead to a reduction in P_{max} and thus increase the probability that plants will be exposed to excess light. However, even the most hardy sun plant will reach P_{max} at less than full sunlight (incident beam normal to leaf surface). At that level (say, 1000µmol quanta m^{-2} s^{-1}) approximately 25% of absorbed energy is used in driving photosynthesis, but at full sunlight (*c*. 2000µmol quanta m^{-2} s^{-1}) as little as 10% is used in this way (Long *et al*. 1994). Individual leaves on plants growing in full sun commonly experience excess light. Such light is potentially damaging, and plants adapted to full sunlight have evolved with a number of mechanisms for either avoiding excess light or for dissipating excess absorbed energy.

Mechanisms for avoiding high light such as leaf angle and surface features, forestall absorption of excess light. Rapid responses, such as changes in leaf angle in *Oxalis* and *Omalanthus*, occur in a matter of minutes and can regulate light interception on a diurnal basis. Slower-acting mechanisms including production of wax on leaves will be useful where there has been a sustained change in light environment. These kinds of mechanisms constitute *external* photoprotection (Figure 12.8).

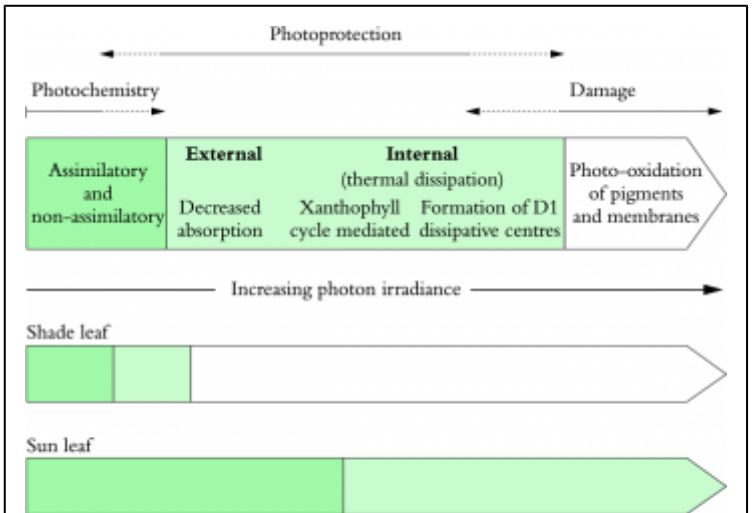


Figure 12.8 As photon irradiance is increased, energy utilisation gives way progressively to energy dissipation. Photosynthetic events shift from photochemistry, to external and then internal photoprotection and finally photodamage. These processes are interconnected and show considerable overlap. Their comparative importance for shade leaves and sun leaves is indicated. Photoprotection is especailly well expressed in sun leaves acclimated to additional environmental and biotic stresses

(Based on Demmig-Adams and Adams 1992; reproduced with permission of the *Annual Review of Plant Physiology and Plant Molecular Biology*)

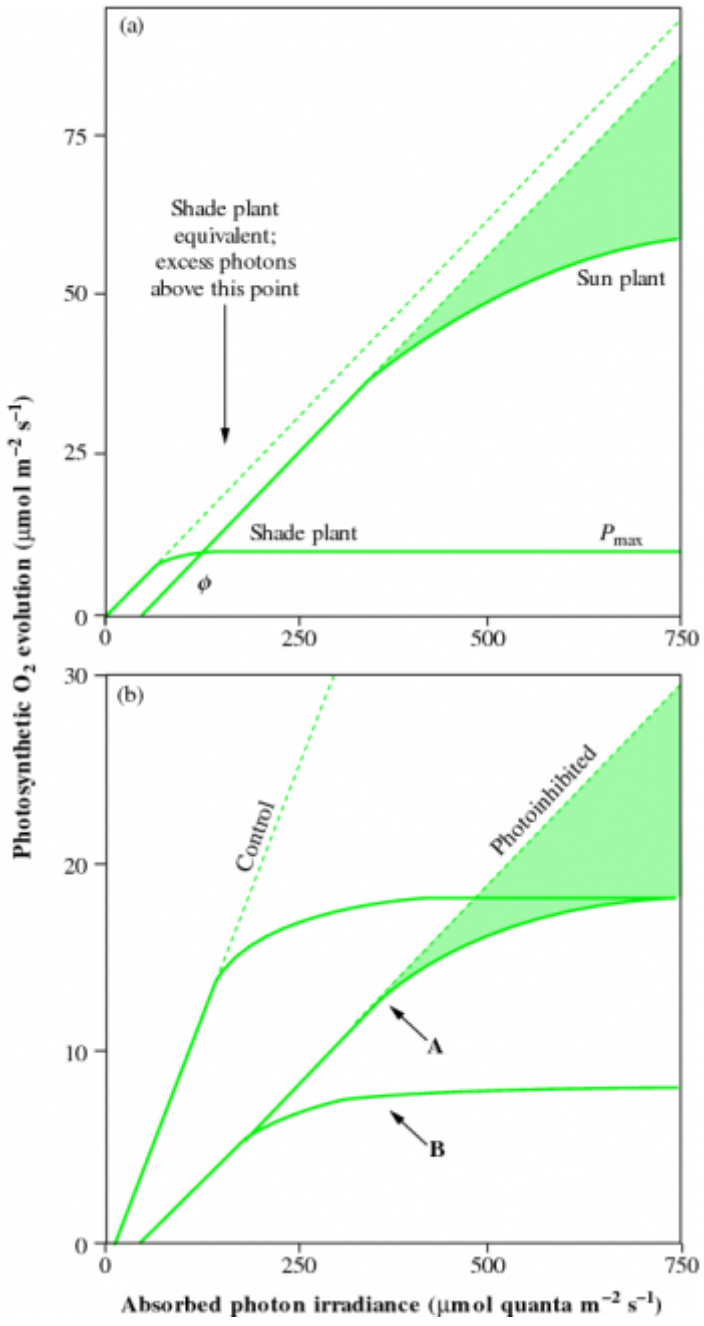
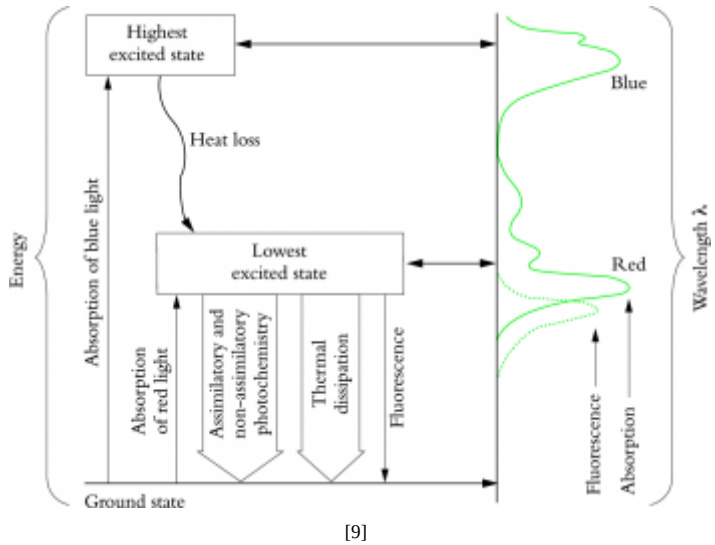


Figure 12.9 Photosynthesis and photoinhibition in sun and shade leaves. (a) shows photosynthesis-light response curves for sun and shade plants as in Figure 12.7. Dashed lines represent light absorbed by each plant. Shaded areas represent absorption of excess energy that has to be dissipated if the sun plant is to avoid damage. Shade plants have an even greater need because they absorb more light (more chlorophyll per unit leaf mass), but need less light to saturate photosynthesis. (b) shows (left side) a non-inhibited control shade leaf corresponding to that in (a) and (right side) the result of prolonged exposure to excess light (note scale expansion on the ordinate of (b)). In curve A, photoprotective processes have reduced the quantum yield of photosynthesis, but P_{max} is unchanged. By implication, more light is required to produce the same amount of O2 (quantum yield is lower) but P_{max} can be sustained by providing more light. Further exposure to excess light results in curve B where both quantum yeld and P_{max} are reduced. Photosynthetic rate is then reduced at all light levels, and recover is slower compared to leaves in curve A

(Based on Osmond 1994, with acknowledgement to Bios Scientific Publishers)

Absorption of excess sunlight often leads to photoinhibition, de?ned here as a light-dependent downregulation of the quantum yield of photosynthesis (Figure 12.9). Ironic as it might seem, photoinhibition is one of the most important regulatory mechanisms in photosynthesis, and results from a series of internal photoprotective mechanisms which act to reduce the amount of light reaching the reaction centres of PSII. One immediate consequence is a reduction in quantum yield (expressed in terms of *absorbed* light).

Photoprotection (Figure 12.8) is normally suf?cient to cope with light absorbed by leaves; photodamage only occurs when the capacity for photoprotection is exhausted. Photodamage is manifest as a decline in both quantum yield and P_{max}, and recovers only very slowly (hours to days), whereas photoinhibition recovers much faster (minutes to hours). Severe photodamage results in bleaching of pigments and damage to membranes (photo-oxidation) and may lead to tissue death.



[9]

Figure 12.10 Absorption of blue or red light (wavebands

corresponding to leaf absorption maxima; Figure 1.3) leads to excitation of chlorophyll from its ground state. Although blue light has higher energy and causes excitaiton to a higher excited state, this energy is quickly lost as heat, and chlorophyll molecules drop to a lower excited state. Utilisation of energy from excited chlorophyll molecules results in either assimilatiory or non-assimilatory photochemistry, thermal dissipation or release of light of a longer wavelength (fluorescence). Arrow thickness indicateds comparative importance of each process for energy utilisation (varies with light exposure; see Figure 12.8)

(Based on Taiz and Seiger 1991)

Consider the alternative fates of light energy absorbed by a leaf and their relevance to photoprotection, photoinhibition and photodamage (Figure 12.10). The proportion of absorbed energy consumed by these different sequences dictates their comparative signi?cance, and in order of importance as protective devices they are:

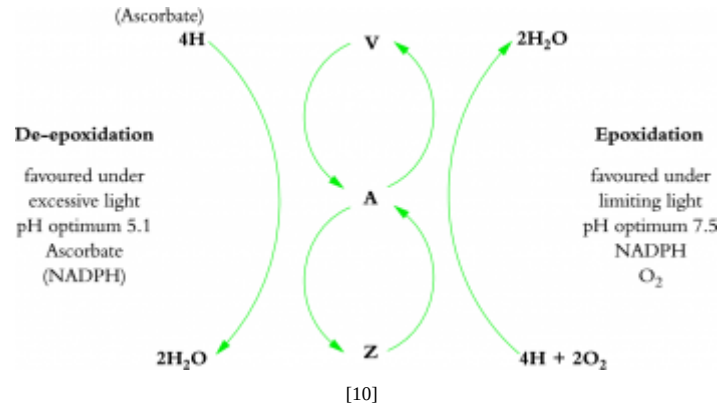
1. assimilatory photochemistry, leading to ?xation of CO_2 into stable chemical products;

2. non-assimilatory photochemistry, that is, energy consumption by metabolic processes that do not result in ?xation of CO_2 into stable chemical products such as photorespiration, nitrate reduction and the Mehler reaction. All consume energy but there is no net gain in carbon as a result;

3. conversion of light energy into heat (thermal dissipation);

4. re-emission of photons as fluorescence. Emission of *in vivo* Chl *a* fluorescence is revealed dramatically during measurements (recall Figures 1.12, 1.13). Such emission still accounts for only *c*. 1% of energy derived from absorbed light.

Most of the NADPH and ATP formed during photosynthetic energy transduction is stored as stable photosynthetic products. Some is consumed in photorespiration and nitrate reduction. Because these non-assimilatory processes also utilise NADPH and ATP they help reduce the need for photoprotection. The Mehler reaction, in which electrons flow to O_2 via photosynthetic system I (PSI) (Figure 1.10), still supports electron flow and thus might also reduce a need for photoprotection (Osmond and Grace 1995).



[10]

Figure 12.11 The xanthophyll cycle summarsied here contributes to dissipation of excess light energy, and involves three pigments, violaxanthim (V), antheraxanthin (A) and zeaxanthin (Z). All occur in chloroplast thylakoid membranes.

This special group of carotenoids undergoes interconversion in response to high light. In low light, viloaxanthin predominates but excess light levels produce chloroplast condition which are conducive to de-epoxidation of violaxanthin to seaxanthin (conditions summarised on the left hand side). Zeaxanthin, and possibly antheraxanthin, provide phtotoprotective thermal dissipation of excess light energy. When light levels are no longer excessive, chloroplast conditions favour epoxidation of zeaxanthin back to violaxanthin (summarised on the right-hand side).

(Original drawing courtesy S.A. Robinson)

However, if photochemical capacity is exceeded by incoming energy, a plant will engage photoprotective mechanisms which increase the amount of energy dissipated as heat. This non-photochemical conversion of light energy is thought to occur in the PSII antennae and involves a group of pigments known as xanthophylls and including violaxanthin, antheraxanthin and zeaxanthin (Figure 12.11). These are a special group of carotenoids which undergo interconversion in response to excess light. Energy is dissipated in the process. In low light, violaxanthin predominates, but when light is in excess, conversion to zeaxanthin via antheraxanthin occurs (Figure 12.11). This conversion requires a low pH, ascorbate and NADPH. Such conditions exist in the lumen of chloroplasts in high light. When light levels are no longer excessive zeaxanthin slowly converts back to violaxanthin via antheraxanthin. Total pool sizes of the xanthophyll pigments increase with increasing exposure to excess light. Sun plants can have three- to four-fold larger pools of violaxanthin, antheraxanthin and zeaxanthin than shade plants and the presence of other stresses can also result in increases in pool size.

Internal differences between sun and shade leaves with respect to energy dissipation are also apparent in different patterns of attenuation of light through mesophyll tissues. This is nicely illustrated by *Cotyledon orbiculata*, the CAM plant cited earlier (Figure 12.5). Here, xanthophylls are mostly found in outermost cell layers where the light environment is strongest. If the reflective wax coating is intact no internal photoprotection is required at growth irradiance and there is no zeaxanthin formed. However, if surface wax (external photo-protection) is removed by hand, internal photoprotection is then needed and zeaxanthin appears in the outermost layer (Figure 12.12).

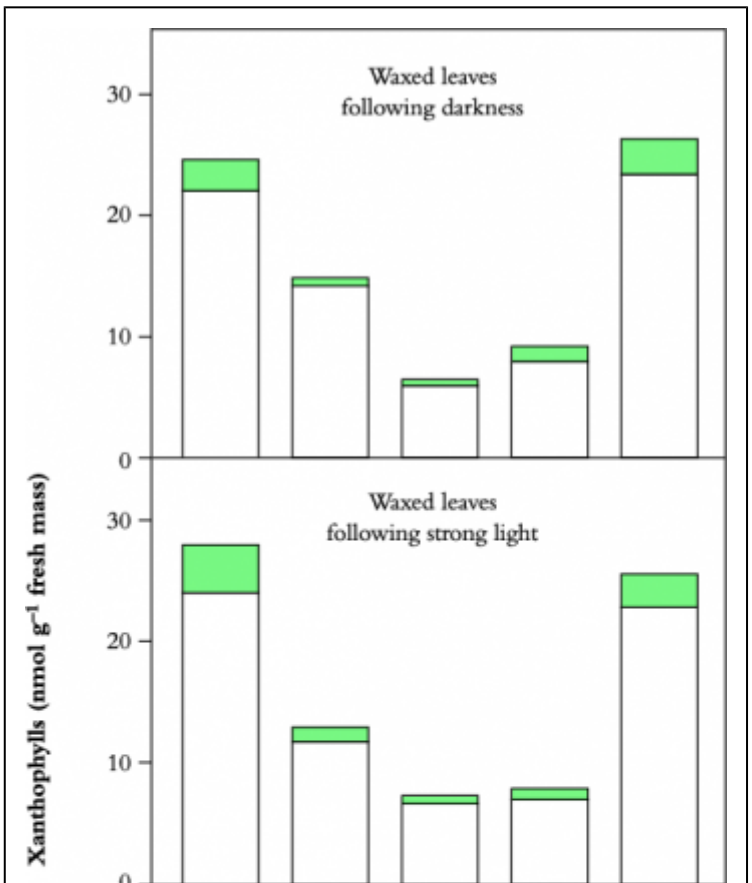


Figure 12.12 External and internal photoprotection in thick leaves of *Cotyledon orbiculata* (cf. Figure 12.5). Removal of protective wax from upper surfaces stimulates synthesis of zeaxanthin. Overall activity of the xanthophyll cycle (Figure 2.11) varies with mesophyll irradiance, while concentration of particular components also varies according to tissue depth. Changes in concentration of the various components of the xanthophyll cycle are shown here for successive (1 mm) layers in thick leaves of *C. orbiculata*, with and without their wax coating. In waxed leaves at the end of a dark period (top figure) xanthophyll cycle pigments are represented mainly by violaxanthin (V) with a small amount of antheraxanthin (A). After 6 h exposure to high light (middle figure) a small amount of violaxanthin is converted to antheraxanthin, but no zeaxanthin (Z) is formed, indicating that the natural wax coating on these leaves (see Figure 12.5) is protecting chloroplasts from excess light. Physical removal of surface wax (brushed leaves in bottom figure) results in zeaxanthin production within the uppermost layer of leaf tissue but not in deeper tissues or lower surfaces. Restriction of this xanthophyll cycle component to the top section confirms that zeaxanthin accumulation is a response to excess light

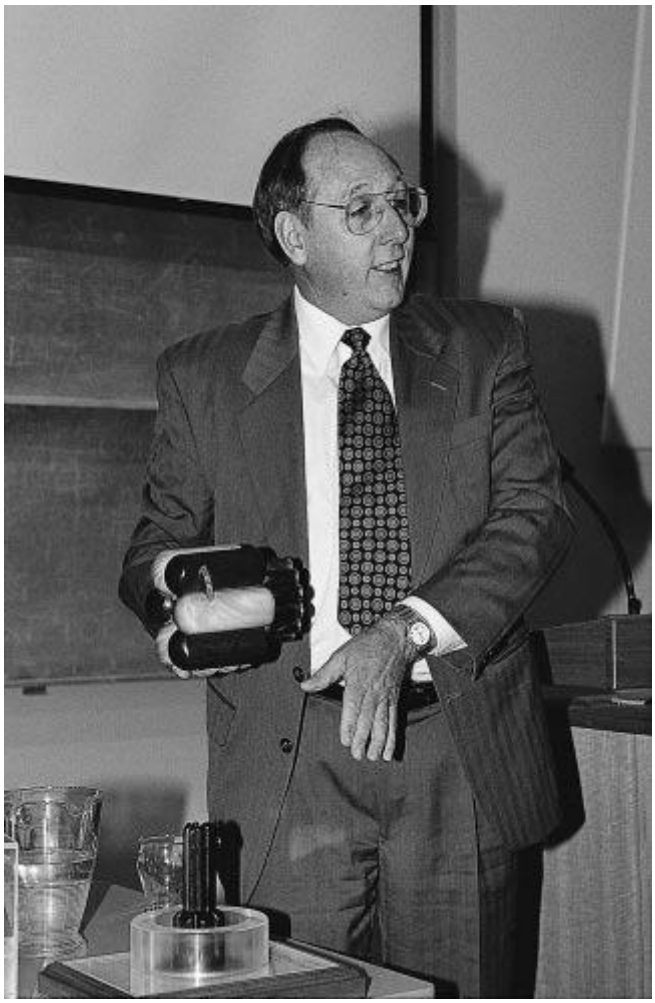
(Based on Robinson and Osmond 1994)

The presence of antheraxanthin and zeaxanthin has been well correlated with increasing thermal dissipation of absorbed light energy. If conversion of violaxanthin to antheraxanthin and zeaxanthin is prevented by treating leaves with DTT (dithiothreitol), then development of thermal dissipation is reduced and the probability of photodamage is increased. The exact mechanism by which zeaxanthin mediates an increase in thermal dissipation is not clear, but it is de?nitely linked to a pH gradient across the thylakoid membranes (?pH from H^+ pumping in Figure 1.11). This link to ?pH makes the mechanism very sensitive to changes in light because ?pH can be dissipated very quickly in low light, whereas reconversion of zeaxanthin to violaxanthin is relatively slow (discussed below in connection with sunflecks).

Traditionally, photodamage has been associated with damage to the Dl protein of PSII (Section 1.2). Most of that research comes from unicellular green algae where photo-damage occurs if D1 degradation is faster than D1 synthesis. However, in higher plants, D1 protein turnover is optimal at growth irradiance and declines at both lower and higher irradiances. When D1 damage occurs in higher plants PSII centres become photochemically inactive. Non-functional PSII centres may then accumulate in the chloroplast grana and somehow increase thermal dissipation of excess light energy (Anderson and Aro 1994). Shade plants with their larger granal stacks may have greater capacity to accumulate non-functional PSII centres, whereas sun plants may rely on a higher rate of D1 turnover and larger xanthophyll pool sizes for their internal photoprotection.

In either circumstance, photoprotection involves a prodigious turnover of PSII reaction centres. W.S. Chow (pers. comm.) estimates that about 1 million damaged centres are renewed every second for each square millimetre of a capsicum leaf, even in low light (20µmol quanta m^{-2} s^{-1}, i.e. near to light-compenstion point). At light saturation (say, 1000µmol quanta m^{-2} s^{-1}), turnover would be about 50 million reaction centres per second! Self-repair on this scale is a prerequisite to continuing leaf function, and a constant drain on plant resources because replacement of D1 protein is part of the repair process.

FEATURE ESSAY 12.1?Perspectives on photoinhibition



[12]

Figure 1 Professor C.B. Osmond, FAA, FRS

Barry Osmond

Plants often harvest more light than they can use in photosynthesis. When they are exposed to excess light there is an ever-present possibility of photoinhibition. This may happen when tree fall produces a rainforest gap and suddenly exposes seedlings adapted to life on a forest floor to sustained 10- or 20-fold increases in photon irradiance, or when water stress or low temperature restricts access to CO_2 in sun plants. The ef?ciency of light utilisation declines rapidly, and in most cases reversibly. Usually the excess light is wasted as heat, instead of being used to drive assimilation. These reversible changes in ef?ciency are known as photoprotection, and, if adequate, photoinhibitory damage is avoided.



Figure 2 Photoinhibitory printing of excerpts from the front page of Ewart's paper on assimilatory inhibition on a leaf of the shade plant *Cissus antarctica*. A microfilm negative of the paper was appressed against the leaf which was exposed to full sunlight for 1 h. Chlorophyll fluorescence was subsequently imaged with a special video camera. Those areas of the leaf exposed to strong light show severely reduced fluorescence due to photoinhibition. This latent print remains on the leaf for several weeks because these shade plants repair photoinhibitory damage only slowly

(Photographs courtesy C.B. Osmond)

Some of the earliest systematic studies of photoinhibition were done by A.J. Ewart in Pfeffer's laboratory in Leipzig and published in 1896 (Figure 2). He examined the effects of excess light on the ability of chloroplasts in leaves to evolve O_2. He detected this by examining the movement of O_2-requiring bacteria towards photosynthetically active cells in leaf sections. Ewart is best remembered because he went on to translate three volumes of Pfeffer's famous textbook (*The Physiology of Plants*) into English, and later became the ?rst Professor of Plant Physiology in Australia (University of Melbourne, 1904).

Modern research on photoinhibition has been strongly influenced by the Dutch biophysicist Bessel Kok (1956), responsible for so many advances in photosynthetic research, and by the early ?eld studies of Björkman and Holmgren (1963) in Sweden. Björkman's sabbatical in Australia in 1971 stimulated renewed interest in photoinhibition, and with Australian collaborators research in his Stanford laboratory has repeatedly changed the way people think in this ?eld (Powles 1984; Björkman and Demmig-Adams 1994). Australian research in photoinhibition continues to attract attention worldwide (Anderson *et al*. 1997; Wydrzynski *et al*. 1995). Although modern research techniques such as *in vivo* chlorophyll fluorescence are much more quantitative and ?eld portable, the questions being probed are remarkably similar to those studied by Ewart!

By and large, leaves on most plants cannot avoid harvesting light, but some have evolved with features to forestall absorption of excess radiation. For example, leaves of desert plants often reflect a large part of incident light, the high reflectivity being due to hairs, salt crusts (as in Australian saltbushes such as *Atriplex nummularia*) or epidermal waxes (see Figure 12.5). Such features are effectively mechanisms for external photoprotection. In others such as Townsville stylo (*Macroptilium atropurpureum*) leaves demonstrate very effective light-avoiding responses when water stressed. Ludlow and Björkman (1984) showed that if leaves of Townsville stylo were restrained perpendicular to incident sunlight, high-temperature-dependent photoinhibition ensued. It was obvious that unrestrained movement in the ?eld preserved green and functional stylo leaves under conditions that accelerated senescence of leaves on adjacent herbs and grasses. By way of contrast, in some species like the compass plant (*Lactuca scariola*) leaves actually track the sun's movement to maximise light interception. Sun plants in which the photo-synthetic apparatus is organised to take advantage of bright light have high capacities for CO_2 ?xation and retain high photosynthetic ef?ciency at relatively high photon irradiance (see Figure 12.9, and Case study 12.1).

Depending on photosynthetic pathway, and environmental conditions, sun plants may also sustain high rates of non-assimilatory electron transport in carbon recycling during oxygenase photorespiration (Section 2.3) and to O_2 in the Mehler reaction. Sun plants are also well endowed with photoprotective mechanisms that facilitate a reversible downregulation of PSII ef?ciency and stimulate wastage of absorbed photons as heat in the antennae pigment–protein complexes, before transfer to the reaction centre of PSII. These processes, linked to the energetic status of thykaloids and the interconversion of

xanthophyll pigments (Section 12.1.2), provide internal photoprotection for PSII reaction centres (Demmig-Adams and Adams 1992; Gilmore 1997).

For the most part, these antennae-based processes seem to accommodate photon excess in most natural environments. However, when photon excess is sustained, especially in combination with other stresses, photoinhibitory damage in PSII reaction centres may follow. The site of damage in most cases seems to be D1 protein which is the *psbA* gene product and the most rapidly turned over protein in chloroplasts. D1 protein is also the binding site for the triazine family of herbicides and accounts for their lethal effects. Turnover of D1 is accelerated in bright light, and it is often described as the 'suicide protein' (Aro *et al*. 1993). Sun plants have high rates of chloroplast protein synthesis, and are thus able to repair damage to the critical D1 protein of PSII reaction centres more readily than in shade plants (Section 1.2).

Photoinhibitory damage at chilling temperatures seems to involve PSI rather than PSII, and is especially signi?cant among C_4 grasses and C_3 plants of tropical origin. In these chilling-sensitive plants, a photon irradiance of only 100 µmol quanta $m^{-2}s^{-1}$ at 0–10ºC for about 5 h is suf?cient to cause a selective photoinhibition of PSI (Sonoike 1996).

Shade plants, in which the photosynthetic apparatus is organised to take advantage of low light, are poorly endowed with all of the above processes. Structural organisation of the photosynthetic apparatus reflects these biophysical and bio-chemical realities, and not surprisingly the very different granal structures of shade and sun plants have important implications for photoinhibitory damage (Anderson and Aro 1994). In the short term, shade plants accommodate bright light in sunflecks without photoinhibitory damage, and even exploit it for additional post-illumination CO_2 exchange (Pearcy 1994; Chazdon and Pearcy 1986). When exposed to sustained bright sunlight, in excess of that encountered during growth, shade-tolerant plants such as *Alocasia macrorrhiza* at the margins of Queensland rainforests suffer photoinhibitory damage. Photoacclimation to bright light, the successful long-term accommodation of photoinhibitory processes, is genetically limited in many species, being dependent on adequate nutrition (especially nitrogen) and permissive temperatures (Anderson and Osmond 1987).

Although unicellular algae such as *Chlamydomonas* sp. have been widely used to research mechanisms of photoinhibitory damage, relatively little is known of photoinhibition in either marine or freshwater environments. Under natural conditions, vertical movement of unicellular algae in water columns is an important determinant of photon exposure and photoinhibitory responses, which almost certainly involve many of the same processes as in higher plants. Thus the ubiquitous marine macrophyte *Ulva* is susceptible to desiccation and high-temperature-dependent photoinhibitory damage in rock pools and estuaries when low tides occur at midday. However, the diversity of photosynthetic pigments among marine macrophytic algae suggests several alternative photoinhibitory mechanisms that are yet to be investigated.

Clearly, photoinhibition is an integral and indispensable component of photosynthesis. The inef?ciencies it produces in light utilisation are essential to the stability of the photosynthetic apparatus in organisms that depend on light for life, and especially in environments where they can do little to regulate the incoming flux of this basic resource. The costs of these inef?ciencies are dif?cult to estimate (Long *et al*. 1994) and the extent to which plant distribution in relation to sunlight is governed by photoinhibitory responses remains controversial. Perhaps one of the most convincing examples is the interaction of bright light and low temperature which restricts re-establishment of eucalyptus seedlings to the shaded south side of parent trees on the Southern Highlands of New South Wales (Ball *et al*. 1991; Case study 14.1).

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12.1.3?Sun/shade acclimation and rainforest gaps

Emergent trees of tropical rainforests have to endure strong sunlight, and leaves comprising the crowns of such trees will have acclimated to full sun. In young-growth forests, such canopy emergents represent early-successional fast-growing species that are adapted for fast growth in full sun on large disturbances. Such species represent an initial phase in forest dynamics that might last 10–20 years. By contrast, in old-growth forests, early-successional species have long since completed their life cycles, and will have been replaced by later-successional species whose seedlings initially tolerated deep shade on the forest floor, but now endure full sun as canopy emergents. Such remarkable plasticity in photosynthesis–light relations is an adaptive feature of late-successional species and involves sun/shade acclimation by individual leaves as discussed below.

A seed germinating in a rainforest understorey (or beneath any closed canopy) starts life in a low light environment. This will not present major problems to an obligate shade species which cannot tolerate strong sunlight. Precluding any other lethal stresses, such species have adapted to life in an under-storey. However, many rainforest species are better described as either shade tolerant (i.e. able to germinate and persist in low light, but requiring higher light to reach maturity) or shade intolerant (unable to germinate or grow in low light). In successional terms, shade tolerance is a feature associated with climax species and shade intolerance with pioneer species. In conjunction with variation in the light environment within a rainforest, and in particular with the formation of gaps, these two types of physiology are in some part responsible for the patterns of distribution of rainforest species and changes in these patterns through time (Denslow 1987; Whitmore 1989).

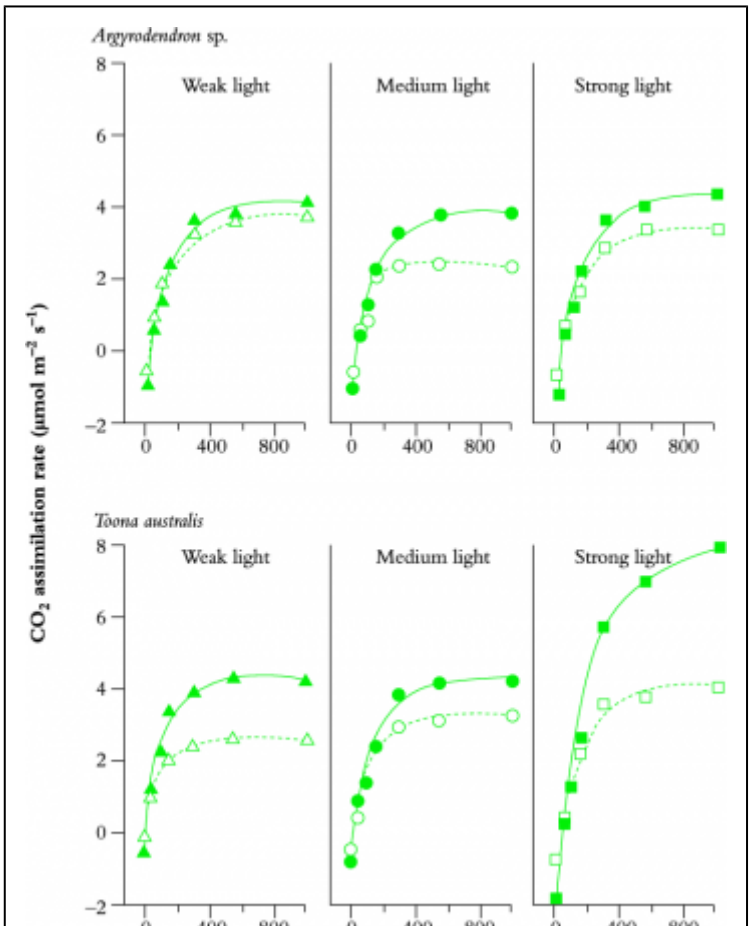


Figure 12.13 Photosynthesis-light response curves for seedlings of a shade-adapted rainforest tree species (*Argyrodendron* sp.) and a sunloving tree species (*Toona australis*). Seedlings were grown under factorial combination of weak, medium or strong light (shown left to right) x either high or low nutrient supply (solid lines with filled symbols, and dashed lines with open symbols respectively). Light-saturated photosynthesis (P_{max}) was little affected by treatment in *Argyrodendron* sp., but P_{max} in *T. australis* was greatly enhanced when cultured under high-nutrient supply x strong light. Highly conserved photosynthetic attributes in *Argyrodendron* sp. fit the late-successional status of this species, while photosynthetic responsiveness to strong light and abundant nutrients in T. *australis* in consistent with successful colonisation of disturbance sites by this early-successional species. (See Case study 12.1 for further details)

(Based on Thompson *et al.* 1992b)

Shade-tolerant species can persist as seedlings in the understorey, often for years, while still being able to respond to an increase in light availability when it occurs. By comparison, shade-intolerant (early-successional) species can only germinate and grow where there is ample sunlight, and consequently they tend to be found in wide gaps and on forest edges. When grown in low light, shade-intolerant species are unable to maintain a positive carbon balance. The change from a high light to a low light environment requires a change in allocation of plant resources as described earlier (Section 6.2). Shade-intolerant plants seem to be unable to make this change and are burdened with the higher costs of construction and maintenance of leaves better suited to strong sunlight. (Taken more broadly, factors beyond photosynthesis contribute to gap dynamics, and shade tolerance in rainforest plants is also associated with features that reduce herbivory and increase resistance to pathogens; Kitajima 1994.)

Wide gaps are relatively rare in old-growth rainforests which have been undisturbed by human activities such as logging or slash and burn agriculture. However, rainforest plants have evolved a range of characteristics which improve their probability of encountering a gap and thus their survival to reproductive maturity. Shade-intolerant species tend to produce numerous small seeds throughout the year which are widely dispersed. Their seeds are also able to remain viable for long periods (years) by going through a period of dormancy which is often broken by high temperature or strong direct sunlight with a high ratio of red to far-red irradiance (R:FR ratio decreases with sunlight attenuation through canopies). Such environmental cues for germination are all likely to be experienced in wide gaps. Following germination, seedlings show rapid growth to maturity, allowing them to become well established in a gap before other slower growing species. These characteristics increase the probability of success for shade-intolerant species in the heterogeneous light environment of a rainforest.

Shade-tolerant species, on the other hand, have evolved a different suite of characteristics. They tend to produce a few large seeds which are generally not well dispersed, with little or no dormancy but with the ability to germinate in low light and persist in the understorey as seedlings for long periods (years). A rarity of gaps and a lack of dormancy found in most shade-tolerant species increases the probability of establishing in a low-light understorey environment. In situations like this the larger seed provides them with a reserve which they can draw upon during early establishment. Osunkoya *et al*. (1993)

In a study of factors affecting survival in North Queensland rainforest tree seedlings found that seedling survival in understorey habitats was positively correlated with seed size, especially in the ?rst few months following germination.

Following establishment in the understorey, seedlings of shade-tolerant species may have to wait for a

very long time before a gap appears overhead. Many succumb to attack from herbivores or pathogens or may be crushed by large animals (including humans!). Those that do survive must be able to acclimate to the new conditions arising on gap formation; their ability to do this will depend on the nature of the new microclimate and the acclimation potential of each species.

As a case in point for rainforest species from North Queensland, Thompson *et al*. (1992b) found that *Toona australis* (an early-successional species) and two species of *Argyrodendron* (late-successional species) showed different acclimation potentials when grown under a range of light conditions (Figure 12.13). When grown under high light, *T. australis* achieved a higher P_{max} and light-saturation point than either of the *Argyrodendron* species. However, *T. australis* was more sensitive to nutrient levels, being unable to acclimate to the same degree in low-nutrient compared to high-nutrient regimes. Moreover, fast growth in *T. australis* was greatly promoted by a positive light x nutrient interaction on leaf expansion and photosynthetic capacity; adaptive features with a clear selective advantage on open sites where soil disturbance liberates nutrients (see Case study 12.1).

CASE STUDY 12.1?Interaction of light and nutrients on rainforest seedlings

Paul Kriedemann

Different species of rainforest seedlings can show strong contrasts in growth response to light x nutrient inputs which relate to their gap-colonising ability and successional status. For example, wide gaps in tropical rainforests of North Queensland that result from major disturbance during forest operations are often colonised by early-successional species such as *Toona australis* (red cedar of commerce). By contrast, narrow disturbance gaps within established forests that have become species rich become occupied by later-successional species such as *Flindersia brayleyana* or *Argyrodendron* sp. These differences in gap-colonising ability relate, *inter alia*, to inherent differences in vigour and thus growth response to light x nutrient inputs, and can be reconciled with leaf attributes. *Toona* is sun loving and fast growing compared with later-successional species of *Argyrodendron* (tulip oak of commerce) which colonise narrow gaps and are shade tolerant as seedling trees. Species in this genus are adapted to life as seedlings in weak light with occasional sunflecks on the forest floor (Figure 12.14). This distinction in seedling vigour between *Toona* and *Argyrodendron* ?ts their respective successional status in forest dynamics and, as shown here, is further expressed in growth and photosynthetic response to light x nutrient inputs.

A priori, strong vigour should have a selective advantage for those species that are recruited to major disturbances where strong sunlight combines with a flush of plant-available soil nutrients to promote fast growth. However, such vigour would be selectively neutral on a forest floor where daily photon

irradiance is a major limitation (notwithstanding sunflecks). In effect, leaf longevity plus resistance to predation would matter more than light-saturated photosynthetic capacity in promoting a positive carbon balance and hence survival. Moreover, strong sunlight may well prove supra-optimal for seedlings of shade-adapted species of *Argyrodendron*, especially when strong sunlight is imposed upon a low supply of nutrients, conditions that would predispose to photodamage.

Thompson and co-workers explored these issues for a number of species including *Flindersia brayleyana*, a rainforest tree with broad tolerance to sun and shade (Thompson *et al*. 1988), *Toona australis*, which is sun loving, and two species of *Argyrodendron* that are shade adapted (Thompson *et al*. 1992a, b). Tree seedlings were held for six months in growth cabinets under a factorial combination of three light ¥ two nutrient treatments (30, 130 and 535 µmol quanta m^{-2} s^{-1} x 1/3 strength or 1/200 strength (modi?ed) Hoagland nutrient solution). Leaf attributes were measured periodically, and dry mass taken at ?nal harvest. The three light treatments provided 1.3, 5.6 and 23 mol quanta m^{-2} d^{-1} respectively, and were designed to correspond with daily photon irradiance on forest floor, mid-canopy and upper crown of a North Queensland rainforest.

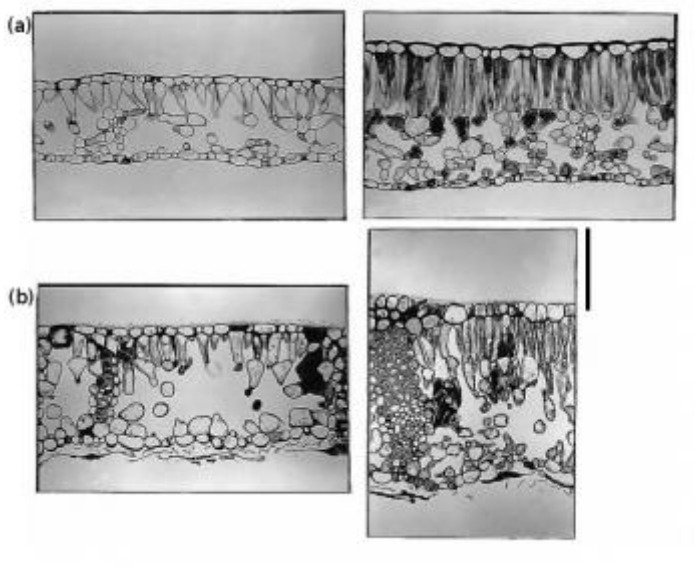


[15]

Figure 1 Figure 1 Growth response to light in (a) *Toona australis* (sun loving) and (b) *Argyrodendron* sp. (shade adapted). Photographs show, left to right, low versus high nutrient supply under strong light for both (a) and (b). Seedlings illustrated here came from a population held for six months under factorial combination of weak, medium or strong light x either low or high nutrient supply. Plants

correspond to those described in Thompson *et al.* 1992a, b. Scale bar = 10 cm (see Colour Plate 49) (Photographs courtesy P.E. Kriedemann)

Consistent with colonising behaviour on disturbed sites in nature, *Toona* seedlings held under strong light showed a spectacular growth response to nutrient supply (Figure 1a). This growth response was accompanied by marked changes in leaf anatomy and light-saturated rates of photosynthesis (P_{max}). Mesophyll depth increased substantially with photon irradiance (Figure 2a), resulting in higher lamina mass:area ratio (Table 1), while P_{max} (area basis) in high-light plants was doubled by high nutrient supply (Figure 12.13).



[16]

Figure 2 Transverse sections of leaves from *Toona australis* (a) and *Argyrodendron* sp. (b) grown on high nutrient supply under either weak light (left side) or strong light (right). *Toona* (sun loving) produces a much greater depth of mesophyll tissue under strong light compared to weak light, which accounts for enhanced photosynthetic capacity. *Argyrodendron* sp. (shape adapted) is much less responsive to photo irradiance during growth, producing consistently thicker leaves regardless of light level, but with lower photosynthetic capacity. Shade adaptation in Argyrodendron is clearly not predicated on leaf adjustments, but probably depends more on carbon retention and leaf longetivity in deep shade than on short-term carbon gain. Scale bar = 100 µm

(Micrographs courtesy I.E. Craig)

Fast growth in *Toona* contrasted with slow growth in *Argyrodendron* (Figure 1b). A light x nutrient interaction on seedling size was apparent in both cases (Figure 1 in Thompson *et al*. 1992a), but overall growth was much more modest in *Argyrodendron* (5 g plant^{-1} in *Argyrodendron* compared with 20g plant^{-1} in *Toona*; both on high light x high nutrients). Furthermore, high light proved supraoptimal for *Argyrodendron* on low nutrient supply, resulting in some photo-oxidative damage and even leaf necrosis (Figure 1b).

Nutrient effects on growth relate mainly to supply and/or utilisation of nitrogen, and nitrogen use ef?ciency for photo-synthesis by *Toona*, *Flindersia* and *Argyrodendron* was inferred from the slope of relationships between light-saturated photosynthesis and leaf nitrogen (both on an area basis; Figure 6 in Thompson *et al*. 1992b). This term was always highest in *Toona*, especially in seedlings grown under strong light, and would contribute to the colonising success of this species in wide disturbance gaps.

Table 1 Lamina mass:area ratio (g m^{-2}) in Argyrodendron *sp. and* Toona australis *as a function of nutrient supply and photon irradiance during growth*

Nutrient supply (mg N L^{-1})	**High (71)**			**Low (1.0)**		
Growth irradiance µmol quanta m^{-2} s^{-1}	Weak	Medium	Strong	Weak	Medium	Strong
	30	130	535	30	130	535
Toona	17	36	48	15	38	53
Argyrodendron	53	74	84	68	76	96
Flindersia	42	73	89	48	92	115

(Based on Thompson *et al*. 1992b)

[17]

Table 1 ***Lamina mass:area ratio (g m^{-2}) in* Argyrodendron *sp. and* Toona australis *as a function of nutrient supply and photon irradiance during growth***

Leaves of sun-loving *Toona* showed major adjustments to light x nutrient treatments (Figure 2a, Table 1) whereas healthy leaves on *Argyrodendron* sp. were much less affected in terms of either P_{max} (Figure 12.13), cross-sectional anatomy (Figure 2b) or lamina mass:area ratio (Table 1). Notably, *Argyrodendron* had consistently thicker leaves (evident in Figure 2, and implied by a greater mass:area ratio in Table 1).

Environmental plasticity in leaf properties of *Toona* underpin this species' responsiveness to well-exposed and nutrient-rich sites where competitive success hinges on carbon gain. Muted responses in *Argyrodendron* seedlings are consistent with requirements for shade tolerance in a closed forest where leaf longevity and carbon retention favours survival.

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12.1.4?Sunflecks

Formation of gaps provides an important opportunity for many rainforest plants to escape from the dim understorey environment and reach maturity as canopy trees. However, a rainforest is not simply a vast shade house with an occasional hole overhead. Rainforest habitats actually present a continuum of light availability ranging from almost total shade (diffuse light) through intermediate levels of direct and diffuse sunlight to a wide gap where direct sunlight is received for most of a day. Input of direct sunlight beneath a closed canopy can be surprisingly high because of sun patches and more transient sunflecks. Sun patches occur when small and variable openings in the overlying canopy permit direct sunlight to penetrate to the forest floor, resulting in the familiar patchwork of sunlight and shade which can be seen in any understorey on a clear day (Figure 12.14).



[18]

Figure 12.14 A cohort of *Argyrodendron* sp. seedlings in a protected niche at the base of a mature tree of that same species growing in a rainforest on Atherton Tableland. Competition for light is intense, and a sunfleck shown passing over this tiny population would be providing a much-needed source of sunlight, namely a few minutes of around 1500 µmol quanta m^{-2} s^{-1} compared with background photon irradiance of around 150 µmol quanta m^{-2} s^{-1}. Scale bar = 15 cm (see Colour Plate 50)

(Photograph courtesy P.E. Kriedemann)

Neither sun patches nor sunflecks occur on fully overcast days when sunlight is entirely diffuse. These patches of sunlight move across the forest floor on bright days, and will illuminate any leaves or parts of leaves which lie in their path (Figure 12.15).

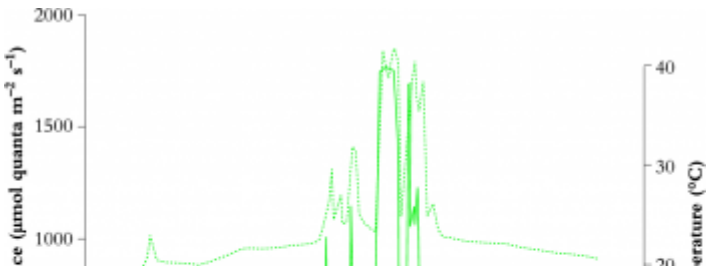


Figure 12.15 Natural variation in photon irradiance experienced by *Alocasia macrorrhiza* growing in the understorey of a North Queensland rainforest (cf. Figures 12.2, 12.3). Daily total photon irradiance on this occasion (from integration) was 6.033 mol quanta m^{-2} d^{-1}). The abrupt increase from a background level of around 50 µmol quanta m^{-2} s^{-1} to to 1750 µmol quanta m^{-2} s^{-1} energises photosynthesis, but is counteracted by increased leaf temperature, especially during prolonged exposure. Transpiration cooling is a significant component of heat budgets for such large leaves, so that adequate soil moisture is a prerequisite for continuing leaf gas exchange during a sunfleck. However, sunfleck frequency will be an additional factor for carbon gain during exposure to strong photon irradiance. Photosynthetic induction state diminishes to a minimum after 30 min in low light (see Figure 12.16) and some minutes are required to reattain full capacity in strong light. Infrequent sunflecks are thus used at reduced efficiency

(Based on Watling *et al.* 1997a, b and additional unplublished data)

Sunflecks and sun patches are of potential use to understorey plants for photosynthesis, but is this potential realised? Growth of understorey tree seedlings has been shown to be correlated with the amount of direct light received in sunflecks, and up to 60% of carbon gain in such environments has been attributed to this source (Pearcy 1983; Chazdon 1986). However, when compared with expected values based on the known steady-state response of plants to light, sunfleck utilisation is often below predicted values (P?tsch and Pearcy 1989). Moreover, species vary in their capacity to utilise sunflecks. Watling *et al*. (1997a) measured the growth of four Australian rainforest species under simulated sunfleck regimes and showed that sunflecks contributed to growth in two species (*Diploglottis diphyllostegia* and *Micromelum minutum*), whereas the other two species (*Alocasia macrorrhiza* and *Omalanthus novo-guinensis*) were unable to make effective use of sunflecks.

Factors underlying this variation in sunfleck utilisation ef?ciency

There are two components of a plant's photosynthetic physiology which will determine how it uses the light in a sunfleck. First, photosynthetic capacity (P_{max}) will set a ceiling on how much light a plant is able to use. Second, a few minutes of illumination are needed for PCR cycle intermediates to reach critical levels, and this 'induction requirement' of photosynthesis determines how quickly a leaf responds to an increase in photon irradiance.

Measured photosynthetic capacities of understorey plants are often low (Figure 12.13). When a leaf experiences a sunfleck, carbon ?xation will increase to the point of light saturation. If an understorey plant could increase P_{max}, it could utilise more light. But there are trade-offs. For example, higher respiration rates would increase the light-compensation point, and increase carbon losses during low light periods separating sunflecks.

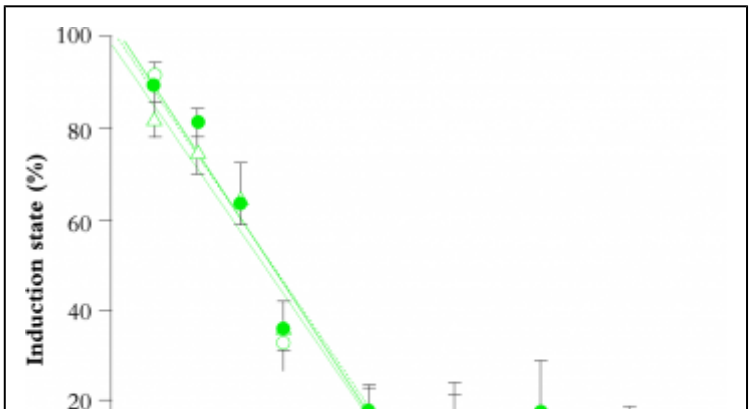


Figure 12.16 Loss of photosynthetic induction state in *Alocasia macrorrhiza* following transfer from saturating light to low light. Fully-induced leaves were transferred to low light (10 µmol quanta m^{-2} s^{-1}) for different lengths of time (up to 60 min). Their induction state was determined as the proportion of light-saturated photosynthetic capacity (P_{max}) achieved within 2 min after return to saturating light. (Replicate determinations represented by different symbols and error bars)

(Based on Watling *et al.* 1997a, b and additional unpublished data)

Regardless of photosynthetic capacity, a plant's ability to use sunflecks is also affected by the induction requirement of photosynthesis. When a leaf that has been in low light for some time is exposed to an increase in photon irradiance the rate of photosynthesis does not increase instantaneously to the new level. Instead, there is a gradual increase in assimilation which can take from 10–60 min for completion. This 'induction period' varies according to species as well as the induction state of the leaf concerned. Three different processes are involved, namely (1) build up of PCR cycle intermediates and in particular ribulose-1,5-bisphosphate (RuBP), (2) light-dependent activation of Rubisco, and (3) light-dependent opening of stomata (Pearcy *et al*. 1994). Each of these processes follows a different time-course. Build up of a metabolite pool is fastest (1–2 min) followed by Rubisco activation (2–5min) and ?nally stomatal opening (up to 60 min). Relaxation in low light is more protracted but generally occurs in the same sequence, leading to a decline in the induction state. Thus, the longer a leaf has been in low light the lower its induction state. Figure 12.16 illustrates this for a leaf of *Alocasia macrorrhiza*, a plant common in rainforest understoreys and forest edges in eastern Australia. Induction loss in *Alocasia* has a half time of about 25min, but other species have been found to be either faster (e.g. *Adenocaulon bicolor*, an understorey herb from the redwood forests of western USA; P?tsch and Pearcy 1989) or slower (e.g. *Castanospora alphandii*, a shade-tolerant tree from Australian rainforests; Watling *et al*. 1997a, b).

Chazdon and Pearcy (1986) showed that continuous light is not needed for induction to proceed. They found that if leaves were subjected to a series of 60s lightflecks (arti?cial sunflecks) separated by 2min of low light, then induction state increased with each lightfleck. In nature, sunflecks are often clustered with a sequence of irregular bursts separated by dull periods of variable duration. Under these circumstances the state of induction might be expected to improve so that a plant will respond more rapidly to closing sunflecks in each sequence. This is supported by the data of Chazdon and Pearcy (1986) where the ef?ciency with which a sequence of lightflecks was utilised increased with successive lightflecks (ef?ciency was calculated as the actual amount of carbon ?xed during a lightfleck relative to the amount predicted if there had been no induction period).

Carbon gain by fully induced leaves during lightflecks can exceed that expected, resulting in improved ef?ciency of light utilisation. This 'intermittency phenomenon' was noted by Kriedemann *et al*. (1973) in grapevine leaves exposed to high-frequency lightflecks. Similar investigations in a number of other species have also shown that such enhancement occurs only with short-duration lightflecks and is more prominent in fully induced leaves. *Alocasia macrorrhiza* showed improved ef?ciency of lightfleck utilisation by fully induced leaves only when lightflecks were of 40s duration or less. Uninduced leaves needed lightflecks 10s or shorter (Chazdon and Pearcy 1986).

This apparent improvement in light use ef?ciency results from continued carbon ?xation in low light (or darkness) following a lightfleck. During a short lightfleck, pools of triose phosphate and RuBP build up because carbon ?xation runs transiently slower than the light reactions. This pool of PCR intermediates

is then used for post-illumination CO_2 ?xation. In rainforest understoreys, where sunflecks are generally longer than a few seconds, this kind of enhancement is unlikely to be important. However, it may contribute signi?cantly to carbon gain under crop canopies, where sunflecks are much shorter and more frequent.

One consequence of generally low photosynthetic capacity in understorey plants is a limited ability to process the light energy they absorb during strong sunflecks. This limited ability can be exacerbated by a low induction state. Under these conditions understorey plants will need to dissipate excess energy if they are to avoid photodamage. Field measurements of chlorophyll fluorescence from *A. macrorrhiza* show a decline in the quantum yield of photosynthesis (measured as F_v/F_m) during saturating sunflecks, indicating that photoprotective mechanisms are probably being engaged. Simultaneous assessment of the xanthophyll pigments shows that interconversion of violaxanthin to zeaxanthin is also occurring. After the sunfleck has passed, conversion of zeaxanthin to violaxanthin is extremely slow in species such as *A. macrorrhiza*, perhaps allowing a more rapid photoprotective response for subsequent sunflecks. However, quantum yield increases more rapidly than xanthophyll reconversion on return to low light, demonstrating a requirement for both high ?pH and zeaxanthin for internal photoprotection (Watling *et al*. 1997b; Section 12.1.2).

Engagement of photoprotective mechanisms by shade-tolerant plants in an understorey environment may seem surprising, but serves to illustrate the extent of spatial heterogeneity in resource availability which is a feature of most habitats.

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