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Introduction

Plants grow as a result of their ability to absorb light energy and convert it into reductive chemical energy, which is used to fix carbon dioxide. Growth enables the species to reproduce its genes, and to do this efficiently the plant must coordinate its development with environmental opportunities.

Plants exist in various associations at a great variety of latitudes and altitudes. They occur under fluence rates which vary daily, seasonally and with shade created by surrounding structures and vegetation. They survive the aquatic environment, the humidity of tropical rain forests and the desiccating effects of the desert. In some environments the stresses upon plants are constant or cyclic, whereas in others they may vary frequently or infrequently. To survive in these habitats plants must retain a high degree of plasticity both as a species and as an individual. Plants must be able to detect the environment and adapt to it.

A significant aspect of a plant's environment is light. As indicated above, a plant has an absolute requirement for light for the purposes of photosynthesis, a process which predominantly requires red (R) and blue (B) wavelengths. If a plant becomes stressed in this regard, it needs to adapt in some way to aid survival. However, these are not the only requirements a plant has of its light environment. Firstly, a plant needs to orientate itself in space so as to present itself to the incident radiation as best it may. Secondly, at higher latitudes in particular, the plant also needs to orientate itself in time so that the various phases of its life cycle are completed within seasons suitable to its habit and ecological niche. Plants need mechanisms capable of detecting a number of variables affecting a large number of processes.

Investigating complex problems such as the relationship between a plant and a varying light environment does not lend itself easily to the scientific process. Although the early workers on photoperiodism were often compelled as a result of the nature of their experiments and available facilities to deal with the variables encountered in the natural environment, the training of the scientist is to ask a single question, design an experiment with a single variable and arrive at an unimpeachable conclusion. The beginning of this painstaking approach to understanding light and plant development has recently been recorded in a booklet entitled *A pigment of the imagination*.¹ This early work is well recorded in almost every text book on plant physiology and will therefore be dealt with only briefly here. It began as the result of the finding of a mutant tobacco plant growing in a field in Maryland, USA. This mutant, which became known as Maryland Mammoth, would continue to grow vegetatively until killed by frost in the winter. Garner and Allard^{2,3} artificially

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shortened the daylength for these plants by bringing them into a windowless shack in the afternoons. After 2 months of this treatment the plants flowered 3 months earlier than plants left under natural light regimes and protected from frost. Simultaneously, these workers were investigating the failure of sequential sowing to produce sequential crops in the soy bean *Glycine max* var. Biloxi. Once again their results showed that daylength was the critical factor controlling flowering. The phenomenon of photoperiodism was discovered, a Pandora's box was opened and some would suggest that hope has not yet emerged.

In the same establishment and not uninfluenced by the presence of Garner and Allard came the work of Borthwick and Parker on the light break of the night period which inhibited flowering of *Glycine max* held under short days. Although this work was originally performed in the late 1930s, it was not published until the early 1950s.⁴ The addition of Hendricks to the team led to the elucidation of several action spectra of photosensitive developmental processes. Their results showed that a good number of light-sensitive responses were controlled by a common photoreceptor.⁵ Perhaps the most important experiment in the history of the discovery of phytochrome resulted from the collaboration of Eben Toole first with Flint and McAlister and then with the Borthwick team. Flint and McAlister,^{6,7} using light-sensitive lettuce seed, had demonstrated not only that maximum stimulation occurred in the R but also that maximum inhibition was found in the far-red (FR). These workers actually used reversibility in their experiments in as much as they raised the germination level of their seeds with R to show the inhibitory capability of FR. It is not possible to judge at this distance in time what significance they attached to this protocol. It was left to Borthwick, Hendricks, Parker, Toole and Toole (1952) to perform the now classical experiment of R/FR reversible lettuce seed germination.⁸ Here they showed that the effects of R and FR were not only opposite to one another, they were also antagonistic.

As a result of their experiments the Beltsville workers were able to suggest that plants contain a blue-green pigment to which they gave the rather uninspired name phytochrome (phyto = plant, chrome = pigment). This pigment was the photoreceptor for a number of light-mediated processes and existed in two interconvertible forms. The first form, now known as Pr (red-absorbing-form of phytochrome), was biologically inactive and capable of absorbing R and in so doing was converted to the biologically active form of phytochrome now known as Pfr (far-red-absorbing form). The Pfr form of phytochrome is capable of returning to the Pr form by the absorption of FR. Although the lack of photoreversibility of a response does not disprove the involvement of phytochrome (see very low fluence response (VLFR), p. 28), the demonstration of R/FR reversibility is still regarded as the hallmark of this system.

It was the photoreversibility of phytochrome which led to the development of an *in vivo* assay of the pigment by Butler, Norris, Siegelman and Hendricks.⁹ This assay is spectrophotometric and can only be used in etiolated tissue. Chlorophyll absorbs and fluoresces in the same region of the spectrum as phytochrome absorbs. This limitation on the measurement of phytochrome, together with the understandable preference for using monochromatic light instead of broad band irradiation, was to influence research in photomor-

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phogenesis. With a few notable exceptions, experimentation was restricted to the study of germinating seeds and etiolated seedlings. Even today the detection of phytochrome in green tissue is an event limited to a handful of laboratories. Although this approach was to retard our understanding of the role of phytochrome in the natural environment, much was to be learned about the control of seed germination and the biochemical events which occur during the early part of the de-etiolation process. Understanding these changes led to two principal proposals. Mohr suggested that phytochrome acted by repressing and derepressing genes,¹⁰ whereas, Smith hypothesised that phytochrome acted by controlling membrane permeability.¹¹ Recent developments in the techniques of molecular biology have added credibility to the involvement of phytochrome with gene expression.¹² Evidence that phytochrome is associated with membranes remains scant despite many distinguished person hours devoted to this problem.

Interest in phytochrome responses of green plants was practically dormant for two decades until a novel approach was provided by the work of Holmes and Smith,¹³ which was to be subsequently exploited by Morgan and Smith.^{14,15} Phytochrome was revealed to have a role of ecological significance in altering the growth strategies of shade-intolerant species. This work has led others to look at the shade strategies of plants from various habitats.

Phytochrome is not the only pigment involved in developmental processes in plants. Reports that B affects plant development are much older than those involving R. Sachs (1864) showed that the bending of plants towards the light was a process stimulated only by B light.¹⁶ Some believe that this process, now known as phototropism, has received more attention from plant physiologists than a developmental option deserves. Although it can be shown that developing plants are capable of detecting small differences between laterally available light,¹⁷ the majority of plants in the natural environment show no sign of phototropic growth during development. Add to this the fact that the most common plant material used in these experiments is the coleoptile (a tissue which despite its suitability for experimentation is of juvenile and transient importance to the Graminae alone) and the accumulation of this knowledge takes on an inane quality. On the other hand, the coleoptile has provided a model system for understanding the interactions between photoreceptor and hormone, and hormone and cell elongation. Certainly the study of a system so subtle as to lead to an understanding of how the photocontrol of a single hormone can influence both straight and curved growth cannot be without benefit to the understanding of growth in general.

While the involvement of B has long been recognised in phototropic studies, the widespread involvement of B photoreceptor(s) in plant development is a concept which has met with a certain amount of resistance. Whether there is more than one B photoreceptor and by what name it should be called is discussed elsewhere (p. 34). Here it will be referred to as blue-absorbing pigment (BAP), but no bias is implied by the use of the singular form. The purification and isolation of phytochrome was aided by the reversibility of the pigment and put an end to sceptical remarks that phytochrome was 'a pigment of the imagination' or 'a R/FR herring'. No such fortune has been experienced in elucidation of the nature of the BAP. The B region of the spectrum contributes to the energy input of photosynthesis, and both the Pr and the Pfr

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forms of phytochrome have absorption maxima in the B. The design of early experiments allowed ambiguous interpretation of results, but in recent years techniques have been developed which unequivocally demonstrate a causal relationship between BAP and plant responses. The nature of the BAP still resists elucidation although flavins and carotenoids are perennial favourites (p. 35).

Now that it is accepted that B acting through BAP can mediate photoresponses, a good deal of interest has been directed towards possible interactions between BAP and phytochrome. Obviously, in the natural environment B, R and FR are simultaneously available albeit in various ratios. It is not known if there is any ecological significance to the interaction of BAP and phytochrome.

Some photoresponses have been shown to be controlled by phytochrome, the influence of B having been eliminated. In other photoresponses, the influence of B is thought to have been eliminated but the appropriate fluence range has not been explored; in others the effect of B has not been investigated once phytochrome control has been established. Key to understanding the influence of light and plant development is identifying what is and is not known to influence a response. Although scientific information is seldom complete, there would appear to be more missing from this subject than most. It may be that some of the blame for this situation lies with the investigators, but it also lies with the nature of the scientific literature, which does not lend itself easily to the publication of negative findings.

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The Natural Light Environment

Light, its nature

Matter, besides having mass, can have electrical charge. Mass acts as a source of a gravitational force field, and charge as a source of an electromagnetic force. The electric field associated with a stationary charge is entirely analogous to the gravitational field associated with a stationary mass. Faraday discovered that moving charges can also produce a magnetic field. Both electric and magnetic fields can accelerate charge. When accelerated, they produce time-varying electromagnetic waves. Maxwell recognized that light is an electromagnetic wave. It has since been realized that not only light but radio waves, infra-red rays, ultra-violet rays, X-rays, and gamma rays are electromagnetic waves. Maxwell's model of light is shown in Figure 2.1. The simple magnetic wave has four properties:

- a) speed of propagation C (in a vacuum), $C = 3 \times 10^8 \text{ ms}^{-1}$ (this is the same for all wavelengths)
- b) direction of propagation
- c) the wavelength
- d) the polarization direction

The direction that E (the orthogonal electric field) points in Figure 2.1 is perpendicular to B (the magnetic field) and the direction of propagation.

At this point the average biologist, having read the above, goes to sit under a tree for about twenty minutes.

Solar radiation

The sun is a star which is approximately 110 times the diameter of the earth and $150 \times 10^6 \text{ km}$ distant. The outer layers of the sun consist of approximately 94 per cent hydrogen, 5.9 per cent helium and 0.1 per cent of all other elements. The inner layers are not thought to be dissimilar to the outer layers, and it is from the interior of the sun that solar energy originates. Here, at very high pressures and temperatures, hydrogen is converted to helium. The vast quantities of energy released during this process reach the sun's surface via convection currents and conduction. The production of energy is constant and thus the output of energy is constant, varying only slightly when solar flares and bursts are produced. Light takes approximately 9 min 20 s to travel the

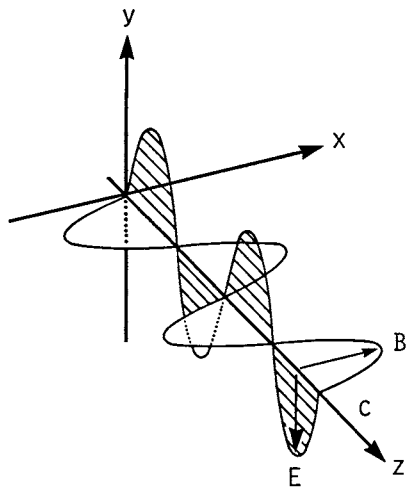


Figure 2.1 Maxwell's model of light.

distance between the sun and the earth. Experimentally determined measurements of the solar spectral distribution agree very closely with those of a black body at $5\,800^{\circ}\text{K}$. These spectra are shown in Figure 2.2.

It has been calculated that X-rays and gamma rays (2 to 10 nm) and ultra-violet rays (20 to 400 nm) provide 9 per cent of the total solar energy, whereas visible radiation (400 to 800 nm) provides 41 per cent and infra-red (800 nm to 3 000 microns) 50 per cent.

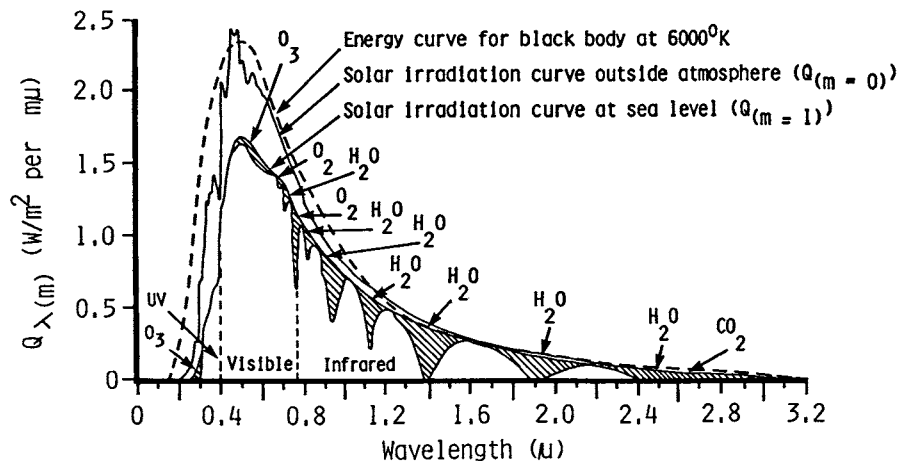


Figure 2.2 Solar spectrum outside the earth's atmosphere compared with that of a black body at 6000°K and with that at sea level (after *Handbook of Geophysics*, revised edition, U.S. Air Force, Macmillan, New York, 1960).

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The earth's atmosphere

There is little in space in terms of molecules or particles to alter the spectral energy of sunlight until it reaches the earth's atmosphere. This begins at about 10 000 km from the earth's surface with a layer of hydrogen. This layer has no distinct outer boundary, but at this distance the density of the hydrogen atoms resembles that found in interplanetary space. This said, hydrogen atoms which rotate about the earth's axis can be found as far out as 35 000 km. The light then travels through a layer of helium for approximately 2 400 km, followed by a 900-km layer of atomic oxygen and a thinner layer of about 110 km of molecular nitrogen.

These layers are arranged in order of mass, the heavier gases being closer to the earth's surface. It may be noted that even at the lowest layer (molecular nitrogen) the density of the atmosphere is only about a millionth of that found at sea level. Below these layers, the atmosphere is divided into thermal regions. The nitrogen layer is often described together with the ionosphere as the thermosphere. The high temperatures found at these altitudes are due to the photodissociation and polarization of molecular oxygen by solar radiation. Some of this energy is transferred downwards into the mesosphere. A significant amount of ozone formation takes place in the lower mesosphere, which causes energy absorption at short wavelengths and a concomitant increase in temperature. The majority of ozone formation/destruction takes place in the stratosphere, which accounts for the very high temperatures in the region. The importance of the absorption of short wavelengths to life on earth can scarcely be exaggerated. Its formation prevents higher temperatures in the troposphere and much of the mutagenic effects of ultra-violet light.

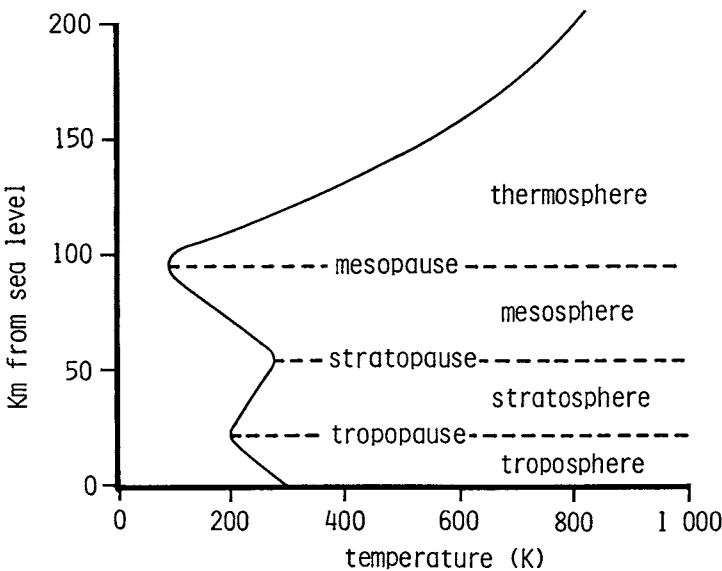


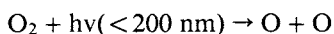
Figure 2.3 The thermal structure of the earth's atmosphere (after Chambers, J.W., 1978).

Atmospheric modifications of solar radiation 9

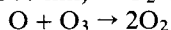
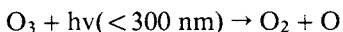
It is the radiant energy of the troposphere, which is finally absorbed by plants, that is of prime consideration here, and will be dealt with in more detail later. The main source of heat in the troposphere is far-red (FR) re-radiation from the land surface of the earth. In consequence, the troposphere is warmest nearest the earth's surface (Figure 2.3). As a result of industrialisation and the concomitant increase in pollution of the atmosphere with the products of combusive processes, the density of the lower layers of the atmosphere has increased. This has resulted in the so-called 'green-house' effect. The presence of these pollutants in the atmosphere causes absorption of the re-radiated energy which had previously disappeared into space. This is resulting in increases in global temperatures which may cause serious problems.

Atmospheric modification of solar radiation

Solar radiation approaches the earth's atmosphere qualitatively unaltered from the photosphere of the sun. Figure 2.2 shows not only the spectrum of the solar radiation outside the earth's atmosphere but also the spectrum as recorded at sea level. A more detailed spectrum of radiation viewed from the earth's surface is shown in Figure 2.4b. Differences between these spectra are caused by the attenuating effects of the atmosphere. The outer layers are rare and have little effect on incoming radiation. The inner layers of atomic oxygen and molecular nitrogen are, however, capable of absorbing X-rays and gamma rays. These layers coincide with those of the ionosphere. As the atoms or molecules absorb these rays they give up an electron and become positively charged. It is this layer of ions which reflects radiowaves and allows long-distance radio communication. Because the inception of the ionosphere depends upon solar radiation, it tends to weaken on the dark side of the earth and disappear. The ozone layer coincides with the lower mesosphere and upper stratosphere (20 to 55 km above the earth's surface). This layer is vital to life on earth since it absorbs a great deal of ultra-violet light (UV) of less than 320 nm and excludes wavelengths dangerous to life (below 290 nm). The ozone layer is produced by the photolytic cleavage of oxygen by wavelengths of less than 200 nm using nitrogen as an activating partner.



UV of longer wavelengths (<300 nm) split the ozone in a slower process, viz.:



The ozone layer is denser in the northern hemisphere (350 D) (Dobson = 0.001 cmbar) than at the equator (245 D). In consequence, UV radiation forms a greater part of the total spectrum in equatorial regions than in northern latitudes. In the late 1970s gaps in the ozone layer were reported over the South Pole. Although the density of the ozone layer was known to vary with factors such as gaseous mixing, solar spot activity and stratospheric temperature changes, the erosion of the ozone layer has now been shown to be due, at least in part, to halogenated hydrocarbons and in particular to chlorinated

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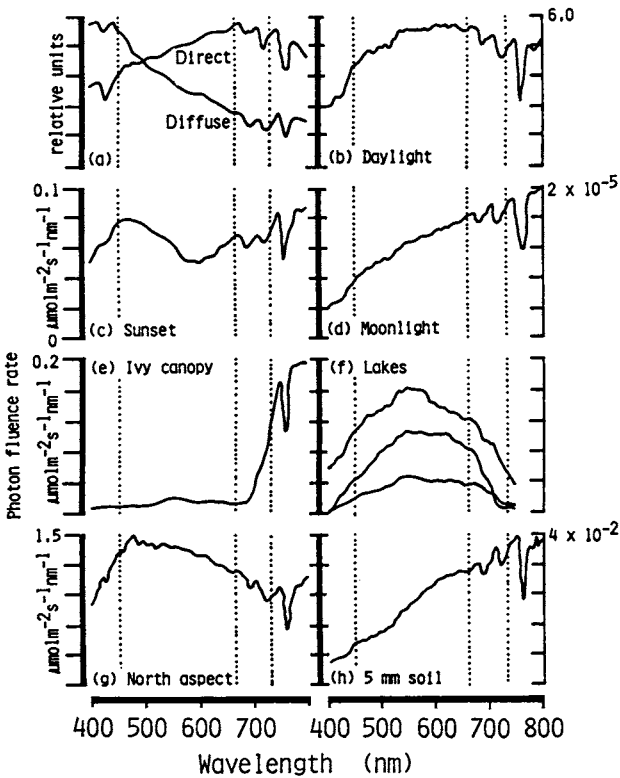
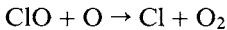
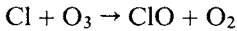


Figure 2.4 Light regimes found in the natural environment (after Smith, H., 1982).
a) Diffuse and direct radiation
b) Clear skies, noon, open situation
c) Sunset
d) Moonlight
e) Ivy canopy-light
f) Lakes
g) North-facing aspect (temperate latitude, northern hemisphere)
h) Soil

fluorocarbons (CFC). These substances are widely used as propellants in aerosol sprays and coolants in refrigeration units and were originally selected for their inert properties. Although long-lived, these compounds finally break down to release chlorine, which interacts with ozone in the following manner:



Further damage to the ozone layer may be caused by nitrogenous oxides, which are produced by combustive processes:

