8 Light Energy and Plant Function

Through the amazing process of photosynthesis, light energy from the sun is captured and stored as carbohydrates, proteins, and fats. We depend on these products of photosynthesis for food, fuel, shelter, clothing, and animal feed. In addition to being the driving force of photosynthesis, light also orchestrates the growth and development of most plant species. Understanding why something as simple as depth of planting at seeding is so important to production success relies on understanding the physics and biology of light. In this chapter the amazing involvement of light in plant growth and development will be examined.

The Physics of Light

Humans have always wondered what light is and how it travels. We know that light is energy, but we really don't know how it moves. There are two major theories of how light travels. One theory proposes that light travels as discrete packets of energy called photons. The other suggests that light travels as waves, just as energy in water travels as waves. Both theories are correct. Light behaves as a wave in some ways and as a particle in others. For plant scientists, it doesn't matter whether light travels as a wave or as a particle. We only need to know how much light there is (intensity or level) and its quality (wavelength).

Light intensity refers to the amount of light at the source while light level refers to the amount of light when it reaches an object. This is an important distinction when discussing light and plants. The intensity of a light source ultimately determines the level when plants intercept the light. We can't control the intensity of our most important light source, the sun, but we can control its level intercepted by plants. We alter plant light levels through pruning, plant spacing, and the use of shading technologies such as lathe houses or shade cloths. We can control both factors when dealing with artificial lighting by bulb selection and altering the distance between plants and the light source.

Light Quality

Light quality is described by its wavelength, measured in nanometers (nm). While many discussions surrounding light often only consider visible electromagnetic radiation, we need to consider the entire electromagnetic spectrum from ultraviolet (UV) through to infrared. Wavelengths beyond these endpoints do not normally impact plant growth and development. Table 8.1 summarizes the wavelengths, color, and importance in horticulture for light from UV to infrared.

Light Quantity

Light quantity is measured as the instantaneous amount of light hitting a unit area per unit time. The units of measurement differ for different types of light. Light we see is measured in foot candles and lux. Total solar radiation is measured in watts (W), and light available to plants for photosynthesis is measured in micromoles (μmol). Quantities of light are measured as particles called photons or quanta. Each photon has a very small amount of energy associated with it, thus we measure photons in units of moles (mol). One mole is equal to 6.02×10^{23} photons. A micromole (μmol) is one-millionth of a mole, or 602,000,000,000,000,000 photons.

An instantaneous measurement of light is not very useful for assessing its impact on plants. A measurement of the total quantity of light at a particular wavelength over time is much more desirable. One such measurement is the daily light integral (DLI) and is the daily total of photosynthetically active radiation (PAR, 400–700 nm) measured in moles per square meter per day ($mol/m^2/day$).

Table 8.1. Impacts on plant growth and development of wavelengths particularly important to horticulturists.

Wavelength (nm)	Color	Impacts on horticulture
280–315	UV	May bleach leaves, may cause sunburn, particularly on fruit, may induce genetic mutation
315–400	UV – blue	Important in photoperiodic responses, some absorption by chlorophyll, thus may influence photosynthesis, inhibits cell elongation, can cause sunburn
400–520	Blue	Photosynthesis
520–610	Green	Mostly reflected by plants
610–750	Red	Photosynthesis and photoperiodism
750–1000	Far-red	Stimulates cell elongation, influences flowering and germination
1000+	Infrared – heat	Heat

In general the middle latitudes receive about 9 mol/day PAR on a sunny winter day, and only about 3 mol/day PAR if it is cloudy. In the summertime, it's about 26 and 12 mol/day for sunny and cloudy days, respectively (Tibbitts, 1994). DLI measurements summed over the season can help in decisions regarding cultivar suitability for specific locations, especially for out-of-season production.

Light Meters

Foot candle or lux meters

Foot candle or lux meters are useless for measuring light in relation to plant productivity. These meters measure light much like the human eye perceives light, mostly in the 500–600 nm range. Much of this is green light, which is not really used by plants but rather is reflected back into space.

PAR/quantum light meter

PAR is radiation effective for driving photosynthesis. Light between 400 and 700 nm is considered PAR. This is the light level most often measured by horticulturists as it provides a good idea of how much light is generally available for plant growth and development. It is often called quantum light and the meter is called a quantum light meter. PAR is measured as the number of moles of light photons striking a surface (in this case the light sensor surface) per unit area per unit time.

Solar radiation meter

A solar radiation meter measures radiation in a very broad spectrum from 300 to 1100 nm. Measurements of this type of radiation are important for estimating evapotranspiration and scheduling irrigation.

UV meter

UV meters are useful in measuring the effectiveness of UV filtering materials that might be used in high tunnel or greenhouse covers. Most UV meters measure radiation in the 250–400 nm range. Meters are available for measuring specific zones within this range.

Red/far-red meter

This type of meter calculates the red:far-red ratio of light by measuring red (660–680 nm) and far-red (720–740 nm) light. These wavelengths are important in phytochrome-mediated responses. These meters are particularly useful for determining the influence of leaf canopy on this ratio as measurements can be made in a number of canopy locations and mapped. Decreasing red:far-red ratios can lead to unwanted stem elongation and 'stretching' of plants. Thus, knowledge of red:far-red ratios is important in determining plant spacing, particularly in greenhouse production which can influence the need for anti-elongation growth regulator applications.

Light Quality and Artificial Lighting

Light quality and quantity are critical choices in artificial lighting situations such as indoor or greenhouse production. Light quantity can be regulated by the number of lamps used and their distance from plant canopies. Light quality is determined by bulb selection.

Lamp technology

There are a number of technologies available for generating light energy from electricity (Dakin, 1994). Many of them have been employed at one time or another for use in horticultural production

systems. After basic spectral requirements are met, the initial cost of the luminaire (the entire lighting fixture consisting of bulb, ballast, and reflector), operating and maintenance costs as well as heat generation must be considered.

Incandescent bulbs

An incandescent bulb has a tungsten filament which heats up to 2800 K as electricity passes through it. Some of the energy is radiated as light while much of it is released as heat. Ultimately, the filament 'burns out' and the bulb must be replaced.

Discharge light sources

In discharge light sources, an electric current passes between two electrodes and heats gaseous plasma contained in a tube made of glass called an arctube. Discharge light sources don't burn out like incandescent bulbs, since they have no filament. They slowly decline due to changes in the electrodes and walls of the arctube. The differences among the discharge types are due to differences in arctube composition, wall temperature, and electrode gap distance. Generally there are two gases involved in each type of discharge source, one is the dominant gas and the other is responsible for radiation. When an electric current passes between the two electrodes, the dominant gas in the tube is ionized, gaining energy from the electric current. When these excited ions collide with atoms in the radiating gas, some of the radiating gas electrons become excited, eventually releasing the energy as photons of light.

FLUORESCENT BULBS Nearly everyone is familiar with the fluorescent discharge light source. The dominant gas is argon (Ar) while the radiating gas is mercury (Hg). This type of lamp is often called a low pressure Hg-Ar discharge lamp. This is also the type of lamp in many neon signs. Low pressure means that the collision rates between gas atoms are relatively low. The radiation emitted is mostly UV (254 nm). Visible light is produced when the UV radiation strikes a phosphor coating on the inside of the arctube wall. The discharge is efficient at creating UV radiation, but the conversion to visible light is inefficient (Langhans, 1994).

HIGH PRESSURE MERCURY LAMPS High pressure discharge lamps are smaller than fluorescent tubes and operate at higher power, temperature, and pressure (Fig. 8.1). The center of the discharge is nearly 5000 K, almost as hot as the sun.

High pressure mercury lamps have Hg as the dominant and radiating gas. While much of the radiation is in the UV range, mercury lamps discharge visible light mostly around 405, 435, and 545 nm.

High pressure metal halide (MH) lamps are similar to high pressure mercury lamps. In MH lamps, there are small amounts of sodium iodide (NaI) and scandium iodide (ScI_3). When the lamp is operating, these salts are molten condensates on the arctube walls with low concentrations of their vapors in the arctube gas. The Na and Sc atoms have lower energy levels than the Hg and radiate more readily than the Hg in the arctube gas. Most of the energy of the Na and Sc atoms is in the visible range. Thus the MH lamp has a higher visible efficiency (more visible light per unit of energy used) than the high pressure mercury lamp.

Both the high pressure mercury tube and the MH lamp utilize high pressure Hg in a fused quartz arctube. Greater visible efficiency in discharge lamps can be obtained by increasing the operating temperature, however, the useful life of the lamp decreases as operating temperature increases. Additionally, in these two lamp types, the high temperature limit for the quartz tube is about 900°C.

High pressure sodium lamps are similar to MH lamps in that they rely on radiation from Na atoms in the presence of Hg. In high pressure sodium lamps, higher amounts of Na in the vapor phase are achieved by using elemental Na rather than

Fig. 8.1. A high pressure discharge luminaire for supplemental greenhouse lighting.

NaI. The arctube wall is made of Al_2O_3 rather than quartz and can withstand temperatures up to 1150°C resulting in higher visible efficiency (Langhans, 1994).

LED LIGHTS Light emitting diodes (LED) are solid-state light-generating fixtures which will probably become one of the biggest advancements in protected plant culture in many years (Bula *et al.*, 1994; Morrow, 2008). LEDs produce light via an electrical current flowing through a solid material with *p-n* junctions. A *p-n* junction is the junction of a *n-type* electron donating semiconductor and the a *p-type* electron accepting semiconductor. The original LEDs were expensive and generated only red (660 nm) light. Current LED structures combine LED units which generate specific wavelengths into a combined lighting structure called an array, analogous to the luminaire of conventional lighting systems.

LEDs are desirable as light sources in horticulture for many reasons: (i) they have a long life; (ii) they are small and rugged; (iii) they have low voltage requirements; and (iv) they do not generate excessive heat. Another unique aspect of LED lights is that wavelength emission can be tailor designed by altering the specific LEDs used in the structure. Programmed wavelengths would be useful for photomorphological manipulation. In addition, LEDs are much safer than conventional lighting fixtures: LEDs do not have glass bulbs with high temperatures that are dangerous and easily broken and they do not contain Hg.

LED arrays are particularly well suited for research applications. In addition, they generate minimal heat and have a low profile, making them ideal for shelving applications often used in tissue culture. Ultimately, LEDs are likely to become widely used in greenhouse applications for supplemental lighting and photoperiod manipulation. The major limitation to their use in horticulture is purchase cost. Another limitation is low output at wavelengths needed for optimum plant growth and development. Both limitations have been decreasing over the last 10 years and will probably continue to do so.

SULFUR LAMPS Sulfur lamps have been considered as a source for lighting in horticulture (MacLennan *et al.*, 1994). Sulfur bulbs work somewhat like other high intensity discharge (HID) lamps, utilizing plasma inside a glass bulb which emits light when heated. The source of energy in a sulfur bulb is microwave energy generated by a magnetron similar to those found in microwave ovens. Electrodes are unnecessary. The sulfur lamp has no discernible spectral shift over the lamps lifetime (10,000 h). They have no large spikes at any wavelength and are very efficient, capable of providing 2000–6000 μmol/m^2/s PAR. Sulfur lamps have not become widely used in horticulture.

Horticultural applications of different light sources

Fluorescent

Fluorescent bulbs have been used extensively in growth chambers and growth rooms. Growth chambers are relatively small boxes equipped with temperature controls and light fixtures to study plant growth and development under controlled simulated outdoor conditions. Growth rooms are similar but much larger. While the spectral quality and intensity of sunlight is difficult to mimic, cool white fluorescent bulbs have become the standard in growth chambers and rooms for good reasons. Cool white fluorescent bulbs have the greatest mole output of photosynthetic photon flux (PPF, light for photosynthesis) of all fluorescent bulb types with an acceptable spectral distribution. Additionally, light levels of 600 μmol/m^2/s can be achieved. However, fluorescent bulbs have a relatively short lamp life (5000–10,000 h) concomitant with a rapid decay in spectral quality and quantity.

Use of fluorescent bulbs in the greenhouse is common. They are relatively inexpensive, readily available and easy to install. Their main liabilities are the same as described for growth chambers and rooms. In addition, lamps can cause excessive shade on benches and lamps must be 1 m or closer to plants in order to provide sufficient PPF levels.

High intensity discharge (HID)

HID lamps include high pressure mercury lamps, high pressure MH lamps, and high pressure sodium lamps. All three types can be used in growth chambers, growth rooms, or greenhouses. If light levels above about 500–1500 μmol/m^2/s are required, HID lamps must be used. HID lamps have a long lamp life (about 30,000 h for high pressure sodium lamps and 15,000 for MH lamps) along with a high efficiency of PPF output. High pressure

sodium lamps produce more PPF μmol/m²/s per unit electricity, but MH lamps have a better spectral distribution. The spectra of MH lamps are satisfactory for plant growth while high pressure sodium lamps are satisfactory only at PPF levels >700 μmol/m²/s. At lower PPF levels, the spectra may be deficient in blue for many species.

At high PPF levels in growth chambers or rooms, heat can be a problem with HID lamps and an air- or water-cooled barrier between the light units and the plants must be installed to catch and remove the heat generated. Because of heat generated at any PPF level, plants must not be closer than about 1 m from the lamps.

In the greenhouse, high pressure sodium lamps are the best choice because bulbs will last around 30,000 h and they have the best efficiency of PPF per unit electricity. The lower levels of blue light in high pressure sodium lamps compared with MH lamps are adequately supplemented by sunlight. When installing HID lamps in a greenhouse limit their installation to 200 μmol/m²/s or ballast heat and luminaire shade will be excessive.

Guidelines for supplemental greenhouse lighting

Most horticulture relies on sunlight for production. With the exception of high tunnel production for season extension, out-of-season production relies on supplemental lighting in the greenhouse to maximize productivity and crop quality (Dietzer *et al.*, 1994; Geiger and Noname, 1994). To develop a framework for lighting requirements, consider the following. Most species will grow productively with a daily light integral of 26 mol/m²/day. This level corresponds to an instantaneous irradiance of 300 μmol/m²/s for 24 h or 600 μmol/m²/s for 12 h. As a point of reference, the summer daily irradiance maximum is around 62 mol/m² in Phoenix, Arizona and in the winter the minimum irradiance is 8 mol/m² at Madison, Wisconsin. The average annual daily irradiance is about 26 mol/m² in Madison, Wisconsin and Washington, DC. At midday in the summertime, the highest solar irradiance is around 2000 μmol/m²/s.

In most greenhouse situations, a total DLI of 26 mol/m² is sufficient for most crops. This total is derived from sunlight plus supplemental irradiance. Lamps should provide a maximum of 200 μmol/m²/s, as levels greater than this add too much heat to the greenhouse and the number of luminaires required would shade plants.

Spectral comparison of horticultural light sources

Table 8.2 allows for a quick comparison of spectral quality among common horticultural light sources. All values were normalized to 100 μmol/m²/s of PAR (400–700 nm) and reflect the percentage of radiated light at a particular wavelength.

How Do Plants Measure Light?

We previously described the different meters used to measure light. Plants in a sense have their own built in light meters called photoreceptors. Photoreceptors are molecules that capture light energy and transform the light energy for utilization by the plant. The energy can be transformed to store energy, as in photosynthesis which is accomplished with the photoreceptor chlorophyll and

Table 8.2. Spectral comparison of common horticultural light sources (adapted from Dietzer, 1994).

Source	UV-B (250–350)	UV-A (350–400)	Blue (400–500)	Green (500–600)	Red (600–700)	Far-red (700–750)
Sunlight	2.88	6.21	29.16	35.20	35.64	17
Incandescent (100 W)	0	0.47	7.52	28.49	63.98	47
Cool white	0.3	1.11	24.85	52.59	22.56	1.4
Gro-Lux	0.16	3.72	24.36	20.22	50.42	1.01
Low pressure sodium	0.03	0.15	0.12	99.33	0.54	0.04
High pressure sodium	0.17	0.53	6.52	56.57	36.91	4.00
Metal halide (MH)	0.66	6.71	20.38	55.82	24.1	4.00
Cool white plus incandescent (100 W) 3:1 ratio	0.02	1.03	22.63	49.22	28.15	8.00

accessory pigments. The energy can also be transformed into a signal to elicit a physiological response. The photoreceptors responsible for this kind of light perception are phototropins, cryptochromes, and phytochrome (Smith, 1982, 1994, 2000; Cashmore *et al*., 1999; Briggs *et al*., 2001; Lin *et al*., 2001; Bouly *et al*., 2007).

While we classify the photoreceptors with specific light absorbance and physiological function, keep in mind that these photoreceptors often overlap in function. For example cryptochromes and phytochromes overlap in regulating such processes as: (i) inhibition of hypocotyl elongation; (ii) anthocyanin production; (iii) sensitivity of flowering to photoperiod; and (iv) entrance into circadian rhythms.

Phototropins

Phototropins (known as phot1 and phot2) are responsible for sensing blue (390–500 nm) and UV-A (320–390 nm) light which elicit a number of different physiological responses in plants (Briggs *et al*., 2001). These responses are generally movement based rather than a developmental response. The major response plants have to blue or UV-A light include: (i) the phototropic response (bending towards or away from a light source); (ii) chloroplast migration in leaf cells; and (iii) solar tracking of leaves of some species. Phototropins are also likely to be involved in the inhibition of stem elongation induced by blue light and blue-light-induced calcium uptake. While phot1 and phot2 are distinct and separate photoreceptors and phot2 only functions at high light intensities, there is considerable overlap in their functions. Neither are photoreversable.

Phototropins, particularly phot1, mediate phototropism, a plant's directional bending in response to light (Whippo and Hangarter, 2006; Holland *et al*., 2009). Positive phototropism is bending towards the light, as in shoot tips, while negative phototropism is bending away from the light, as in root tips. The bending response is due to unequal growth on opposite sides of the affected organ. The phototropic response is usually limited to differentiating tissue only. Mature tissue will not usually show a phototropic response. This is generally due to a loss in cell wall elasticity and a hardening of cell walls which makes them resistant to change. Hardened cell walls prevent uneven cell wall expansion which causes the bending of the organ involved.

Phototropins also mediate chloroplast migration within the cell in response to light levels. Under low light conditions, both phot1and phot2 induce chloroplast migration within the cell to minimize shading and maximize light interception. Under high light, chloroplasts are rearranged to minimize light interception to avoid photodamage. This high light response seems to be controlled exclusively by phot2. The molecular form of the molecule, phot1 or phot2, is determined by the amino acid sequence.

Phototropin molecules (either phot1 or phot2) exist as one of three forms: LOVD447, LOVL660 or LOVS390, depending on light conditions. LOVD447 is the dark form, ready to absorb blue light. The absorption of a single photon of blue light converts LOVD447 to the energized, intermediate form, LOVL660, which can absorb red light. This intermediate form rapidly decays to LOVS390 in darkness or after absorbing a second near UV photon. LOVS390 is the lit form which is responsible for signaling physiological responses.

Another interesting characteristic of phototropins is their movement within the cell in response to light signals. When LOVS390 is formed in response to blue light hitting LOVD447, the entire molecule moves within the cell. For example most phot1 (LOVD447 form) is normally associated with the plasma membrane in the dark. Once lit by blue light, some of the phot1 (now in the LOVS390 form) moves intracellularly. The actual movement of the molecule is a response to blue light. Similar movements have been observed for phot2.

Cryptochromes

Another group of blue and UV-A photoreceptors are the cryptochromes (Cashmore *et al*., 1999; Bouly *et al*., 2007). While phototropins regulate movement-based responses to blue and UV-A light, cryptochromes regulate developmental responses to blue and UV-A light. Additionally, cryptochromes interact significantly with phytochromes in these regulations of development. Cryptochromes are not reverseable photoreceptors.

There are a number of cryptochromes with those of *Arabidopsis*, CRY1 and CRY2, receiving the greatest attention for research. Cryptochromes regulate plant developmental responses to blue and UV-A light. Some developmental responses mediated by cryptochromes include: (i) hypocotyl elongation; (ii) entrainment in circadian rhythms especially those related to phytochrome-mediated

flowering responses; (iii) cotyledon expansion; (iv) anthocyanin production; (v) inhibition of stem elongation; (vi) stimulation of leaf expansion; and (vii) regulation of gene expression. CRY1 functions mainly under high light conditions while CRY2 functions mainly under low light levels. CRY2 is rapidly degraded at high intensities of blue light. In the light, most of the CRY1 is in the cytoplasm while the CRY2 is in the nucleus. CRY1 may be imported to the nucleus in the dark, but is quickly exported to the cytoplasm in the light.

CRY2 particularly interacts with phytochrome in photoperiod measurement. *Arabidopsis* is a long-day plant that flowers in response to short daily dark periods. Continuous illumination with blue or far-red light promotes flowering. Continuous illumination with red light inhibits flowering. CRY2 seems to promote flowering by interfering with the inhibition of flowering caused by an abundance of phytochrome far-red (P_{fr}) under red-light conditions and also by some unknown mechanism directly promoted by blue light.

As a seed germinates it undergoes a process called de-etiolation in response to exposure to light, blue light in particular. De-etiolation includes inhibition of stem elongation, enhanced leaf expansion, stimulation of chloroplast development and changes in gene expression. Cryptochromes trigger anion channels in the plasma membrane which results in depolarization of the membrane and a subsequent reduction in cell expansion.

Cryptochrome, at least CRY1, appears to exist in at least two interconvertable forms. Inactive CRY1 accumulates in the dark. Exposure to blue light reduces the inactive CRY1 to an active form. The activation can be inhibited with green light, and as such, green light can inhibit plant responses to blue light. This occurs in nature in plants growing under the canopy of another species. The low-growing plants are subject to light rich in green wavelengths. This helps explain why plants often elongate in response to shading.

Mystery blue and green light receptors

Responses to photoreceptor stimulation follow a very precise curve when comparing response to wavelength exposure. This curve is called an action spectrum and each known photoreceptor has a specific curve for activity. If a plant response is controlled by a particular photoreceptor, the response should closely follow that photoreceptor's action spectrum.

There are several examples of plant responses to blue light that do not seem to be under the control of any known photoreceptor. Blue-light regulation of stomatal aperture is controlled by an unknown photoreceptor. Zeaxanthin, a xanthophyll pigment, may be involved as a light receptor in stomatal function. The action spectrum driving its synthesis is similar to that regulating stomatal opening. Another 'mystery' blue-light receptor regulates leaf-base folding in *Oxalis*. The action spectrum for this phenomenon does not match any known photoreceptor.

Green light can affect hypocotyl elongation and leaflet folding in the sensitive plant (*Albizzia julibrissin*) (Folta and Maruhnich, 2007). Green light can also induce changes in mRNA transcription in plastids. Both of these responses appear to be controlled by an unknown photoreceptor.

Phytochrome

Phytochrome is the most widely studied photoreceptor in plants (Smith, 1982, 1994, 2000). It is responsible for photoperiodic responses in growth and development. Photoperiodism is the ability of a plant to measure daylength as a relative amount of light to darkness. Most photoperiodic responses are controlled by length of the dark period (nyctoperiod), not the light period. Photomorphogenesis is a plant's developmental response to night length.

There are a number of different phytochromes in plants with five different phytochromes (A, B, C, D, and E) isolated from the model plant *Arabidopsis*. It is likely that most higher plants have the same or similar phytochromes. Phytochrome is localized in the cytoplasm of the cell, the nucleus, and in plastids. Not all cells contain the same amount of phytochrome. In the epidermis, most of the phytochrome is in the guard cells of the stomata.

Phytochrome occurs in plants in two basic forms: (i) phytochrome red (P_r) which absorbs red light (660 nm); and (ii) phytochrome far-red (P_{fr}) which absorbs far-red light (730 nm). When a molecule of P_r absorbs a photon of red light, it is immediately transformed into P_{fr}. P_{fr} is very unstable and degrades slowly in the dark back to P_r. Additionally, P_{fr} is converted to P_r upon exposure to far-red light (730 nm).

The phytochrome molecule consists of a protein which binds to a chromophore, or light-absorbent molecule. The protein is encoded in nuclear DNA which is transcribed in the nucleus and translated

on ribosomes in the cytoplasm. The chromophore is manufactured in plastids. The two components are brought together to form a phytochrome molecule in the cytoplasm.

This assembled molecule of phytochrome is a molecule of P_r. When the molecule is exposed to red light, its structure is modified by the energy in the red light, and the phytochrome molecule is transformed to the P_{fr} form. In addition, the P_{fr} molecule autophosphorylates. The phytochrome is now the physiologically active P_{fr}. The amount of P_{fr} remaining after the dark period determines whether or not a photoperiodic response is observed.

Photoperiodic responses controlled by phytochrome are often classified as inductance responses or high irradiance responses (HIR) based on the photon flux density required to initiate the response and the timing of irradiance.

The inductance responses are further classified as very low fluence responses (VLFR) and low fluence responses (LFR). Both VLFR and LFR reactions can occur with only a few seconds of irradiation and the response will occur even if the seed or plant is returned to darkness. VLFR responses are mediated by phytochrome A, activated by red light, and are not reversible by exposure to far-red light. Very weak pulses of light equivalent to one to three firefly flashes are all that are required for VLFR to occur.

LFR responses are controlled by phytochrome B, regulated by red and far-red light and are reversible. A few seconds to a few minutes of light equivalent to a common flashlight are needed to induce this type of response. Many of the typical responses attributed to phytochrome control are LFR responses.

HIR responses are not reversible and are controlled by phytochromes A and B. They require prolonged high intensity irradiation and the response is in proportion to the irradiance received by the plant. If the tissue is etiolated, as in a germinating seedling, far-red and blue light are effective in mediating the response. If green tissue is involved, red light is active. HIR responses generally take minutes to hours of high fluence irradiation to occur. Two of the typical HIR responses are: (i) anthocyanin production; and (ii) inhibition of hypocotyl elongation.

A useful parameter to describe light quality, especially with respect to phytochrome-mediated responses, is to describe the ratio of red to far-red light. It is important to remember when discussing this ratio, the ratio describes the ratio of light, not the ratio of the phytochrome forms. A high R:FR light ratio (high red light) would yield a low P_r:P_{fr} ratio (high P_{fr}) while a low R:FR light ratio (high far-red light) would yield a high P_r:P_{fr} ratio (high P_r).

Daylight contains about equal amounts of red and far-red light (approximate red:far-red of 1:1.2) when the sun is more than 10° above the horizon. A small but detectable change in the red to far-red light ratio of sunlight occurs when the sun is less than 10° above the horizon (dawn and dusk). With the sun less than 10° above the horizon, sunlight has a longer path through the earth's atmosphere leading to greater light absorption and scattering. The sunlight spectrum at dawn and dusk is enriched in the blue and far-red regions, and poor in the orange-red regions. Thus, at dawn or dusk, the R:FR ratio is around 0.7–0.8.

In addition to sun angle, vegetation itself affects the relative amounts of red and far-red light. Vegetation absorbs red light but not much far-red light. Consequently the R:FR light ratio in canopies is often very low (high levels of far-red light) in the order of 0.09–0.7. The higher far-red light leads to higher levels of P_r which promotes etiolation (or conversely P_{fr} inhibits etiolation). Thus shoots will elongate more to effectively compete for available light as the canopy becomes more dense.

Plants enter the dark period with a certain P_{fr}:P_r. Any photoperiodic response will be governed by the amount of P_{fr} remaining relative to P_r at the end of the dark period. Long-day responses require a short dark period. This leads to a high P_{fr}:P_r ratio at the end of the dark cycle. Short-day responses need a long dark period leading to a low ratio of P_{fr}:P_r after the dark period.

Photoperiod, Phytochrome, and Plant Growth

True photoperiodic responses

In discussing plant developmental responses to daylength it is important to distinguish between responses attributable to the daily light period and those attributed to the daily dark period. This distinction is particularly important for long-day responses. Is the observed response due to a long period of photosynthesis or is it due to a high level of P_{fr} at the end of the dark period? The former does not imply a photoperiod response, but rather a photosynthetic response. The latter suggests a true photoperiodic response. But how can we separate the two?

The night interruption (NI) effect

A long-used method for separating photosynthetic and photoperiodic responses is called the 'night interruption (NI) technique' (Fig. 8.2). Plants are grown under three different conditions: (i) a short day (SD) (typically 8 h light with 16 h darkness); (ii) a long day (LD) (16 h light, 8 h darkness); and (iii) a photoperiodically long day (also called the NI treatment) (8 h light, 16 h dark with the dark period interrupted briefly, for as little as 1 min, in the middle with low-level red light). The plant response in question is compared among the three conditions. If the NI treatment produces a response much like the SD treatment, the response is due to photosynthesis differences between long and short days. If the NI response mimics that observed under long days the response is likely to be a true photoperiodic response. If the response is qualitatively but not quantitatively similar to long day, the response is likely to be due to both photosynthesis and photoperiod. A good example of this is the runnering response of photoperiod-sensitive strawberry (*Fragaria* × *ananassa*) cultivars. These cultivars will not produce runners under SD conditions. Under LDs, they produce runners profusely. NI treatment causes runner production, but not to the extent LD does. Clearly, the runnering response is a qualitatively true photoperiod response to short nights, but a quantitative response to length of the light period.

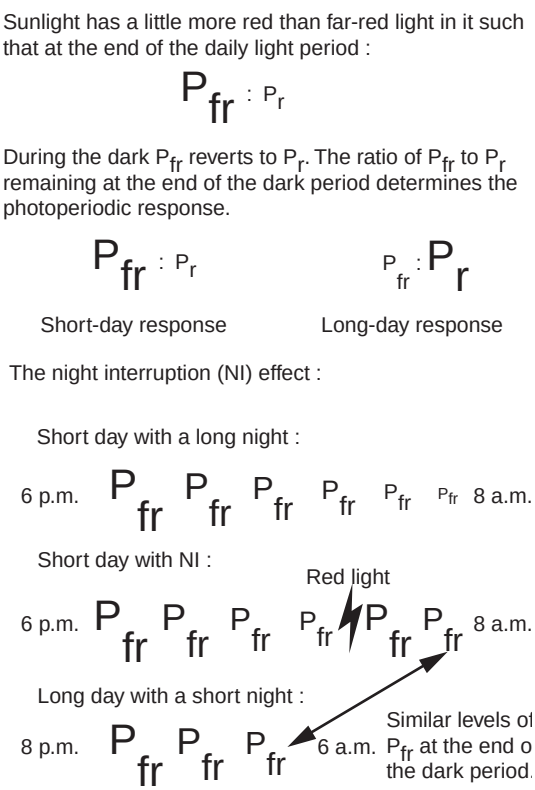

Fig. 8.2. Schematic representation of phytochrome conversions during night interruption (NI) with red light. (Lightning symbol courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science, ian.umces.edu/symbols/.)

Physiology of the NI effect

The physiological mechanism for the NI effect is simple and elegant. Under SD, there is little P_{fr} remaining at the end of the dark period. Under LD, there is abundant P_{fr} remaining at the end of the dark period. With the NI treatment, P_{fr} levels decline until the interruption treatment with red light converts all P_r back into P_{fr}. It thereby resets the P_{fr} level to what it would be at the start of the dark period. Since the LD dark period and the second half of the NI dark period are both 8 h, the level of P_{fr} at the end are similar. If the response is due to P_{fr} level (and hence a true photoperiodic response to the length of the dark period) it will be similar under LD and NI. The key to achieving the photoperiodic result anticipated with the NI treatment is using red light in the middle of the dark period. No other color and no other timing will work.

This NI treatment is useful in out-of-season production where a long-day response is desired under short-day conditions but the expense of supplemental daylength extension is not acceptable. The response desired must be a true photoperiodic response. A simple string of low wattage incandescent light bulbs will work (Fig. 8.3). A standard NI treatment in greenhouse production utilizes 15 W incandescent bulbs lit for 3 h in the middle of the dark period. The 3 h interruption is to ensure adequate conversion of P_r to P_{fr} with the incandescent bulbs.

Some responses to phytochrome

Many horticultural crops depend on photoperiodic signals for induction of a specific growth process directly related to harvest. The most notable and most widely studied process is flowering. Other processes include: (i) seed germination; (ii) de-etiolation of seedlings; (iii) tuber formation in potatoes; and

Fig. 8.3. A string of low wattage incandescent bulbs used for inducing the NI effect in fall-grown (New Jersey, USA) high tunnel strawberries (*Fragaria* × *ananassa*).

(iv) bulb formation in onions. Another photoperiodically controlled process important for propagation rather than harvest is stolon production in strawberry.

Seed germination

Seed germination is at least partially controlled by phytochrome in many species. Most species exhibit a classical P_r/P_{fr} reversibly reaction with exposure to red light and accumulation of P_{fr} leading to germination which is a LFR mode of phytochrome action.

A classic example of this is found in lettuce (*Lactuca sativa*). The photoperiodic control of germination is so strong in lettuce that germination of lettuce seed after exposure to red and far-red light is a classic laboratory experiment for many plant physiology classes. Seed germination of lettuce requires the presence of an adequate amount of P_{fr}. P_r is synthesized by plant tissues, including germinating seeds, and is converted to P_{fr} by exposure to red light. In order to germinate, lettuce seed must be exposed to red light, thus shallow coverage is essential for good stands. Many lettuce cultivars are primed before sale, and during the priming process the photoperiod requirement is met as well as any temperature treatment to break thermodormancy. Seed coverage is not such a big issue for primed lettuce seed.

The absolute requirement for red light is readily illustrated in a laboratory setting by imbibing lettuce seed in the dark and then exposing them to either red or far-red light, or cycles of red and far-red light. Only lettuce seed with a final exposure to red light will germinate. Those exposed to far-red light will not, since most of the P_{fr} is converted to P_r with the far-red light exposure.

Many seeds that are imbibed in darkness express the VLFR mode of phytochrome action. They remain dormant and are extremely sensitive to light. They will germinate only after light exposure. In seeds that can germinate in complete darkness, germination can be inhibited by exposure to prolonged far-red light, which is probably a reflection of the HIR type of the phytochrome response.

Seedling de-etiolation

As a seed germinates, the seedling is normally elongated with closed and unexpanded cotyledons that lack photosynthetic capacity. Once moved to the light, shoot growth is inhibited, cotyledons expand and the photosynthetic machinery revs up. All of this is in response to red light perception by phytochromes A and B, and blue light perception by cryptochrome and phytochrome A.

Shade avoidance

Plants have a unique ability to modify their architecture and reproductive strategy in response to shading, helping them avoid competition for light under crowded conditions. When a shade-intolerant species detects shading, it will initate internode and/or petiole elongation, increased apical dominance, retarded leaf development or accelerated flowering. All of these mechanisms are an attempt to elevate leaves to a better light environment, and to ensure seed production under marginal conditions. Many times the responses begin long before shading actually occurs due to far-red light reflecting off leaves of nearby neighbors. These physiological responses to shading are mediated through phytochrome, predominantly phytochromes B, D and E.

Flowering

Plant development usually proceeds along a fairly well-defined pathway from seed germination, through

vegetative growth, flowering, fruiting, senescence, and finally death. In some species the entire process occurs in several weeks while others live for years, cycling between vegetative growth, flowering, and fruiting many times before entering senescence leading to death. Many species rely on environmental cues for switching from one phase of growth to another, especially the transition from vegetative growth to flowering. One major environmental signal for undergoing the transition from vegetative growth to sexual reproduction is photoperiod.

There are three photoperiod types of plants with respect to flowering: (i) short-day; (ii) long-day; and (iii) day-neutral. Short-day plants begin the flowering process when days are as short or shorter than a given critical daylength. Long-day plants respond when the daylength is as long as or longer than a critical photoperiod. Day-neutral plants are not affected by daylength.

Remember, since flowering is a true photoperiodic response, the length of the dark period (skotoperiod, nyctoperiod) regulates flowering, not the daylength. The critical daylength is defined for each species through observation or research. It is often useful to determine not only the critical photoperiod but also the number of light/dark cycles need for floral induction. Generally short-day plants require fewer cycles for floral induction if days are significantly shorter than the critical photoperiod. Similarly, long-day plants require fewer cycles if the daylength is significantly longer than the critical photoperiod.

In addition, the critical photoperiod and number of required cycles can be affected by temperature. As a general rule of thumb, relatively cool temperatures can substitute for part of a short-day requirement and relatively warm temperatures can substitute for some of the long-day cycles. Generally fewer inductive cycles are needed when the photoperiodic requirement is substituted with temperature exposure. When considering flower induction in short-day plants, a minimal daylength is required for adequate photosynthesis.

While we often categorize species as long-day, short-day, or day-neutral, some species may include more than one photoperiodic type. A classic example of this phenomenon is the cultivated strawberry (*Fragaria* × *ananassa* Duch.) (Fig. 8.4). In strawberries, all three photoperiodic types are represented in standard commercial cultivars. Traditional 'Junebearing' cultivars are short-day plants, 'Everbearers' are long-day plants and 'Day-neutral' are day-neutral plants. Day-neutral cultivars are often called everbearers, however, the two are distinct cultivar types. The physiology of strawberry flowering is greatly influenced by temperature. Junebearers are most sensitive to temperature, everbearers are moderately sensitive to temperature and day-neutrals are relatively insensitive to temperature with respect to flowering.

Fig. 8.4. A strawberry (*Fragaria* × *ananassa*) plant with stolons (runners) and fruit. Both flowering and stolon production are true quantitative photoperiodic developmental responses to light.

In all photoperiodically sensitive crops there are two processes at work which result in the manifestation of the photoperiodic response. One is the circadian rhythm, regulated by cryptochromes and the other is the photoperiodic response regulated by phytochrome. The circadian rhythm maintains a 24 h cycle of light sensitivity, which must be considered in any scheme where photoperiod is to be manipulated for horticultural production. Timing of light, dark, and NI cycles is crucial for success. Phytochrome controls the sensitivity to light and dark within the 24 h. There is a periodicity to the wavelength sensitivity of many species. In other words, the plant will only respond to specific wavelengths (i.e. red or far-red) if given at the appropriate time during the 24 h cycle.

Plants can be qualitative or quantitative in their photoperiodic requirement and also absolute or facultative. In addition, there can be combinations of the two. Quantitatively photoperiodic means

that the intensity of flowering is directly related to the daylength treatment imposed on the plant. Qualitatively photoperiodic means that the intensity of flowering is not directly related to the photoperiod treatment. Absolute means that there is an absolute requirement for a specific number of photoperiodic cycles at a particular daylength for flowering. Facultative means that the photoperiodic requirement is not an absolute requirement, but rather that flowering is greatly stimulated with the prescribed treatment.

Putting this all together, plants are usually one of the following with respect to flowering: (i) absolute quantitative short-day plants; (ii) absolute qualitative short-day plants; (iii) facultative quantitative short-day plants; (iv) facultative qualitative short-day plants; (v) absolute quantitative long-day plants; (vi) absolute qualitative long-day plants; (vii) facultative quantitative long-day plants; (viii) facultative qualitative long-day plants; and (ix) day-neutral plants. Most discussions of photoperiodic type with respect to flowering are limited to long-day, short-day, or day-neutral.

Some common long-day plants include *Rudbeckia*, California poppy (*Eschscholzia californica*), radish (*Raphanus sativus*), lettuce (*L. sativa*), and spinach (*Spinacia oleracea*). Short-day plants include chrysanthemum (*Chrysanthemum* spp.), poinsettia (*Euphorbia pulcherrima*), and Christmas cactus (*Schlumbergera* spp.). Day-neutral crops include tomato (*Solanum lycopersicum*), corn (*Zea mays*), and cucumber (*Cucumis sativus*).

Besides flowering, some other responses to photoperiod that are horticulturally important include, but are not limited to, tuber formation in potato (*Solanum tuberosum* L.), bulb formation in onion (*Allium cepa*) and garlic (*Allium sativum*), and runner or stolon formation in strawberries (*Fragaria* × *ananassa*).

Circadian Movements and Rhythms

Rhythmic growth patterns in plants often follow a general 24 h cycle. These rhythmic patterns are part of the circadian rhythm present in nearly all living organisms. When a particular growth movement is truly part of the circadian rhythm, it remains even if the plant is transferred to constant darkness for several 24 h cycles in a row. A great example of such a growth pattern occurs with leaves of the common bean (*Phaseolus coccineus*) which rise and fall following a rhythmic cycle. This movement is temperature independent. Opening and closing of flowers of some species are highly regulated by the time of day, for example in morning glory (*Ipomea* spp.) and angel's trumpet (*Brugmansia* spp.).

This rhythmicity is controlled by two factors: (i) genetics; and (ii) some factor in the environment which triggers the start of the cycle. This trigger is normally light in the blue or UV-A range and is perceived by cryptochrome. The genetic component is an autonomous regulation of growth that is not affected by external stimuli. Phytochrome may also be involved in setting the length of the circadian rhythm. Far-red light tends to shorten the length of the periods and also induces a quick subsiding of the rhythm.

Photosynthesis, Plant Growth, and Yield

So far in this chapter we have looked at how light regulates growth and development utilizing the photoreceptors phototropin, cryptochrome, and phytochrome. Light is also important as it drives one of the most important biochemical processes on earth, photosynthesis. Rather than study photosynthesis from a purely biochemical basis, we will approach it from a horticultural perspective by investigating aspects of plant biology that influence photosynthesis and ultimately, plant productivity.

A quick general review of photosynthesis

Photosynthesis, simply put, is the transformation by organisms in the *Plantae* kingdom of light energy into stored chemical energy. This stored energy can now be utilized by the storing organism or by organisms that do not possess the ability to directly use light as a source of energy. This includes human beings. With few exceptions, all living organisms on earth rely on photosynthesis for survival.

Though this is a simple description of photosynthesis, it is not a simple process. Photosynthesis is a very complex process requiring specific physiological and anatomical characteristics for completion. The physiological processes of photosynthesis are usually divided into two major categories: (i) the light reactions; and (ii) the dark reactions. The light reactions only occur in the light and result in the formation of high energy compounds (temporarily storing light energy from the sun) which are utilized in the dark reactions. In addition, oxygen is released from water molecules, thereby providing

the oxygen needed for aerobic respiration. Some of this oxygen is converted to ozone in the upper part of the earth's atmosphere, protecting the earth from UV radiation. The light reactions take place on the thylakoid membrane of the chloroplast. The dark reactions can occur in the light or the dark and take the stored energy from the light reactions and transfer it to biologically stable storage compounds. The dark reactions take place in the liquid part of the chloroplast called the stroma.

The light reactions

In order to accomplish these tasks, most photosynthesizing organisms of horticultural importance have very specialized organs (leaves) containing the principal components of the photosynthetic machinery. The first step in photosynthesis is capturing light energy. This is accomplished by specialized pigments which absorb light in the 400–700 nm range. Recall this part of the spectrum is called PAR. The two major pigments that absorb light energy for photosynthesis are the chlorophylls and the carotenoids. Chlorophyll molecules are anchored to the thylakoid membrane of the chloroplast. The chlorophyll molecule contains a magnesium atom, hence its importance in soil fertility discussions. Chlorophyll absorbs blue and red light while reflecting or transmitting green light.

Carotenoids are yellow-orange accessory pigments that absorb light in the blue portion of the spectrum, where chlorophyll does not, to extend the range of the light-spectrum energy participating in photosynthesis. Accessory pigments are those pigments other than chlorophyll that participate in photosynthesis. Carotenoids also help protect chlorophyll molecules from ROS.

When a photon of light at the appropriate wavelength hits a pigment molecule, an electron in the pigment molecule absorbs the energy and becomes 'excited'. The energy of this excited molecule can be passed from one molecule to another in a carefully orchestrated manner in the thylakoid, ultimately being passed to a specialized structure in the thylakoid called a reaction center. There are two types of reaction centers: (i) photosystem I (PSI or P700); and (ii) photosystem II (PSII or P680). These reaction centers collect and concentrate the energy absorbed by pigment molecules. Energy is passed from pigments to reaction centers. In addition, energy from PSII is passed to PSI. When a molecule of chlorophyll in the reaction center is excited, it passes this energy along a series of carrier molecules. As the energy is passed along, it is used to synthesize adenosine triphosphate (ATP) and nicotinamide adenine dinucleotide phosphate (NADPH). The ATP and NADPH now store the energy from the sun until it can be used to reduce CO_2 to form sugars, where the energy can be stored in a biologically stable form for a longer time.

In this process of energy movement within the thylakoid from pigment to reaction center to either ATP or NADPH, electrons are removed from PSII. These electrons must be replaced in order for the process to continue. Water molecules are split, releasing oxygen, which diffuses out of the chloroplast and eventually exits the leaf through open stomata. The H^+ replace the electrons removed from PSII.

The dark reactions

At this point we have light energy from the sun temporarily stored in ATP and NADPH. The processes in photosynthesis that transfer this energy from ATP or NADPH to CO_2, reducing the CO_2 to a carbohydrate are called the dark reactions. Remember, the dark reactions can take place in either the light or the dark but they require the products of the light reaction (ATP and NADPH) to proceed. This conversion of CO_2 to carbohydrate is accomplished in a series of biochemical reactions called the Benson-Calvin cycle, the Calvin cycle or the reductive pentose phosphate pathway. These reactions take place in the stroma of the chloroplast.

This reduction of CO_2 to carbohydrate takes many steps, each of which is accomplished by a specific enzyme. CO_2 combines with a five carbon compound called ribulose-1,5-bisphosphate (RuBP) to form a six carbon molecule which quickly splits into two three carbon molecules of 3-phosphoglycerate. Energy from ATP or $NADPH_2$ convert the molecules of 3-phosphoglycerate into two molecules of glyceraldehyde 3-phosphate (G3P). For every three molecules of CO_2 incorporated into the Calvin cycle, one molecule of G3P is produced to be converted into a sugar for storage, or another compound needed for general metabolism. For each G3P synthesized, the cycle spends six molecules of ATP and six molecules of $NADPH_2$. The remaining G3P are used along with three more ATP to regenerate RuBP so that it can fix more CO_2. The enzyme which catalyzes the first step of the Calvin cycle is RuBP carboxylase or RuBisCo and it is the most abundant protein on earth.

With a basic knowledge of the processes occurring in photosynthesis, we can now look at a vast array of factors that affect photosynthesis and ultimately horticultural productivity.

Factors affecting photosynthesis

Leaves are the primary photosynthetic organ of a plant. Their unique structure, shape, position, and biochemistry provide them with the opportunity to absorb a maximum amount of solar radiation for manufacturing growth and storage compounds. Just how much of this solar energy is converted into biologically useable energy depends on many factors, some of which are environmental others are plant based.

Plant-based factors affecting photosynthesis

LEAF STRUCTURE, BIOCHEMISTRY, AND PHOTOSYNTHESIS Photosynthesis occurs primarily in the leaf lamina or blade. Stomata orchestrate gas exchange between the interior of the leaf and the environment and their position and number vary widely among species. In addition, the epidermis of a leaf may include a waxy cutin and/or hairs to minimize water loss. Leaf position may change via specific plant movements to maximize light interception.

Inside, leaf anatomy is an amazing array of palisade cells near the adaxial (upper) surface vertically oriented to maximize light interception subtended by a collection of spongy mesophyll cells with abundant air spaces for gas exchange. Within the spongy mesophyll are intricate networks of vascular tissue to bring water to the leaf and shuttle products of photosynthesis off to awaiting sinks.

At the cellular level, leaves are equally amazing. Within mesophyll cells are the powerhouses of photosynthesis, chloroplasts, each cell containing from 20 to 100 of them. Chloroplasts can change their position within the cell, adjusting to changing light conditions. Each individual chloroplast increases the photosynthetic area of the leaf.

Plants have four main biochemical/anatomical avenues for fixing CO_2: (i) C3; (ii) C4; (iii) C3-C4 intemediates; and (iv) crassulacean acid metabolism (CAM) photosynthesis.

Most monocots and dicots of the temperate zone have C3 photosynthesis. It is called C3 photosynthesis because the first stable product of carbon fixation is a three carbon molecule. C3 plants generally have a low water use efficiency and waste much of the energy they fix in a process called photorespiration. Photorespiration is the process where the enzyme normally fixing CO_2 instead fixes O_2 wasting much of the energy harvested in the light reactions and releasing CO_2, rather than fixing it. This is important: not only is O_2 taking the place of CO_2 in reactions with the RuBisCo enzyme, in the process it is releasing CO_2 previously fixed. As much as 30–50% of the energy stored in ATP and NADPH in the light reactions can be wasted in photorespiration. Photorespiration occurs when the concentration of CO_2 falls to 50 ppm or lower. This can occur under hot, dry conditions when stomata close to conserve water.

In photorespiration, instead of forming two three carbon G3P molecules like it does when RuBisCo fixes CO_2, only one molecule of G3P is produced and a toxic two carbon molecule called phosphoglycolate is produced. Since it is toxic, the plant must get rid of the phosphoglycolate. It does so through a series of reactions involving peroxisomes and mitochondria. First the phosphoglycolate is converted to glycolic acid, transported to the peroxisome and converted into glycine. The glycine is then transported to a mitochondiria and converted into serine and then glycerate. The glycerate is shuttled back to the chloroplast, phosphorylated and re-enters the Calvin cycle. In this process, substantial metabolic energy is used and CO_2 is lost from the plant.

Most grasses and cereals common to the tropics have C4 photosynthesis. They are generally much more efficient than C3 species because they have an anatomical/biochemical mechanism for maintaining high CO_2 levels around the RuBisCo enzyme which is only found in specialized cells surrounding vascular tissues. These specialized cells are called bundle sheath cells and this arrangement of leaf cells is called Kranz anatomy. Since RuBisCo is not present in mesophyll cells, photorespiration cannot occur. The first stable products of carbon fixation which occurs in mesophyll cells is a four carbon compound, oxaloacetate, thus they are called C4 plants. The oxaloacetate is converted into malate or aspartate, both four carbon compounds, which are then shuttled to bundle sheath cells where CO_2 is released from the four carbon compound and fixed by RuBisCo in the Calvin cycle. C4 plants use water more efficiently and are generally more productive than C3 plants.

Some species (*Flaveria, Panicum*) have Kranz anatomy but lack the C4 biochemistry. These species

are called C3-C4 intermediates. Their photosynthetic and photorespiratory pathways are identical to C3 species, and RuBisCo is found in both mesophyll and bundle sheath cells. Any CO_2 released during photorespiration is refixed via an enzyme called glycine carboxylase of bundle sheath mitochondria. Species in the C3-C4 intermediate group use water more efficiently than C3 species and are therefore more productive than C3 species.

CAM species have the biochemistry of C4 species and the anatomy of C3 species. Carbon fixation is separated in time, rather than anatomically as in C4 plants. Mespophyll cells of CAM plants do not differentiate into palisade and spongy layers, but rather, they are all spongy. They have fewer stomata than C3 or C4 plants and the stomata stay open at night to fix CO_2 to be stored as malate in the vacuole until the following day. During the day, stomata are closed to minimize water loss, malate from the vacuole is converted into phosphoenolpyruvate and CO_2 is released to be fixed by RuBisCo in the Calvin cycle. CAM plants are generally inefficient since they exhibit photorespiration and they do not use water very efficiently.

LEAF POSITION Leaf exposure to solar radiation can be greatly affected by the leaf's position in the plant canopy. Leaves at the top or exterior of the canopy generally have high levels of electron transport in the light reactions of photosynthesis and concomitantly high rates of RuBisCo activity and carbon assimilation. Leaves lower or more interior in the canopy generally have much reduced light reactions and subsequently, reduced carbon fixation in the dark reactions.

LEAF AGE Photosynthetic rates steadily decline with leaf age. In fact, leaf age is more of a factor in photosynthetic rates than light intensity. Younger leaves may not be light saturated at 1800 μmol/cm^2/s while older leaves might be nearly 90% saturated at 600 μmol/cm^2/s. Light saturation of photosynthesis occurs when increasing the light intensity will not increase the rate of photosynthesis. Some other factor of photosynthesis is limiting photosynthetic rate, in this case, leaf age.

In addition, older leaves of C4 species may exhibit photorespiration due to a diminished capacity to concentrate CO_2 in the bundle sheath cells. When chlorophyll and RuBisCo content of senescing C4 leaves reaches 50% of normal mature leaves, photorespiration can approach that in C3 plants.

Environmental factors influencing photosynthesis

Plants are immobile and as such are subjected to a wide array of environmental conditions which may enhance or hinder photosynthesis. In this section we will look at environmental factors that may have either a direct or an indirect effect on photosynthesis and plant productivity. These factors include: (i) CO_2 levels; (ii) temperature; (iii) light (and shading of leaves); (iv) water stress (drought, excess water and anaerobiosis); (v) soil salinity; (vi) gaseous pollutants; and (vii) heavy metal contamination of soil.

CO_2 CONCENTRATION

DEFICIENCY CO_2 is the basic substrate of photosynthesis. Regardless of species, low CO_2 levels lead to lower rates of photosynthesis. Some species are just much better at utilizing lower levels of CO_2 than others.

ELEVATED In general, increased CO_2 leads to increased growth and productivity of most species. The levels of RuBisCo ultimately determine the amount of photosynthesis that can occur. In general, increasing CO_2 concentration does not induce a change in RuBisCo content of leaves. The effect of CO_2 concentration on the activity of RuBisCo in leaves is not clear, with some studies indicating an increase, some a decrease, and still others no change with increased CO_2.

Increases in yield observed with elevated CO_2 may be a reflection of physical changes in leaves that often occur with elevated CO_2. These changes include an increase in leaf area and fresh weight, thicker leaves, and a greater number of palisade cells.

TEMPERATURE

HEAT An increase of 10–15°C above the normal growing temperatures (15–45°C) for a crop generally leads to a reduction in photosynthesis. In general, photosynthesis inhibition at higher temperatures is greater in C3 plants compared with C4 and CAM plants. The reduction in photosynthesis is caused by a myriad of factors including: (i) disruption of thylakoid membranes; (ii) reduction in electron transport chain activity; (iii) disruption of PSII; (iv) grana unstacking; (v) reduced O_2 evolution from photosynthesis; and (vi) denaturation and inactivation of many enzymes, especially RuBisCo and to a lesser degree phosphoenolpyruvate carboxylase (PEPCase). In addition, photosynthetic

rate is reduced more than respiration rate during heat stress leading to a general loss of carbon during heat stress.

CHILLING Chilling (exposure to temperatures between 0 and 15°C) inhibits photosynthesis particularly in tropical and subtropical species. Temperate species may also suffer chilling injury, however, the temperature range defining chilling is usually reduced to 0–5°C. The extent of the injury depends on: (i) temperature; (ii) length of exposure; (iii) developmental stage of the crop; and (iv) species and cultivar.

Inhibited photosynthesis results from changes in membrane fluidity, reduced enzyme activity, slower protoplasmic streaming, chloroplast swelling, inhibition of PSI and PSII, and increased susceptibility to photoinhibition at low temperatures. High light levels during chilling damages PSII and photoinhibition readily occurs. Photoinhibition may also occur under low light conditions at chilling temperatures. One of the major reasons for photoinhibition at chilling temperatures is a decrease in the activity of oxygen-scavenging enzymes.

In many crop species, photosynthesis at 10°C is much lower than at 20°C. Chilling injury begins to occur when membranes acquire more saturated fatty acids in direct response to exposure to low temperatures. Increased saturated fatty acid content makes membranes less fluid leading to disrupted light harvesting, electron transport and enzyme activity. RuBisCo and to a much lesser extent PEPCase activity is inhibited by chilling temperatures. Chilling causes an accumulation of starch and sucrose and sucrose may play a bioprotective role during chilling.

LIGHT Light drives photosynthesis. Increasing light levels will increase photosynthetic rates accordingly but only up to a point. When all other factors are not limiting and increasing light levels does not increase photosynthesis rates, we have reached the *light saturation point*. Many C3 species are saturated at low light levels due to photorespiration while most C4 species are never light saturated. Reducing light levels of leaves at or below the saturation point results in decreased photosynthesis. These responses to light are instantaneous. Long-term changes in light level can also influence photosynthesis. Under reduced light levels, photosynthesis is reduced due to lower stomatal conductance and reduced mesophyll area.

Shading of leaves can greatly influence their photosynthetic potential. Shade leaves generally have a lower light saturation point compared with similar leaves grown in the sun. Thus even if these leaves were to become well lit their photosynthetic rate would still be compromised. Shading itself causes a reduction in RuBisCo activity and electron transport which leads to reduced photosynthesis.

WATER STRESS

DROUGHT One of the first plant responses to water stress is stomatal closure. When a leaf becomes dehydrated due to water stress, abscisic acid (ABA) transported from roots as well as ABA formed in mesophyll cells induces stomatal closure. Stomatal closure leads to decreased internal leaf CO_2 content and a concomitant reduction of photosynthesis.

Lack of sufficient water leads to a decrease in leaf water content which causes cells to shrink. Solutes become more concentrated and the plasma membrane becomes compressed. These conditions lead to decreased cell expansion and decreased leaf size. Over time, fewer and smaller leaves are produced leading to an overall reduction in leaf area per plant (i.e. a reduction in LAI). Photosynthesis on a whole-plant basis is thereby reduced.

Permanent scars occur on membranes of the grana due to water stress to chloroplasts. In addition, many thylakoid proteins are damaged by oxidation and deleterious structural changes occur in the chlorophyll–protein complexes of the thylakoid. PSII photochemistry is only slightly altered by drought stress, even though efficiency of PSII may be reduced by drought stress. The reduced efficiency is brought on by aberrations of the electron transport system and photoinhibition rather than a direct effect on PSII. Chloroplasts of bundle sheath cells seem to be more resistant to drought stress than those of mesophyll cells.

Water stress also leads to reduced photophosphorylation and decreased ATP synthesis caused by a reduction in the synthesis of the ATP synthase which is brought on by an increase in magnesium concentration in the chloroplast. Reduced ATP content limits RuBP biosynthesis which leads to reduced photosynthesis.

Reduced photosynthesis under drought stress results from inhibited regeneration of RuBP and reduced levels and activity of RuBisCo. C4 plants require less RuBisCo than C3 plants for a similar rate of photosynthesis, thus C4 plants are less sensitive to drought stress than C3 plants.

However, PEPCase is inhibited under water stress, and ultimately drought stress reduces C4 photosynthesis too. Dehydration of chloroplasts under water stress may lead to conformational changes in these enzymes, further limiting their activity. Sulfate and phosphate anions accumulate in the dehydrated chloroplasts and can directly inhibit RuBisCo activity. Chloroplasts also become more acidic under water stress which might reduce RuBisCo activity.

Water stress often leads to elevated sucrose and reduced starch levels in leaves largely due to a remobilization of starch into sucrose under carbon limiting conditions. The activity of the two enzymes important in sucrose biosynthesis, cytosolic fructose-1,6-bisphosphatase (FBPase) and sucrose phosphate synthase, declines in water-stressed leaves. Production of assimilates is reduced by water stress, but their translocation is relatively unaffected.

EXCESS WATER AND ANAEROBIOSIS Poor soil drainage or excessive rainfall or irrigation leads to anaerobic soil conditions. Plants grown under anaerobic conditions exhibit reduced photosynthesis, slow growth, and drastically reduced yield. A shortage of oxygen in the roots is believed to stimulate ABA production in the roots which is then translocated to leaves causing stomatal closure. With closed stomata, CO_2 diffusion into the leaves is severely restricted creating a lack of substrate for photosynthesis. In addition, anaerobiosis accelerates carbohydrate breakdown, further reducing the already decreased carbon reserves within the plant.

SOIL SALINITY Salts, particularly chlorides and sulfates of sodium, magnesium, and calcium, often accumulate in the soil due to irrigation with poor quality water. This problem is often exacerbated by poor drainage and the lack of periodic flushing of salt from irrigated soils and draining away of the flushing water. Sodium chloride is a particular problem due to its very high solubility.

Excessive soil salinity induces osmotic stress, direct ion toxicity, and ionic imbalance in plants. Osmotic stress results from the increasingly negative osmotic potential of the soil solution with increasing salinity. Direct ion toxicity from sodium, chloride or sulfate ions taken up from the soil solution also occurs. Nutrient imbalances develop as unwanted ions compete with desirable nutrient ions for uptake by the roots. All three products of saline soil have deleterious effects on photosynthesis, particularly in arid and semi-arid regions where soil salinity is a particular problem.

Plants under salt stress conditions exhibit a decrease in photosynthesis primarily due to a decrease in stomatal conductance due to stomatal closure as a result of osmotic stress, sodium toxicity, and elevated ABA content of guard cells induced by osmotic stress in the roots. When stomata close, the internal CO_2 concentration declines and photosynthesis is reduced. The initial response to salt stress is the osmotically induced closing of stomata, followed after further salt exposure by ion toxicity responses.

Species vary widely in their tolerance of saline soil. Spinach (*Spinacia oleracea*) can tolerate high levels of salt toxicities with no decrease in photosynthesis even though stomatal conductance and internal CO_2 concentrations are reduced under the stress. On the other hand, rice (*Oryza sativa* L.) exhibits a marked reduction in photosynthesis with a decrease in stomatal conductance under saline conditions.

Reduced photosynthesis under saline conditions can also be attributed to alterations in chloroplast structure. Salinity induces an accumulation of sodium and chloride ions within chloroplasts leading to shrinking of the thylakoid membrane and stacking of adjacent membranes in the grana. Chlorophyll a molecules are destroyed by saline conditions thus total chlorophyll levels decline. In addition, chlorophyll tends to become loosened from its protein. Salt-tolerant species tend to avoid degradation of chlorophyll molecules under saline conditions by sequestering sodium in vacuoles and producing osmolytes such as putrescine and quaternary ammonium compounds in the chloroplasts.

Salinity increases a plant's susceptibility to photoinhibition which leads to the production of toxic singlet oxygen in chloroplasts and degradation of PSII under excessive light conditions. With a compromised PSII, photosynthesis is greatly inhibited. Electron transport is inhibited by salinity in some species but not in others.

The level and activity of RuBisCo decreases under saline conditions. The activity of PEPCase, which is important in C4 photosynthesis and a host of other plant processes including C/N partitioning in C3 leaves, guard cell carbon metabolism, seed formation and germination, and fruit ripening, rises considerably under salt stress.

Photosynthesis produces primarily sucrose and starch. Salinity induces an accumulation of starch and sucrose attributable to impaired carbohydrate in respiration. In addition, sucrose may serve an osmoprotectant role under salt stress conditions. Accumulation of photosynthetic products tends to inhibit photosynthesis.

GASEOUS POLLUTANTS When wood, coal or petrochemicals are burned for fuel, gases such as CO_2, CO, SO_2, NO, NO_2, H_2S, HF, and ethylene are released into the atmosphere. In high concentrations these pollutants reduce photosynthesis and inhibit plant growth.

Increased CO_2 in the atmosphere leads to increased absorbance of infrared light resulting in global warming. In addition, high levels of CO_2 may cause stomatal closure, resulting in decreased photosynthesis.

SO_2 enters leaves through stomata and dissolves in the cytoplasm forming bisulfite and toxic sulfite ions. NO and NO_2 are also absorbed by leaves through stomata and may directly inhibit photosynthesis.

One of the most phytotoxic agents produced through a reaction of sunlight with air containing hydrocarbons and nitrogen oxides is ozone. Ozone levels are most often high during the summer months near urban areas. Ozone is a very potent oxidizing agent, leading to a number of physiological problems. Ozone inhibits translocation of photosynthates by interfering with phloem loading. This leads to excessive starch accumulation, reduced photosynthesis, destruction of the chlorophyll molecule followed by bleaching of photosynthetic pigments. Ozone also damages the chloroplast envelope and thylakoid membranes directly, leading to further reduction in photosynthesis. The level and activity of RuBisCo decreases upon exposure to elevated ozone levels and photoinhibition is promoted even at moderate light levels. Ozone also interferes with efficient guard cell regulation of stomatal opening.

Degradation of ozone in the cytoplasm leads to the production of ROS such as the superoxide anion, singlet oxygen, and hydroxyl radicals. These ROS lead to damaged proteins and nucleic acids along with peroxidation of lipids.

Beneficial ozone, located high in our stratosphere, forms through a reaction of oxygen with UV light. Once present, the ozone layer helps filter out UV rays that would be harmful to life on earth. Humans must not return to activities which result in a depletion of the stratotospheric ozone like that which occurred with the use of chlorofluorocarbons as aerosol spray propellants. Depletion of this ozone layer allows UV-B light to reach the earth's surface in ever increasing amounts. UV-B light causes stomatal closure, reduced RuBisCo production, and it directly damages the photosynthetic machinery reducing photosynthesis in C3 and C4 plants. Reduced photosynthesis leads to not only reduced photosynthates but reduced oxygen production as well.

HEAVY METAL CONTAMINATION OF SOIL Heavy metals such as cadmium, nickel, mercury, copper, zinc, lead, and aluminum have serious negative consequences for plant productivity. The presence of one or many of these metals in the soil may lead to reduced chlorophyll content and disorganized or destroyed chloroplast structure which leads to reduced photosynthesis. Most of these metals interfere with PSII. Cadmium and lead inhibit chlorophyll and carotenoid synthesis and alters the ultrastructure of chloroplasts. Excess copper inhibits the electron transport between PSII and PSI and significantly reduces oxygen evolution from PSII. Mercury and nickel inhibit both photosystems. Manganese toxicity reduces photosynthesis through peroxidative damage to the thylakoid membrane. Cadmium and nickel lead to reduced carbon fixation through direct effects on Calvin cycle enzymes. Many heavy metals also induce the formation of free radicals leading to severe oxidative damage.

Plant productivity and photosynthesis

Our interest in photosynthesis is linked to our interest in maximizing horticultural productivity. In this section we will examine many of the components that determine and regulate productivity of horticultural crops and how they relate to photosynthesis. A good place to start our investigation is to look at the whole plant, its canopy, and subsequent crop productivity.

THE CROP CANOPY AND PRODUCTIVITY A crops canopy consists of all above-ground organs which intercept sunlight including leaves, flowers, fruit, and the stem which supports them all. Of these components of the canopy, we are mostly interested in leaves and how they affect productivity and yield.

LEAF AREA INDEX (LAI) A common measure discussed in relation to productivity is the LAI.

This is a measure of the amount of leaf area covering a unit area of ground. Crop productivity does not rely on leaf size or leaf area per plant, but rather, on this measure of leaf area per unit land. LAI is usually expressed as square meters (m^2) of leaf area per square meter (m^2) ground area. LAI is important as a measure of the potential leaf area for intercepting solar radiation per unit land area.

It is also important to know not only how much light hits the canopy, but what happens to the light of different wavelengths once it hits and penetrates the canopy. PAR (400–700 nm) hitting the canopy is either reflected (15%), absorbed (75%), or transmitted (10%). UV radiation (<380 nm) and long wave (>4000 nm) are both nearly 100% absorbed. Less than 25% of near infrared radiation (750–1200 nm) is absorbed. The rest is reflected and transmitted.

While leaf absorption characteristics are important in understanding what happens inside a canopy, how much radiation penetrates the canopy and how far it gets is the most important factor to consider with yield. A formula for calculating the solar penetration into a canopy is:

$$I = I_0 e^{-kL}$$

Where:
I = solar penetration into a canopy (the approximate percentage of the solar radiation hitting the top of the canopy that reaches the height determined by the calculation of L)
I_0 = the solar radiation at the top of the canopy in W/m^2
e = the base of the natural logarithm (approximately equal to 2.71828)
k = the extinction coefficient for a particular crop canopy
L = the cumulative LAI from the top of the canopy down to the selected height
The extinction coefficient is a measure of the amount of light lost to scattering and absorption as light passes through a medium, in this case, the plant canopy. The extinction coefficients range from 0.57 for fescue (*Festuca arundinacea*), 0.59 sugarcane (*Saccharum officinarum*), 0.76 for clover (*Trifolium repens*), 0.84 for rape (*Brassica napus*), and 0.88 for alfalfa (*Medicago sativa*). Grasses or other crops with somewhat vertically oriented leaves have extinction coefficients less than 0.6 while broadleaf species or those with more horizontally positioned leaves may have extinction coefficients over 0.7. More horizontally oriented leaf blades absorb more light, thus less of the incident light travels through to leaves below.

As an example, if the extinction coefficient is 0.5, then the solar radiation reaching the bottom of a canopy with a LAI of 3 m^2/m^2 is 22% of the light level hitting the top of the canopy. If the LAI is higher, say 5 m^2/m^2, then that level drops to 8.5%. Higher LAIs result in reduced light penetration into the canopy. While it is good to have a high LAI for productivity, LAIs that are too high can be detrimental to productivity.

Some of the incident radiation is re-reflected, generally in the range from 15 to 25%. Vertically oriented narrow leaves reflect less while horizontal leaves reflect more radiation. Sun angle is also a factor. When the sun is closer to the horizon, reflection increases.

When considering LAI, it is important to understand that it changes during the growing season. With annual crops and deciduous perennials, LAI starts out at or near 0 m^2/m^2 in the spring. Depending on growth habit and planting density, this value steadily increases to its maximum then begins to decline as senescence sets in. When the LAI reaches about 3 m^2/m^2, nearly all solar radiation is absorbed by the leaves. In most crops, maintenance of a LAI near 3 m^2/m^2 is desired for maximum production. Even though some leaves are lost during the growing season to pests or natural senescence, newly emerging leaves generally replace the lost ones. While leaf senescence is undesirable for much of a plant's growth, crops which store large amounts of protein often rely on leaf senescence for the translocation of the protein from the leaf to the storage organ.

SOLAR ENERGY AND PRODUCTIVITY A high LAI does not necessarily lead to high yield. Leaves must use the solar radiation they receive efficiently and convert that energy into usable biological energy. The efficiency of solar radiation use by leaves has not really changed over the last 100 years, even though yields have increased dramatically. The yield increases observed are mostly due to increases in dry matter allocation within crop plants to the harvested portion of the plant. This is often measured in harvest index (HI) which represents the yield of harvested commodity per unit total plant biomass, both usually expressed as dry weight. In a very general sense, the HI has increased from about 0.3 to 0.6 in the last 100 years. Further increase in the HI is limited since a certain portion of a plant's

biomass is required for activities other than existing as the harvested commodity. In other words, a wheat plant cannot produce only wheat kernels; it must also have roots, stems, and leaves to produce the grain. Further enhancements to yield will probably come from increases in solar use efficiency which would allow higher plant densities without a concomitant reduction in production per plant.

Solar energy efficiency of leaves considers that for every 1 mol of CO_2 fixed into plant biomass, 8–10 mol of PAR light quanta are needed. This is approximately a 20% conversion ratio or energy efficiency. The global solar efficiency looking at total incoming radiation and total global biomass produced is around 0.1% total or 0.2% PAR. Most crops have solar efficiencies of about 0.5–3%. This corresponds to about 1–3 g dry matter/MJ PAR received. Theoretical estimates of solar efficiencies suggest that it could be increased to 4–6 g dry matter/MJ PAR. Such an increase would probably be achieved through genetics and to a lesser degree by modified production practices.

Assimilate production efficiency is higher under lower light levels and decreases as light levels increase. More efficient use of incident radiation comes from a well-designed canopy, as in many pruned and trained orchards and vineyards. The total light hitting the plant is more evenly distributed among all the leaves. In order to achieve this optimum light distribution among leaves, a much larger LAI is needed.

To more fully understand this idea, consider several different canopy arrangements. In a canopy where leaf orientation is at 90°, all leaves would intercept direct radiation, their rate of photosynthesis would be high, but their solar use efficiency would be relatively low because of the high light irradiance. If leaves in another canopy were oriented at a 20° from vertical their rate of photosynthesis would be low, but their solar efficiency would be relatively high, due to the lower irradiance.

In an ideal situation, leaves should be neither vertically nor horizontally oriented, but rather, be oriented at different angles at different levels of the canopy (Fig. 8.5). Leaves high in the canopy should be oriented more vertically while a more horizontal component should occur as one descends the canopy height. This arrangement produces moderate rates of photosynthesis with moderate efficiencies in all leaves of the canopy.

The most desirable situation for an annual crop would be one where the first leaves to emerge would be primarily horizontally oriented to cover the ground area quickly. As the plants grew, leaves would take on a more vertical orientation to achieve the desired distribution. While production methods for the most part cannot initiate such growth, plant breeders can select for plants exhibiting this trait or any tendency towards it. Many modern cereal cultivars have nearly vertical leaves, allowing LAIs of close to 6 m^2/m^2. Nearly all leaves, sheaths, and internodes contribute to assimilate production, since they are all moderately irradiated. Cereal crops also have the advantage of producing tillers for filling in space rapidly leading to high LAIs as compared with higher density seeding which would cost more to implement.

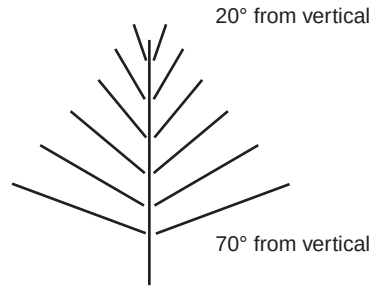

Fig. 8.5. Leaf orientation should transition from more vertical higher in the canopy to more horizontal lower in the canopy for optimum productivity.

Excessively high LAIs are not desirable since on days of low irradiance, lower leaves would respire more carbon than they fix, resulting in a net carbon loss.

SOURCES, SINKS, AND PHOTOSYNTHESIS The first product of carbon fixation in the leaf, triose phosphate, can be converted into starch in the chloroplast or shuttled to the cytoplasm to form sucrose. The formation, translocation, and storage of carbohydrates is an important topic of horticultural physiology since we rely on many crops for sucrose and starch for food or feed. The partitioning of carbohydrate into starch (immobile) or sucrose (mobile) occurs not only at the cellular level, but at the whole plant level as well. Organs of active photosynthesis, mainly leaves but sometimes stems and fruit, are called 'sources' while recipients of translocated photosynthates are called 'sinks'. How efficient a plant is with respect to carbon partitioning among sources and sinks often determines crop productivity.

Metabolism of starch in the chloroplast is dynamic. Up to 30% of the CO_2 fixed by a plant is incorporated into starch during the day and accumulates as granules in the chloroplast. The cytoplasm is not involved in starch synthesis. At night, starch is decomposed in the chloroplast into triose phosphates and exported to the cytoplasm where sucrose is synthesized and loaded into the phloem for translocation to other plant tissues (sinks) for metabolism or conversion back into starch for storage.

The carbon fixed in photosynthesis must be allocated among:

- sucrose for translocation;
- starch for storage; and
- carbohydrates for metabolism.

Some of the factors that regulate this process include: (i) rate of assimilate translocation; (ii) respiratory needs; (iii) use of carbon in other biosynthetic pathways; (iv) variations in photosynthetic rates; and (v) nutrient availability to the plant which regulates general plant growth and carbon needs. Changing growth rates in different parts of the plants cause fluctuating demands for skeletal carbon and energy. Different stages of tissue growth also cause differences in both assimilate supply and demand. Starch formation is highly dependent on photosynthesis: high rates of photosynthesis translate into high rates of starch formation. On the other hand, sucrose synthesis is somewhat independent of photosynthetic rates. Sucrose synthesis is fairly constant throughout the diurnal cycle. The source of substrates change from newly fixed triose phosphates in the light to those derived from degraded starch in the dark.

Both starch and sucrose syntheses are subjected to endogenous rhythms in plants. When plants are moved from normal growing conditions to continuous lighting, the accumulation of starch shows a remarkable decrease as the plant enters the time of day near the end of its normal light period, even though it was under continuous lighting. In addition the photosynthetic rate slowly declines as a plant enters the time of its normal dark period even though it was still illuminated.

Part of the photoassimilated carbon remains in the photosynthetic tissue and is utilized to satisfy the many biosynthetic reactions occurring within the leaf cell. In particular, much of the carbon flows into the respiratory metabolism. Respiration plays an important function in green cells, even under light conditions. For instance, routing carbon to the tricarboxylic acid cycle provides carbon skeletons for amino acid biosynthesis.

The general mechanism for sucrose movement from the source to the sink is the pressure flow or mass flow mechanism. Sucrose can move from the mesophyll cells to the phloem either symplastically through plasmodesmata or apoplastically via active phloem loading into sieve cells or through a combination of the two routes. There is extensive evidence supporting a mostly apoplastic mechanism for phloem loading via an ATP-driven transporter which concomitantly pumps H^+ into the apoplast and sucrose into the sieve cell.

Sucrose unloading at the sink may be apoplastic in tissues where plasmodesmata are not fully formed and functional such as embryos or endosperm. In other tissues, sucrose unloading may be entirely symplastic, driven by a steep sucrose concentration gradient from the sieve cell to an awaiting sink cell. The relatively low level of sucrose in the sink cell is maintained by the conversion of sucrose to starch or storage of sucrose in the vacuole.

Once sucrose arrives at the cytoplasm of sink cells, it may undergo any of a number of transformations depending on what type of sink tissue is involved. It may be converted to and stored as starch or fructans in the vacuole if the tissue involved is storage tissue such as roots, fruits, tubers, or seeds. It may also be used for energy or used to supply carbon for different biosynthetic pathways, particularly in growing tissue such as embryos or non-photosynthesizing shoots. In many sink tissues, sucrose may enter multiple pathways, some providing energy and growth components and some being stored.

When sucrose reaches a sink, it is hydrolyzed to glucose and fructose, which are then phosphorylated. These hexose phosphates, primarily glucose phosphate, then move into the amyloplast to be converted into starch. In some storage tissues, particularly potato tubers and the endosperm of cereals, amyloplast-bound starch may comprise up to 80% of the dry weight of the tissue.

One factor limiting improvement of yield in crop plants is not the rate of photosynthesis but rather the translocation of sucrose from source to sink. Translocation rate is governed by mass flow and maxes out at a rate that is species specific. The amount of translocated photoassimilate is directly related to the amount of phloem available. Improving yield may require increasing the amount of phloem in plants as well as improvements to photosynthetic efficiency.