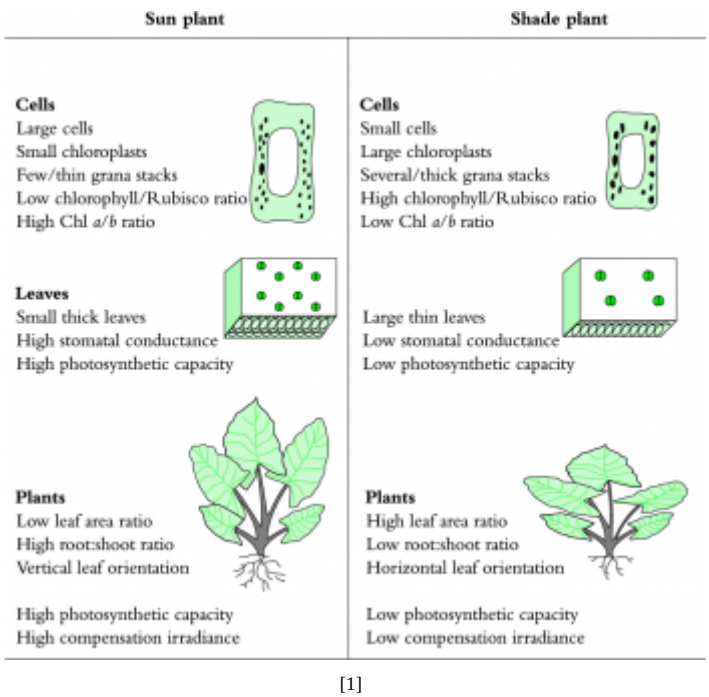
12.1.1?Light interception and utilisation

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.



[1]

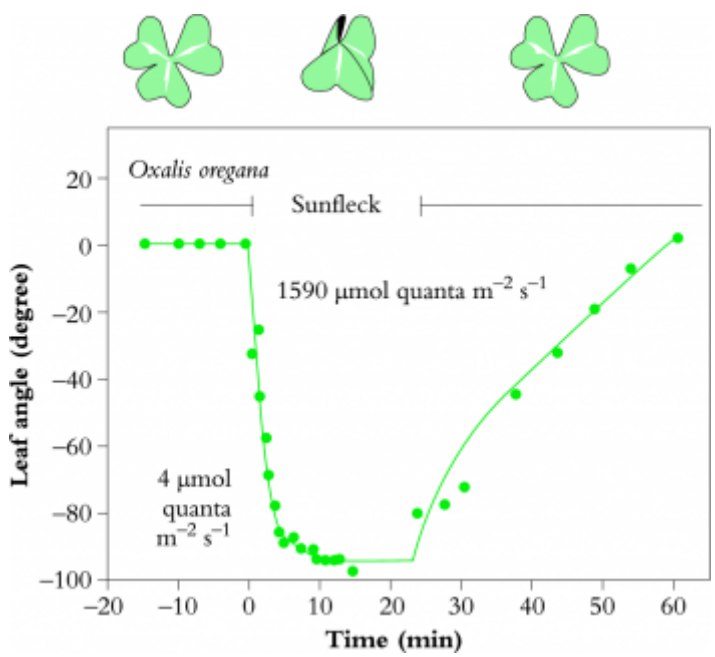
Figure 12.2 A comparison of photosynthetic structure and function in sun and shade plants. Major characteristics are described for cells, leaves and whole plants (Original drawing courtesy S.A. Robinson)



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.



[3]

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?

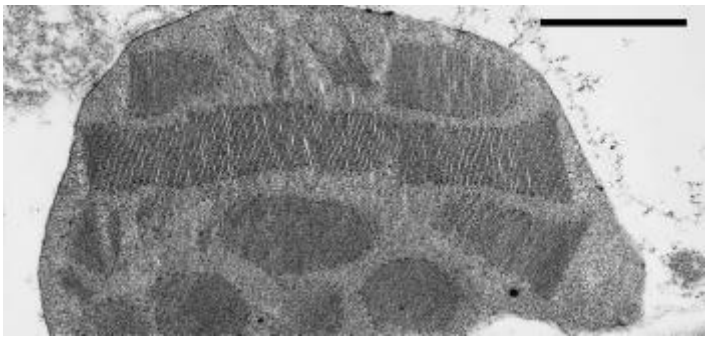
Epidermal cells in some rainforest shade specialists are shaped to enhance light capture by acting as a lens. The optical properties of such cells focus incident sunlight into the layer of photosynthetic tissue just below the epidermis, reducing light lost due to reflectance and transmittance.

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).

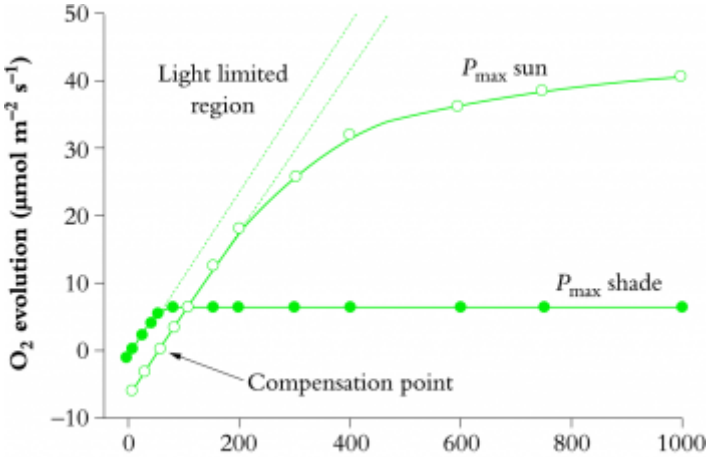


Figure 12.7 Photosynthesis-light response curve for typical shade and sun plants, showing relationships between photosynthetic rate (measured as O_2 evolution) and absorbed light (expressed as a photon irradiance). Dashed lines are extrapolations of initial linear slopes where photosynthesis is light 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.

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