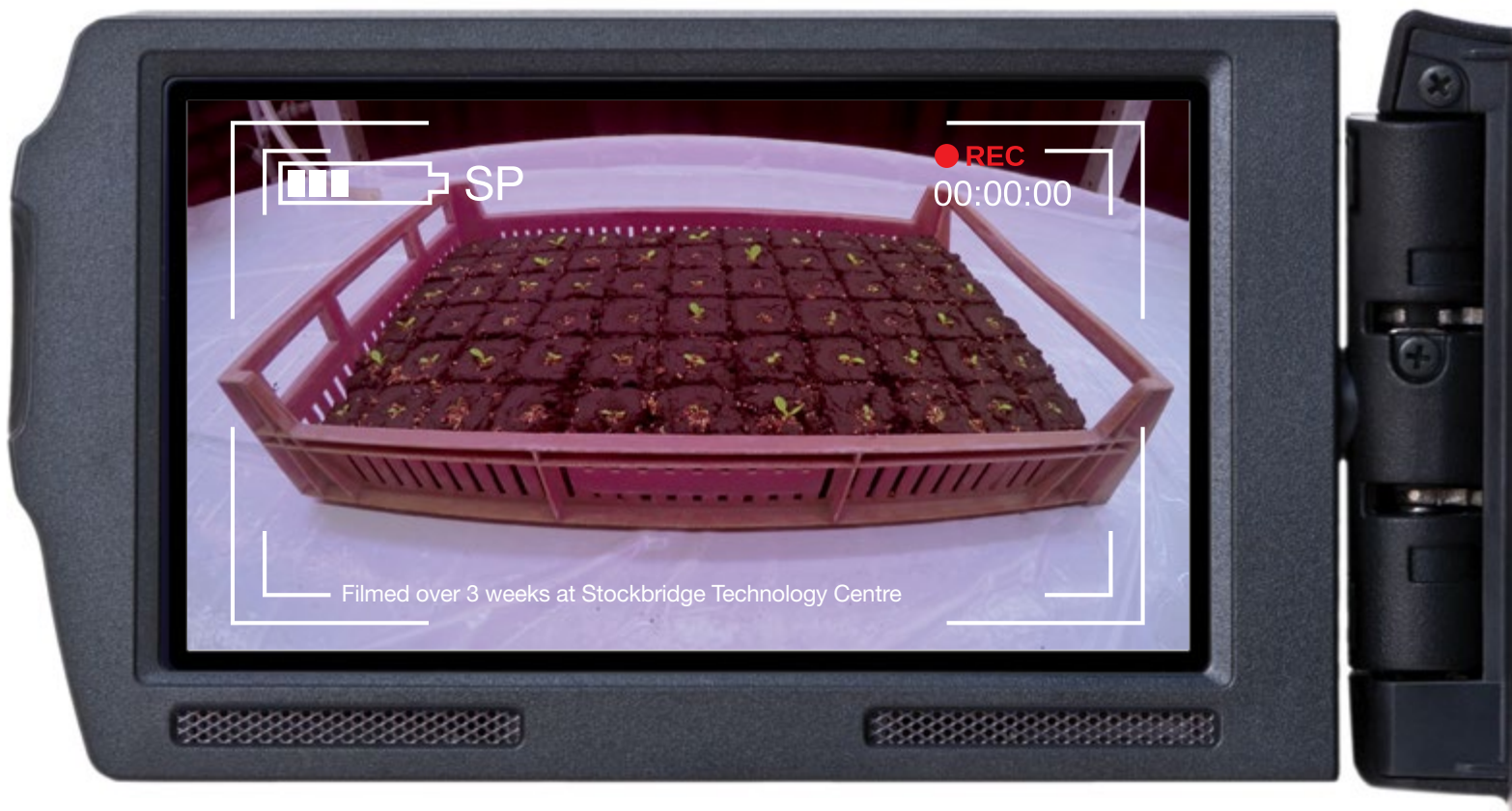


AHDB Fellowship CP 085
Dr Phillip Davis, Stockbridge Technology Centre

Lighting: The principles





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GLOSSARY

Cryptochrome

A photoreceptor that is sensitive to blue and UVA light.

Daily light integral (DLI)

A value of the total amount of light received over a 24-hour period. The values can be calculated using measurements made in different units. If irradiance (Wm^{-2}) values are used, the DLI has units of J m^{-2} . If photon-irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$) values are used, the DLI has units of mol m^{-2} .

Irradiance

A measurement of the amount of light energy incident on a surface, which has units of Wm^{-2} .

Photon irradiance

A measurement of the number of photons incident on a surface, which has units of $\mu\text{mol m}^{-2} \text{s}^{-1}$.

Photoreceptor

Light-sensitive proteins that initiate light responses.

PAR

Photosynthetically active radiation (PAR) is light with wavelengths in the range of 400–700nm that can be used by plants for the process of photosynthesis.

Photomorphogenesis

The processes that causes plant morphology and pigmentation to change following exposure to light. These processes are activated and controlled by several photoreceptors.

Phototropin

A photoreceptor that detects blue and UVA light.

Phytochrome

A photoreceptor that can sense the red:far-red ratio of light.

Rubisco

The enzyme that fixes CO_2 during the process of photosynthesis.

UVR8

A photoreceptor that is able to detect UVB light.





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SECTION ONE

Light and lighting

1.1 What is light?

Electromagnetic (EM) radiation is a type of radiant energy that moves through space in the form of a wave. The energy associated with EM radiation is contained within small packages called photons. The amount of energy contained within a photon is proportional to its wavelength, with the wavelength decreasing in size as the amount of energy it contains increases. The term 'light' is generally described as the region of the EM spectrum that is visible to the human eye, but for the purposes of this report we will use the term 'light' to refer to regions of the EM spectrum that can be perceived by plants.

1.2 The natural light environment and its impact on plant light responses

The main source of light is the Sun, which produces photons with a wide range of wavelengths (Figure 1). The atmosphere filters out some wavelengths of light and the majority of the photons reaching the Earth's surface have wavelengths between 150nm and 4000nm (Eltbaakh *et al*, 2011). Photons are classified based on their wavelengths: UVC = 100–280nm, UVB = 280–315nm, UVA = 315–400, visible or photosynthetically active radiation (PAR) 400–700nm, far-red = 700–800nm and infrared 800v4000nm. Within the visible range of the spectrum, the wavebands can be further divided into colours. For the purposes of this report we will use three colour bands: blue, 400–500nm; green, 500–600nm; and red, 600–700nm. The biological importance of each of these wavebands will be described in section two.

The amount of light available for plants is highly variable across the globe and through the seasons. The two most obvious variables in natural light that affect plants are day length and amount of light received. Close to the equator, the day length and amount of light received is relatively constant throughout the year, with weather patterns providing the main factor affecting light availability. With increasing latitude (both Northward and Southward) day length and light intensity become increasingly variable throughout the year. In North Yorkshire, day length varies from 7.3 hours long at the winter solstice to 16.8 hours at the summer solstice, a variation of 9.5 hours. The total amount of light available also varies considerably through the seasons (Figure 2). At Stockbridge Technology Centre, Cawood, North Yorkshire, the mean daily light integral for December measured over a seven-year period was 3.6 mol d⁻¹ (185 J cm⁻¹ d⁻¹) and the mean value for July was ten times greater, at 30 mol d⁻¹ (1540 J cm⁻¹ d⁻¹). Location within the environment can also have a significant influence on the light environment. In the northern hemisphere, south-facing slopes receive more light than north-facing slopes.

There are also more subtle changes to light spectrum that occur though the day and seasons. At low solar elevations

the light must pass through a larger volume of the atmosphere before it reaches the earth's surface. This causes changes in the spectrum as the atmosphere filters proportionally more of the shorter wavelengths of light: the atmosphere filters more UV than blue and more blue than green or red light (Eltbaakh *et al*, 2011; Paul & Gwynn-Jones 2003). The amount of UVB radiation is particularly variable through the seasons and this also varies with altitude. The amount of UVB is much higher at high altitudes (mountain tops) as there is less atmosphere to filter out these harmful rays. Changes in spectral composition with season and location are likely to influence plant light responses and the light quality encountered at dusk (end of day) can have large effects on stem extension (Kasperbauer & Peaslee, 1973; Blom *et al*, 1995; Chia & Kubota, 2010; Yang *et al*, 2012).

Especially large changes in spectral composition of light are observed within plant canopies and these have large influences on plant light responses. Within a plant canopy, the light intensity decreases rapidly with depth as the leaves absorb, reflect, and scatter the light. Leaves preferentially absorb red and blue light. This causes a dramatic change in the spectrum of light with increasing canopy depth, with green and far-red light forming a much greater proportion of the light as depth increases (Figure 3). The red:far-red ratio of sunlight is 1.2, but below a forest canopy the ratio is much lower, at ~0.4 (Turnbull & Yates 1993).

1.3 The measurement of light

When any parameter is measured it is important to report the values in units that are relevant to the final use of that data. For example, if the price of a glasshouse is quoted on price per square metre, it is impractical to measure the desired footprint of the glasshouse in feet and inches. It is possible to make conversions between different units, but it should be avoided where possible. For a simple metric such as distance, it is relatively easy to convert between the different units; however, conversions between units with respect to light are more complex and inaccurate conversions can lead to significant errors. In this section, we will briefly review the different units used to measure light and examine why some units should be avoided for horticultural purposes.

1.3.1 Photometric light measurement – lumens and lux

The majority of artificial lighting systems have been developed with human vision as the main focus. As a consequence, most technical data is reported in photometric terms that characterise light with reference to the human eye. Luminous flux (also called luminous power) has units of lumens and defines the total output of a lamp (light emitted in all directions) that could be detected by the human eye. The energy efficiency of lamps is often reported as the 'luminous efficacy',

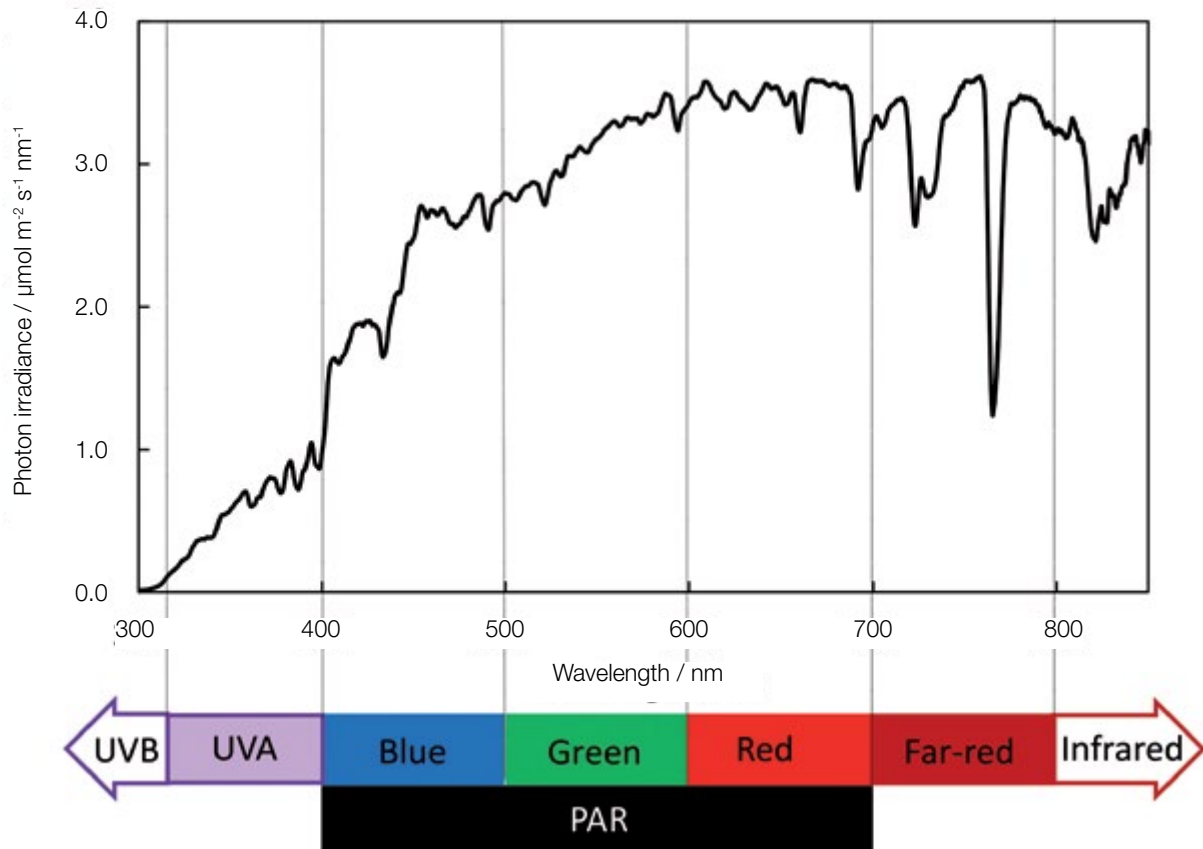


Figure 1. Spectra of the Sun measured at Stockbridge Technology Centre, Cawood, North Yorkshire on 28 April 2014

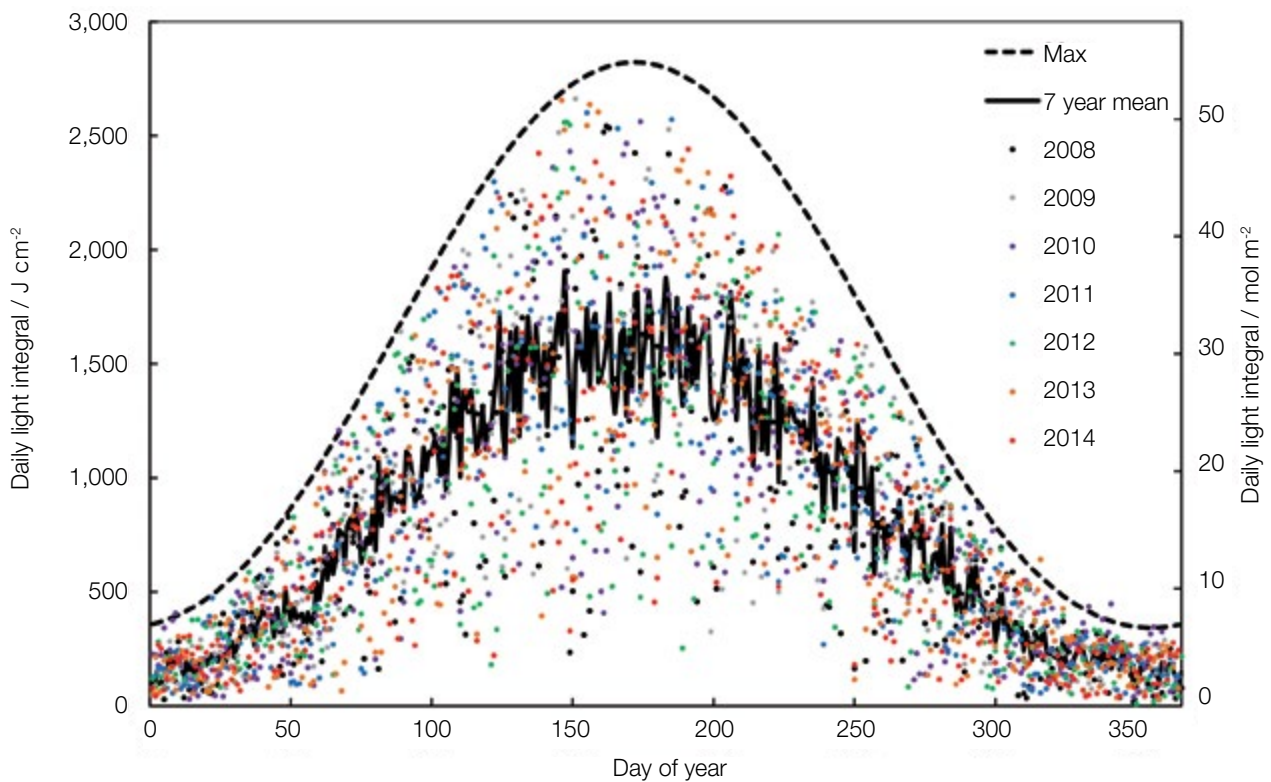


Figure 2. The measured daily light integral (DLI) over a seven-year period at Stockbridge Technology Centre. Individual points indicate the value measured on each day. The solid line indicates the mean value over the seven years. The dashed line shows the calculated maximum daily value DLI assuming no cloud cover

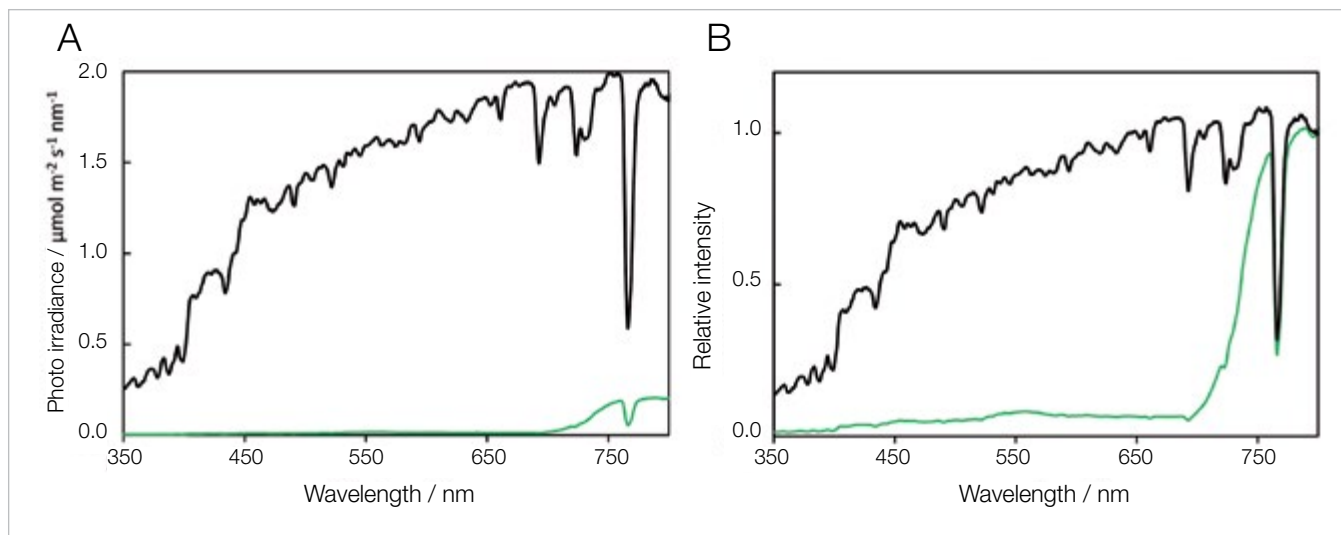


Figure 3. A) Measured spectrum in full sunlight (black line) and in deep shade below a tree canopy (green line) demonstrating the large decrease in light intensity. B) Same spectra as in A but normalised to a wavelength of 800nm to demonstrate the large change in spectral composition

which has units of lumens per Watt of electrical input (lm/W). Lumens are useful for defining the total output and efficiency of lamps but for most practical purposes it is the amount of light reaching a surface (eg, the light intensity received at the top of a plant canopy) that is of greater relevance as this will account for the design and efficiency of the lamp reflectors as well as the number and spacing of lamps installed. Illuminance is a measure of the light incident on a surface. Illuminance is measured using lux (lx) units, which are defined as the number of lumens per meter squared ($\text{lux} = \text{lm m}^{-2}$). Instruments that measure lumens or lux are designed to have the same sensitivity to different regions of the electromagnetic spectrum as the human eye (Figure 3), which is most sensitive to green light (~550nm). Lux meters are widely used in horticulture to measure the intensity of high-pressure sodium lights. Good quality lux meters will provide an accurate assessment of the light output of HPS lamps; however, because these measurements are designed to describe the light in reference to the human eye, the measurements cannot be used to make any direct interpretation of how the light will influence plants. Lux meters provide accurate assessments of HPS lamps because their emission spectra are similar to the response spectra of the lux sensors. For many of the horticultural LED lamps, especially those with predominantly red and blue LEDs, the emission spectra falls in regions where lux meters are relatively insensitive. The result of this is that lux meters provide very low estimates of red and blue LED-based lighting systems even if the 'actual' intensity is high. Photometric measurements of light should be avoided in horticulture, where possible, and should certainly not be used to measure red and blue LEDs.

1.3.2 Radiometric light measurement – Watts per metre squared or Joules per metre squared

While artificial light sources are often defined in photometric terms (lumens and lux), sunlight is more commonly measured in radiometric terms that measure the amount of energy contained within light. The radiometric equivalent of illuminance is irradiance (sometimes called radiant flux density), and this provides a measure of how much light energy is incident on a surface in units of Watts per meter squared (W m^{-2}) or, sometimes, Watts per centimetre squared (W cm^{-2}). While the spectral sensitivity

of photometric sensors is defined by the spectral response of the eye, not all radiometric sensors measure over the same wavelengths. Light sensors that measure the photosynthetically active radiation (PAR: 400–700nm) waveband are most suitable for horticultural purposes. However, many commonly used sensors measure over a wider waveband, so care must be taken when comparing measurements made with different sensors or when making conversions between measurement units.

While measurements of irradiance can provide good estimates of the light energy supplied to plants, there are some challenges associated with comparing light sources that have different light spectra. This is because the energy contained within a photon decreases as the wavelength increases (Figure 4). For example, a photon with a wavelength of 400nm (blue) contains 75% more energy than a photon with a wavelength of 700nm (red). This means that light from a red LED could contain less radiant energy than light from a blue LED, even though the red light may contain more photons.

1.3.3 Photon counts – Moles

The most suitable light measurement for use with plants is the PAR photon irradiance (also termed the photosynthetic photon flux density, PPF). PAR photon irradiance provides a measurement of the number of photons that are incident on a surface and has units of micromoles per metre squared per second ($\mu\text{mol m}^{-2} \text{s}^{-1}$, NOTE: the SI symbol for micro is 'µ' (10^{-6}) not 'm' which stands for milli (10^{-3})). Photon irradiance is more appropriate than irradiance or illuminance because photosynthesis uses light on a photon-by-photon basis and is largely independent of the energy contained within a photon. Once absorbed by chlorophyll, a red photon can drive the same amount of photosynthesis as a blue photon despite its lower energy level. Therefore, the effect that different light sources have on plants can be compared more easily when PAR photon irradiance is used. In addition, because photosynthesis is measured in similar units ($\mu\text{mol} [\text{CO}_2] \text{m}^{-2} \text{s}^{-1}$), use of PAR photon irradiance allows direct comparisons between the amount of light and the amount of photosynthesis to be made.

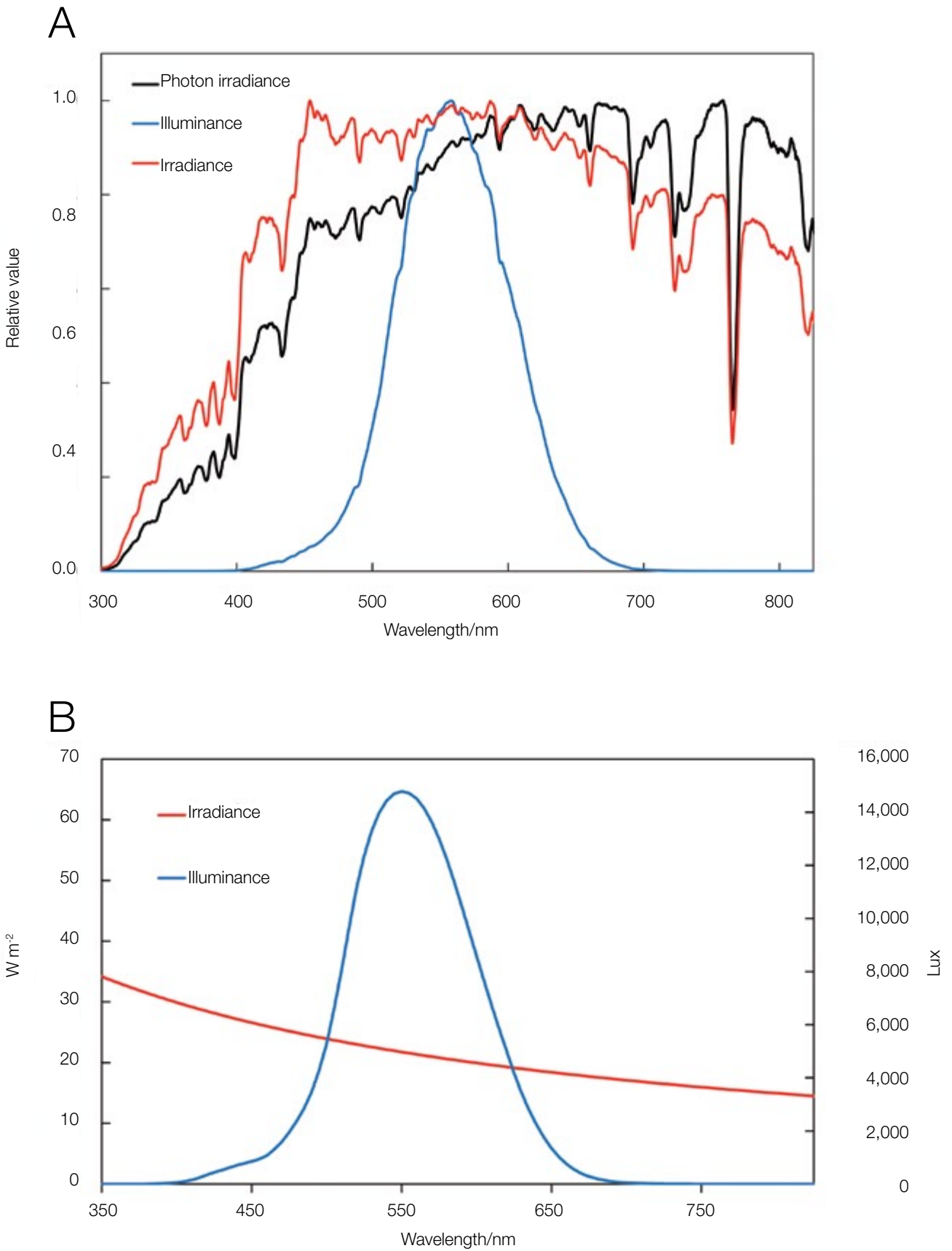


Figure 4. A) The relative spectrum of sunlight when expressed in terms of three relevant measurement units: illuminance = Lux, irradiance = Wm^{-2} , Photon irradiance = $\mu mol m^{-2} s^{-1}$. All spectra are normalised to the maximum value over the wavelengths presented. B) Example of how Irradiance (Wm^{-2}) and Illuminance (Lux) vary with wavelength for monochromatic light when the photon irradiance is a constant $100 \mu mol m^{-2} s^{-1}$ across the spectrum

1.3.4 Daily light integrals (DLI)

The DLI is a measure of the total amount of light received over a 24-hour period. Plant lighting requirements are often defined in terms of daily light integral (DLI), and these vary widely between species and at different growth stages. For example, tomato crops require 30–35 mol m⁻² d⁻¹ to achieve peak production (Spaargaren, 2001), whereas 13 mol m⁻² d⁻¹ is sufficient for vegetable seedling production (Fan *et al*, 2013). These values are provided as guidance and often function as minimum values for good quality plants that limit shade avoidance responses or light overexposure responses. In general, plant growth increases as more light is provided. In previous experiments (Faust *et al*, 2005), increasing the DLI integral from 5–43 mol m⁻² d⁻¹ resulted in an increase in plant biomass in several bedding plant species such as Petunia, Salvia, Vinca and Zinnia. Growth increases were seen in begonia and impatiens when DLI increased from 5–25 mol m⁻² d⁻¹. In addition, higher DLIs also increased flowering rates (Faust *et al*, 2005). Most DLI estimates have been determined in natural light environments. With spectral modification, it may be possible to produce good quality plants using lower DLI, and this may help to either reduce production periods or extend growing seasons.

The DLI is calculated by summing all the measured values made throughout the day and multiplying this value by the number of seconds between each measurement. If light has been measured as irradiance with units of Wm⁻², then the DLI will be a fluence value (also called radiant exposure) with units of joules per meter squared (J m⁻²). If the measurements are made as photon irradiance (μmol m⁻² s⁻¹), the DLI value will be a photon fluence and will have units of moles per metre squared (mol m⁻²).

1.4 Conversions between different measurement units

While it is recommended that light is measured in terms of photon irradiance (μmol m⁻² s⁻¹), there are many cases where this is not possible. For example, data was historically recorded as irradiance (Wm⁻²) and many lamp manufacturers only provide measurements in lumens. In these cases, it is useful to be able to convert between the different units. In order to calculate conversion factors the spectrum of the light must be known. The 'Principles of Radiation Measurement' publication provided by Li-Cor gives a detailed description of how to convert between units as well as other relevant information regarding light measurements. A series of conversion factors for a range of different light sources is provided in Table 1. All values are calculated over the PAR range (400–700nm) using spectra measured with an Ocean optics Jaz spectroradiometer. Before attempting to use any of the conversion factors provided, the specifications of the sensor used must be double-checked to ensure that the spectral ranges are appropriate for the conversion factors provided. The values provided will work for all lux meters. These conversion factors cannot be used directly for measurements of sunlight made with global radiation sensors that measure in Wm⁻² over the full spectrum (200–4,000nm). However, it is possible to convert these measurements to W[PAR]m⁻² by multiplying by 0.42 (the proportion of the solar spectrum within the PAR range) before using the conversion factors. If you desire to convert measurements from lux or μmol m⁻² s⁻¹ back to Wm⁻² global radiation, first convert the values

to W[PAR] m⁻² and then multiply the value by 2.381 to convert W[PAR]m⁻² to W[global radiation]m⁻². Note that some values are reported as W cm⁻² or J cm⁻², and these values must be multiplied by 10,000 to convert them to W m⁻² or J m⁻².

1.5 Assessing light quality

The red:far-red ratio (R:FR ratio) of light is one of the most regularly discussed parameters of light quality, with much research having focused on spectral filters that can modify this ratio (Rajapakse *et al*, 1992) or the effect of different types of light for night break lighting (Adams *et al*, 2012). Different calculations have been used to determine the red:far-red ratio: Smith (1982) used R = 655–665 nm and FR = 725–735 nm; Kasperbauer *et al*, (1963) used R = 640–650 nm and FR = 725–735 nm; Mortensen and Stromme (1987) used R = 600–700 nm and FR = 700–800 nm. For sunlight, where the spectrum of light is relatively flat across the red and far-red region, all these calculations give similar estimates of the R:FR ratio. However, with LEDs, where the spectrum is 'peaky', the use of different calculations could provide very different results depending on the peak emissions of the LED under examination. For LEDs where different models/makes are expected to have slightly different emission peaks, the method of Mortensen and Stromme (1987) is likely to provide the most stable and best measurement. It should be noted that the red:far-red ratio values differ slightly when calculations are made using spectra measured in units of Wm⁻² and when spectra are measured using μmol m⁻² s⁻¹. All values reported here will use values determined with units of μmol m⁻² s⁻¹.

1.6 Overview of light technologies

1.6.1 Incandescent and halogen bulbs

Incandescent bulbs function by heating a wire filament (made from tungsten) until it glows. The filament is protected from damage and oxidation by enclosure in a glass bulb filled with inert gas. These lamps are the oldest and least energy efficient type of electric light and are gradually being phased out in Europe as regulators push for greater energy use efficiency. Halogen bulbs differ from incandescent bulbs in that they contain a halogen gas (iodine or bromine) that increases the life of the tungsten filament and can allow a higher operation temperature. One reason for the low energy efficiency of these types of bulb is that much of the light they emit is beyond the visible (low luminous efficiency) and PAR spectrums. These lamps produce a relatively large amount of far-red light (red:far-red ratio of ~ 0.6) and it is this spectral property that has made them of use to the horticulture industry for night break lighting.

1.6.2 Fluorescent tubes

Fluorescent tubes generate light by passing an electric current through a gas-filled glass tube containing mercury vapour. The electric current excites the mercury vapour which then emits short wave ultraviolet light. The UV light is absorbed by the phosphor coating on the inside of the glass tube. The phosphor coating then fluoresces to produce the required light. The colour of the light emitted can be altered by changing the mixture of phosphors contained within the lamps or by adding filters to the glass. The luminous efficacy of fluorescent tubes

Table 1. Conversion factors for switching between measurement units for different light sources. ALL VALUES IN THIS TABLE ARE CALCULATED FOR PAR WAVELENGTHS (400–700nm). Multiply the measured value by the relevant conversation factor for the light source of interest.

Instantaneous measurements						
Measured units ->	Lux		W [PAR] m ⁻²		μmol [PAR] m ⁻² s ⁻¹	
Desired units ->	μmol [PAR] m ⁻² s ⁻¹	W [PAR] m ⁻²	Lux	μmol [PAR] m ⁻² s ⁻¹	Lux	W [PAR] m ⁻²
Daily light integrals						
Measured units ->	-		MJ [PAR] m ⁻²		mol [PAR] m ⁻²	
Desired units ->	-		-	μmol [PAR] m ⁻²	-	MJ [PAR] m ⁻²
Conventional lamps						
Sunlight (April @ Stockbridge Technology Centre)	0.0178	0.0038	260.2	4.62	56.3	0.22
HPS	0.0139	0.0028	360.0	4.99	72.2	0.20
Fluorescent	0.0141	0.0032	316.7	4.48	70.7	0.22
Incandescent	0.0211	0.0041	242.5	5.12	47.4	0.20
Individual LEDs						
Far-red (735nm)						
Red (660nm)	0.1204	0.0217	46.0	5.54	8.3	0.18
Green (550ishnm)						
Blue (457nm)	0.0769	0.0200	49.9	3.84	13.0	0.26
Commercial LEDs – Predominantly red and blue LEDs						
Philips Lo blue top light	0.098	0.018	54.6	5.36	10.2	0.19
Philips MB + white top light	0.060	0.012	85.7	5.10	16.7	0.20
Fionia FL300	0.091	0.017	57.9	5.29	11.0	0.189
Commercial LEDs – Predominantly white LEDs						
Philips RW production module	0.0320	0.0062	160.0	5.13	31.2	0.20
Solidlight CWW	0.0169	0.0037	268.3	4.52	59.3	0.22
Solidlight DPM	0.0161	0.0034	291.3	4.67	62.3	0.21
Solidlight DPA	0.0211	0.0045	221.9	4.69	47.3	0.21
Valoya NS2	0.0155	0.0033	298.9	4.62	64.7	0.22
Valoya AP673	0.0214	0.0043	231.8	4.95	46.8	0.20
Commercial LEDs – Multicoloured lamps						
Phytolux Attis 7	0.036	0.007	133.52	4.79	27.9	0.21

can be greater than 100 lumens per Watt. Fluorescent tubes are often used in controlled environment growth facilities, as required for micropropagation, as they can provide uniform lighting and be placed relatively close to plants. Many plant factories were initially constructed using fluorescent tubes.

1.6.3 High intensity discharge lamps

There are two major types of high intensity discharge (HID) lamps commonly used in horticulture: high pressure sodium (HPS) and metal halide (MH) lamps. HID lamps function by passing an electrical arc between two tungsten electrodes that are separated by a transparent tube filled with gas and metal salts. The heat generated by the arc evaporates the metal salts, which at operating temperature form a plasma that emits light. The spectral output the HID lamps is controlled by is characteristic of the metal salts contained within the arc tube. HPS lamps contain mercury and sodium. During ignition, HPS lamps emit a pinkish glow: at this stage, only mercury vapour is

emitting light as evaporation of sodium only occurs at operating temperature. MH lamps contain mercury and metal halides (metal compounds containing iodine or bromine). HID lamps are more energy efficient than fluorescent and tungsten lamps because a greater proportion of the light they emit is in the visible/PAR region of the spectrum.

The spectrum of HPS lamps is not ideal, however, as they are deficient in blue light (Figure 5). While good-quality plants can be grown under HPS lamps, the lack of blue light can lead to plant etiolation. Metal halide (MH) lamps have a better spectrum for plant growth as they emit more blue light (Paul 2006). However, several significant limitations associated with HID lamps restrict their application. HID lamps operate at high temperatures, preventing them from being located close to plants. In extreme cases, HID lamp failures can lead to fires. HID bulbs have a relatively short lifespan, but can be replaced relatively easily.

1.6.4 Plasma and sulphur lamps

Plasma lamps are a type of gas discharge lamp that generates light by heating a gas contained in a sealed glass vessel using high frequency radio waves. In a sulphur lamp, the glass vessel contains sulphur, which is heated to form the plasma. These lamps contain no internal electrodes and are much smaller than the bulbs of HPS and MH lamps. The small bulbs mean that more efficient reflectors can be developed. As with other types of gas discharge lamps, the spectrum can be altered slightly by altering the gas mixture in the lamp but, once constructed, the spectrum is fixed.

1.6.5 LED technology

Unlike all other artificial lighting systems, light emitting diodes (LEDs) contain no glass or gaseous components: all the components are solid-state. LEDs are, therefore, less fragile than other types of lamp and they can be located in places where other lamps may become damaged and pose a health and safety risk. LEDs are constructed from two layers of semiconducting material that are in contact with one another. When an electrical current is passed through an LED, electrons move across the junction between the two materials. As the electrons cross the junction they fall to a lower energy level and release a photon in the process. The chemistry within the LED controls the size of the energy drop and, therefore, the wavelength of the photon emitted. LEDs are now available with almost any wavelength between ~240nm and 4,000nm, though their energy conversion efficiency differs with colour (red and blue LEDs are the most energy efficient). While the narrow emission spectrum of LEDs provides many opportunities, there are many cases where a white light may be more appropriate. White LEDs are manufactured by adding a phosphor coating to blue LEDs. The phosphor absorbs some of the light emitted by the LED and re-emits the light with a longer wavelength (this is the same process that occurs at the wall of a fluorescent tube). The colour of white LEDs can be adjusted during manufacture by altering the mixture of phosphors. White LEDs are less efficient than standard LEDs for two main reasons. First, the phosphor coating scatters the light emitted by the LED and this effectively traps some light within the LED. Second, as phosphors absorb blue photons and re-emit the energy as longer wavelength photons, some energy is converted to

heat (this energy loss is referred to as a Stokes shift loss). The most efficient phosphor (YAG) has a Stokes shift loss of ~10% (Stokes shift losses may be up to 30%) and, thus, in 'white' LEDs that generate a significant amount of red light there is a considerable loss when compared to a red LED. One of the major advantages of LEDs is their high efficiency (light energy output/electrical energy input) compared to other lighting sources. While there are many areas to be aware of when estimating the efficiency of LED lighting systems it should be noted that LED technology is advancing at a considerable pace. Each decade, the efficiency of LEDs has increased approximately 20-fold, while the cost per lumen emitted has fallen by a factor of 10 (Haiz law). An example of the rapid rate of LED development is provided by the recent release (January 2015) of the second generation of Philips Greenpower LED production modules. These modules are reported as having a 25% lower power consumption for the same light output compared to the first generation modules. Such rapid advancements will drive down running costs, though the ongoing development costs will reduce the rate at which lamp costs decrease, at least in the near future.

The power of LED technology can be seen in the design of the lamps they are used to construct. Unlike other types of lighting systems, the light emitted from LED is directional, and optical design of LEDs lamps, therefore, differs from other lamp designs. The need for reflectors is reduced as no light is emitted from the back of the LED, although reflectors can still be of use in shaping the light beam. Instead of reflectors, many LED-based systems implement lenses to direct the light beam to the desired location. Good optics can reduce the amount of stray light and ensure that the maximum amount of light reaches the crop. The emission spectrum of LEDs, like other types of lighting technology, cannot be changed. However, the overall spectrum of LED lamps can be modified for different applications by changing the number and colours of LEDs installed in the unit. Lamps can also be designed with the ability to alter the intensity of each colour of light so its emission spectrum can be modified at will. A single lighting source could then be used to adjust crop morphology at different stages of development or to control the habit of different crops with different lighting requirements. The range of potential benefits and applications for LED lighting will be investigated in detail in section three of this report.

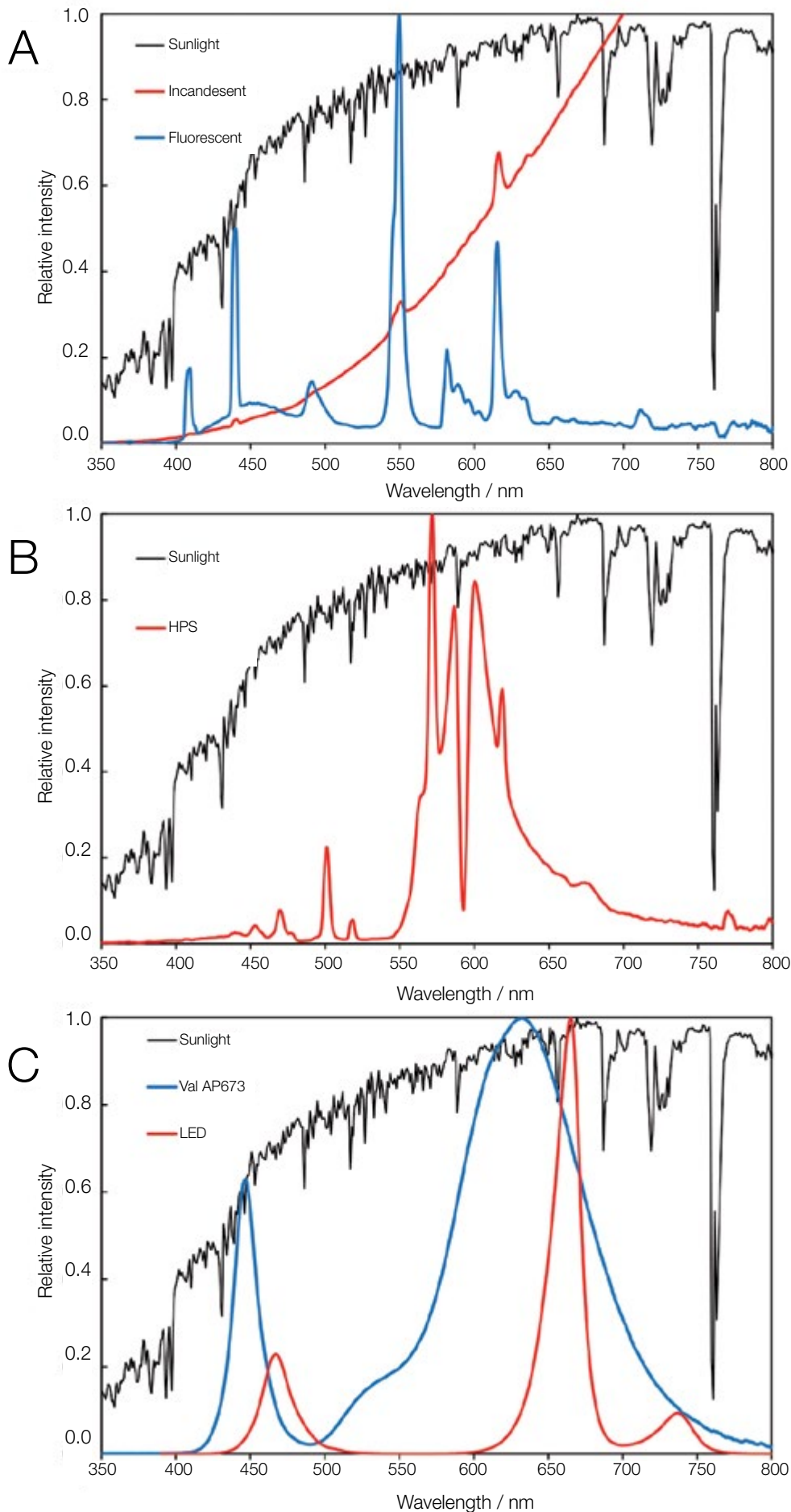


Figure 5. Selected lamp spectra. All graphs show the solar spectrum for comparison.
 A) Fluorescent tube and incandescent light bulb. B) 600W HPS lamp. C) Two types of LED light, Phillips red blue and far-red Greenpower research modules and a Valoya AP673 lamp



SECTION TWO

Plant light responses

Plant light responses have evolved to help plants acclimatise to the wide variety of light climates that plants find themselves in. Not only are individual plant species able to acclimate to maximise performance in different light environments, but different species are optimised to respond to light environments associated with different niches. All plants will respond differently to high and low light conditions but some species are adapted to perform optimally under full sun conditions while others are adapted to live in shaded conditions (Schmitt 1997). In this section, we will briefly examine the mechanisms by which plants are able to sense and respond to changes in light intensity and quality and provide some examples of potential uses/benefits of different colours of light.

2.1 Photosynthesis

Photosynthesis is the process by which plants are able to use light to produce energy and carbohydrates through the fixation of CO₂. Photosynthesis provides all the energy and carbohydrates that the vast majority of plants need in order to grow and reproduce. In darkness, plants respire and produce CO₂. As the light intensity increases, the photosynthetic rate also increases and, at a certain light intensity (the light compensation point), the rate of respiration is equal to the rate of photosynthesis (no net uptake or loss of CO₂). The photosynthetic rate increases in a linear fashion up to photon irradiances of 100–200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 7). With further increases in photon irradiance, the photosynthetic light responses level off until the light saturation point is reached, above which any further increases in light intensity do not increase photosynthesis. Under light saturation conditions, other factors such as temperature and CO₂ concentration influence the maximum photosynthetic rate. In addition to light intensity, the colour of light also influences the rate of photosynthesis. Plants are able to use light of wavelengths between 400nm and 700nm for photosynthesis. This waveband is described as the Photosynthetically active radiation (PAR). PAR accounts for about 26% of the photons and 42% of the energy received from the sun (calculations based on the ASTM G173-03 Reference Spectrum). Within the PAR range, the ability of plants to utilise light also varies between different wavelengths. Plants are most effective at using red and blue light for photosynthesis (see Box 1 overleaf for details), but are also able to utilise a significant amount of green light for photosynthesis. The majority of green leaves absorb at least 70% of the green light and a plant canopy could absorb over 90% of the available green light (Paradiso *et al*, 2011). The lower rate of absorbance of green light compared to red and blue light means that it can penetrate deeper into leaves (Terashima *et al*, 2009) and canopies (Paradiso *et al*, 2011) and can, therefore, drive photosynthesis in places where blue and red light cannot penetrate (Sun *et al*, 1998). In the non-linear region of the light response curve (Figure 7),

the addition of green light can increase photosynthetic rates with the addition of the same amount of red or blue light. If crop photosynthetic rates are to be maximised, light spectra may require the inclusion of some green light. The benefits of including green light in the spectrum would need to be evaluated with regard to the energy required to generate this light, as red and blue LEDs are currently more energy efficient than green or white LEDs.

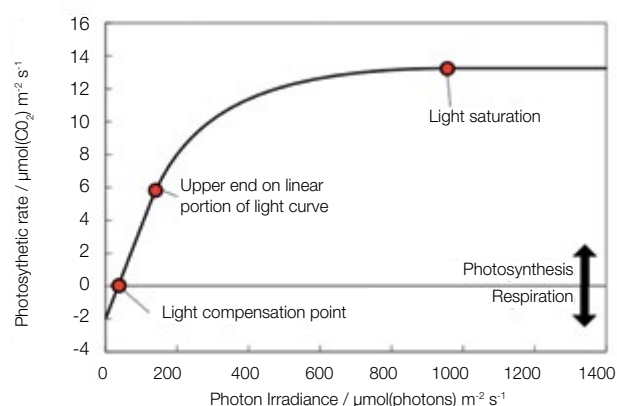


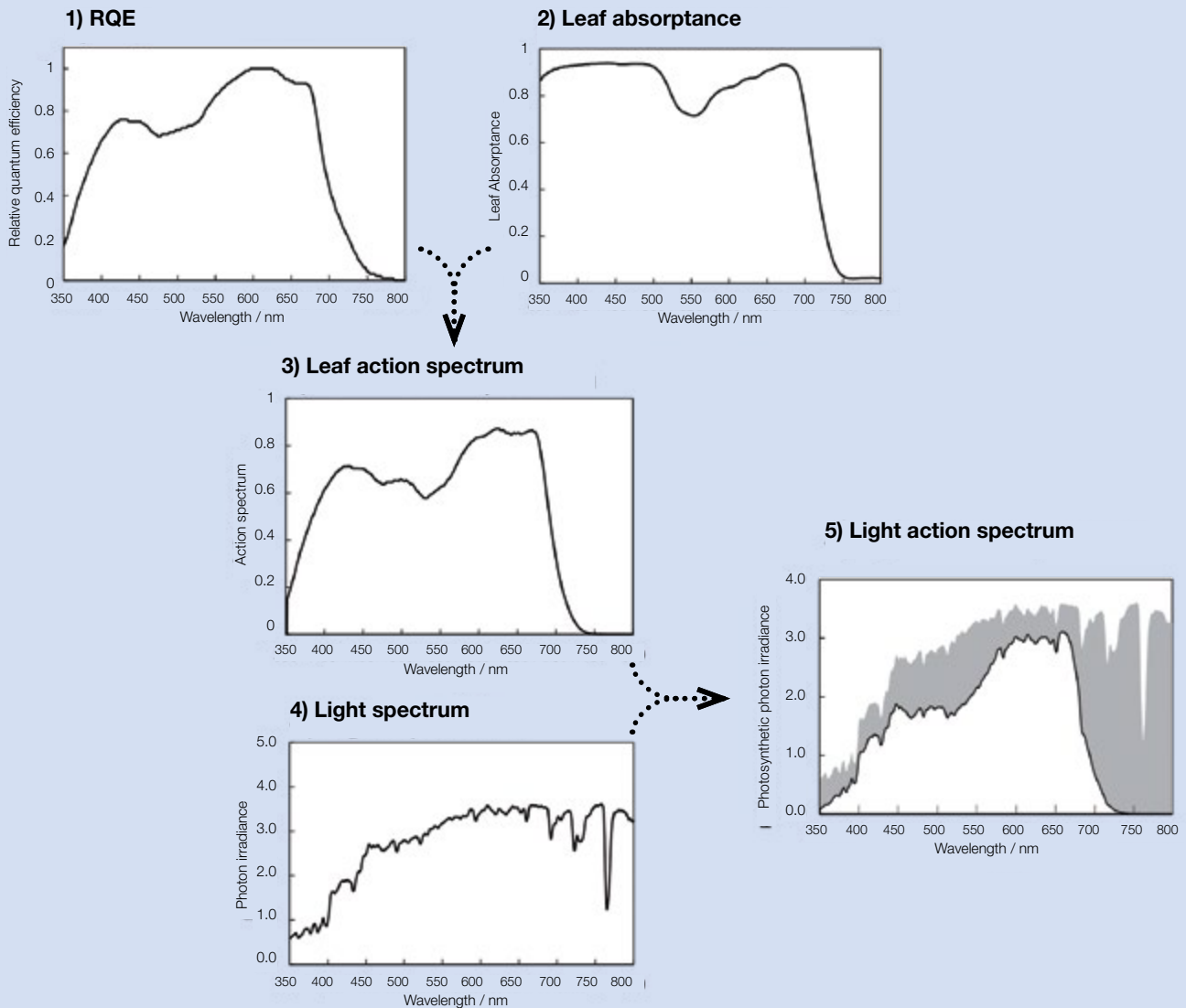
Figure 6. Idealised net photosynthetic light response curve of a single leaf. Negative values indicate that the rate of respiration is greater than the rate of photosynthesis

2.2 Light stress – Photoinhibition

Even when exposed to low light intensity, the complex protein structures (photosystems) involved in photosynthesis can become damaged by the light they absorb through a process called photoinhibition. Plants must continually repair their photosystems in order to maintain efficient photosynthesis. Under most conditions, plants are able to adjust the rate of repair to match the rate of damage and no evidence of damage can be observed. Under stress conditions such as bright light, particularly combined with drought, cold or heat stress, the rate of photoinhibition can exceed the rate of repair. Mild cases of photoinhibition result in reduced photosynthetic rates, but more advanced symptoms result in leaf bleaching or loss and, in extreme cases, plant death. This is one of the reasons that plants must be hardened-off before transplanting, as this allows plants to produce protective pigments and increase their ability to repair damaged photosystems. Light quality/colour also influences rate of photosystem damage, with the rate of damage rapidly increasing as wavelength decreases. UV light causes very high rates of photoinhibition and blue light causes photoinhibition at higher rates than red or green light (Sarvikas *et al*, 2006). These wavelength-dependent differences in photoinhibition may be exploited to help harden-off plants before transplanting: provision of additional blue or UV light can increase plant stress tolerance (Ouzounis *et al*, 2014).

BOX 1. Spectral effects on photosynthetic rates

A considerable amount is known about how plants utilise different regions of the spectrum for photosynthesis. The advent of LED technologies has sparked a renewed interest in this field. It is possible to calculate the amount of photosynthesis that different light sources can potentially drive by following the procedure outlined in the figure below. For the process to be accurate for a specific crop, measurements of leaf light absorbance should be made on plants grown under the conditions of interest. However, by using mean leaf absorbance spectra made on wide range of plant species, it is possible to assess how effectively different light sources can drive photosynthesis.



1) The relative quantum efficiency (RQE) spectrum shows how effectively different colours of light drive photosynthesis once absorbed by chlorophyll (McCree 1971). 2) The leaf light absorbance spectrum gives the proportion of each colour of light that a leaf can absorb (note the dips in the green and the far-red regions of the spectrum). The data shown is the average leaf absorbance values of 25 plant species (Davis *et al*, 2011). 3) By multiplying the RQE and the leaf absorbance spectra together, the photosynthetic action spectrum of a leaf can be determined. 4) Solar spectrum as shown in Figure 1. 5) By multiplying a light spectrum with the calculated leaf action spectrum it is possible to assess the proportion of available light that can be used for photosynthesis, termed here the 'light action spectrum'. The shaded area indicates the light incident on a leaf that is not used for photosynthesis, instead this light is either reflected or turned into heat.

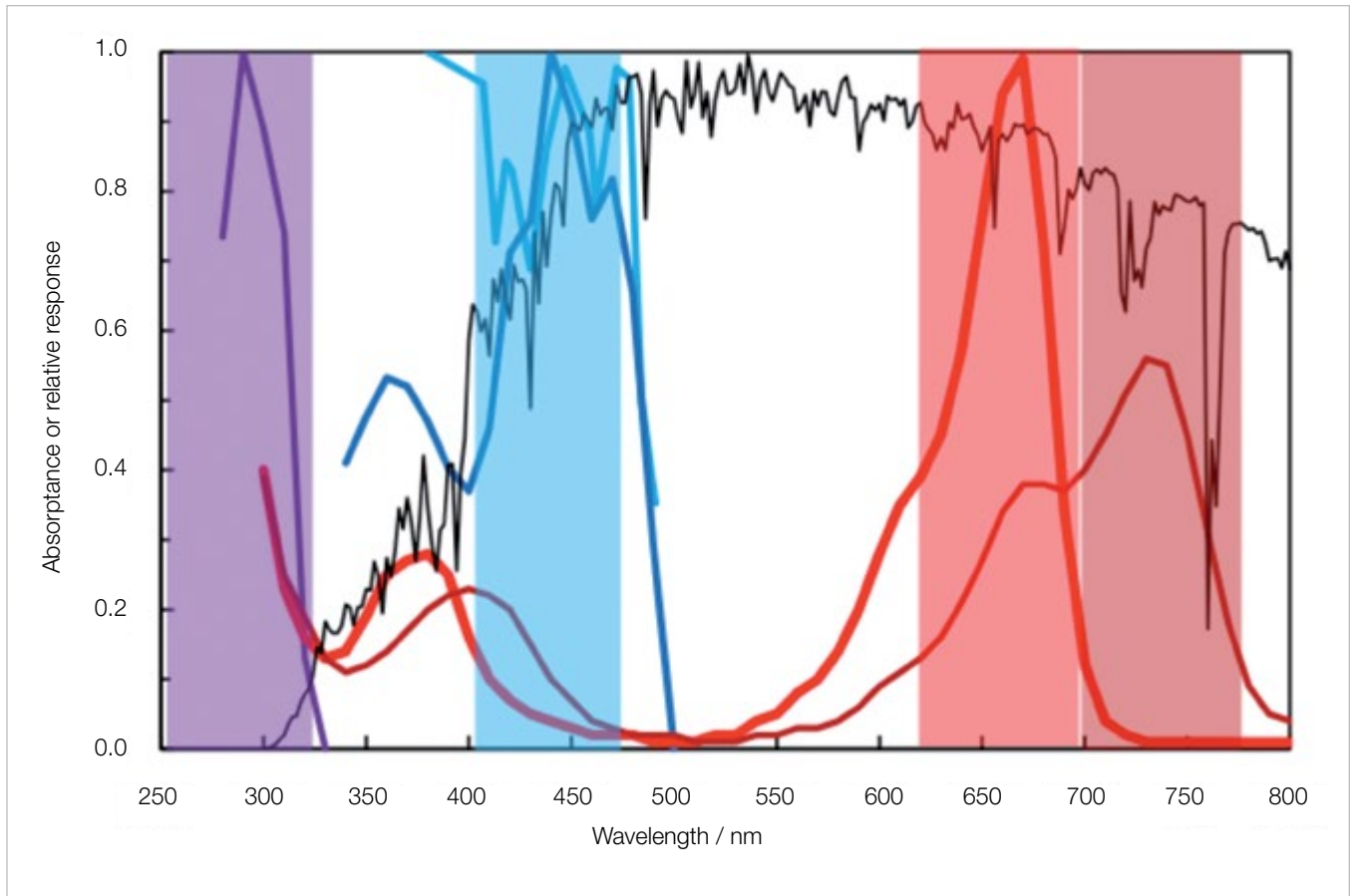


Figure 7. Action spectra of different photoreceptors. Purple line – the action spectra of UVR8 (Gardner *et al.*, 2009). Blue lines indicate the action spectra of phototropin and cryptochrome (Briggs and Christie 2002). Bright red line shows the absorption spectra of the inactive form of phytochrome B and the dark red line indicated the absorption spectrum of the inactive form of phytochrome B. The coloured panels indicated the regions of the spectrum that are important for controlling plant morphology

Table 2. Plant light responses and the regions of the spectrum as well as the photoreceptors that have important roles in regulating those responses.

Plant response	UVB	UVA/ Blue	Green	Red	Far-red	The photoreceptor
Photosynthesis	✗	✓	✓	✓	✗	Chlorophylls Accessory pigments
Photoinhibition	✓	✓	✓	✓	-	Chlorophyll and/or the water splitting complex of photosystem II
Reduce stem elongation	✓	✓	✗	✓	✗	Phototropins Cryptochromes UVR8 Phytochromes
Stomatal opening	✗	✓	✗	✗	✗	Phototropins
Chloroplast movement	✗	✓	✗	✗	✗	Phototropins
Phototropism	✗	✓	✗	✗	✗	Phototropins
Pigment synthesis	✓	✓	✗	✓	✗	Cryptochromes UVR8 Phytochromes
Flowering time	✗	✓	✗	✓	✓	Cryptochromes Phytochromes
Germination	✗	✓	✓	✓	✓	Phytochromes

2.3 Sensing light quality

Photosynthesis provides the energy and carbohydrates required for plant growth. Plants are also able to sense the intensity and quality/colour of light and modulate their growth and development to match the conditions in their environment. Plant light responses have been studied for over a hundred years (Whippo & Hangarter 2006), but in the last 30 years great advances in our understanding of the molecular basis of these responses have been made. Plants become etiolated when grown in darkness, having long internodes and undeveloped yellow leaves. This form of development aids plants to grow towards the light as fast as possible (useful if seeds germinate underground, under leaf litter or in deep shade). When exposed to light, plant tissues undergo the process of photomorphogenesis and several independent processes occur simultaneously. Stem elongation is reduced, stems and leaves bend towards the light, and leaves open, expand, and turn green. These photomorphogenic responses help the plant orient towards the light and maximise their chances of absorbing light for photosynthesis.

Photomorphogenesis is mediated by several types of photoreceptor. Photoreceptors are light-sensitive proteins that initiate signal cascades that eventually lead to light responses. Each photoreceptor is sensitive to specific wavelengths (Figure 7) and is responsible for a different subset of responses (Table 2). There are some overlaps and certain plant light responses can be mediated by several photoreceptors. In darkness, the photoreceptors are inactive but, following the absorption of a photon, their conformation/shape changes and they become activated. The mechanisms by which the different photoreceptors drive photomorphogenic changes are diverse and in many cases not fully understood. Some photoreceptors induce changes in gene expression while others cause changes to other cellular processes such as polar auxin transport. If returned to darkness, active photoreceptors will return to their inactive states. Some photoreceptors can also be inactivated by the absorption of a second photon (usually of a different colour to the activating photon) that causes it to revert to its inactive state while in the light. Photoreceptors that can be photo-inactivated cycle between the active and inactive states when illuminated and the spectral composition of the light can influence both how rapidly the cycling occurs and what proportion of a photoreceptor population exists in its activated state. These properties allow plants to be particularly sensitive to changes in the light environment.

2.4 UVB light responses

The Earth's atmosphere removes a large proportion of the short-wavelength radiation emitted by the sun. Virtually no UVC radiation reaches the ground and much of the UVB radiation is also removed. However, levels of UVB sufficient to cause damage to living organisms are present, especially in the summer months and at higher elevations. UVB is extremely damaging to organic molecules (proteins, DNA and RNA can be damaged by UVB radiation) and, because of this, plants are sensitive to low intensities of UVB light. In the presence of UVB light, plants produce a range of pigments and other secondary metabolites that act like sunscreen to provide protection against damage (Chalker-Scott 1999). Flavonoids and anthocyanins in particular are increased following exposure to UVB (Tevini *et al*, 1981; Beggs & Wellman 1985), and this causes leaves

and flowers to have stronger colours (Paul *et al*, 2006). In addition to changes in pigmentation, UVB light also causes plants to remain compact in morphology (Gardener *et al*, 2009), produce tougher, more robust, leaves (Wargent *et al*, 2009), and increase the concentration of essential oils in herbs (Kumari *et al*, 2009; Hikosaka *et al*, 2010). The photoreceptor for UVB light (named UVR8) is sensitive to light with wavelengths between 280nm and 330nm with peak sensitivity at ~290nm (Figure 5: Gardener *et al*, 2009). Small amounts of UVB light have large effects on plant morphology and this may provide a way of inducing large changes in plants for minimal energy inputs (Ballare *et al*, 1991). Currently, UVB LEDs are prohibitively expensive for use in practical applications in horticulture, but cheaper light sources such as fluorescent tubes could be used to good effect. A major limitation of adding an artificial source of UVB light in glasshouses is the potential to cause a health hazard as UVB can cause sunburn and skin cancer.

2.5 Blue and UVA light responses

Blue light photoreceptors influence many plant responses including phototropism, anthocyanin production, chloroplast movement, stomatal opening, inhibition of shoot elongation, and leaf flattening. Plants possess several blue-light photoreceptors, each of which utilises a different set of mechanisms and functions to influence photomorphogenesis and development. Two families of blue-photoreceptors, the phototropins and the cryptochromes, have been the subject of a great deal of research and much is known about the responses they control and how changes are induced. The phototropins function by altering cellular processes without altering gene expression, while the cryptochromes function by changing gene expression. The spectral sensitivity of the two groups is similar (Figure 7; Briggs & Christie 2002), with both functioning across the blue and UVA regions of the spectrum. Cryptochromes can be deactivated by green light: this would inhibit some of the blue light responses and allow a greater ability to detect differences in light quality (Sellaro *et al*, 2010).

The phototropins control a wide range of plant responses including stomatal opening, phototropism (bending towards the light), chloroplast movement, leaf flattening, and inhibition of hypocotyl elongation. The cryptochromes are involved in regulating pigment synthesis, entraining the circadian rhythm, flowering, and inhibition of hypocotyl elongation. Plants grown in the absence of blue light become etiolated and leaves tend to hang downwards and remain partially curled.

2.6 Green light responses

The presence of a green-light photoreceptor has been in debate for some time, but none has been discovered to date. While there is currently no known green-specific photoreceptor, phytochromes are able to sense green light and there is some evidence that cryptochromes can be deactivated by green-light (Sellaro *et al*, 2010). Regardless of the presence or absence of a green light sensing mechanism, there is an increasing number of studies highlighting the effects of green light on plants. Addition of green light has been reported to increase plant growth rates, although whether this is due simply to a direct effect of green light on photosynthesis (see section three for more details) or to some other factor remains to be seen. Interestingly, Sommer and Franke (2006) observed that

exposing seeds of cress, radish, and carrots to bright green laser light caused the plants to grow considerably larger. No biological explanation for this observation has been elucidated, but further investigation may identify some useful practical applications. Green light is not always found to benefit plant growth. For example, tomato seedlings are inhibited by exposure to green light (Brazaityte *et al*, 2010). For a detailed review of the influence of green light on plant production see Wang & Folta (2013).

2.7 Red and far-red light responses

Phytochromes are known to be responsible for several photobiological responses: germination (photoblasty), hypocotyl elongation inhibition, apical hook straightening, leaf expansion, flowering time, circadian rhythm entrainment, and chlorophyll biosynthesis. Plants possess more than one type of phytochrome (arabidopsis has five, rice has three, and maize has six). Phytochromes influence plant light responses by inducing changes in gene expression. Two types of phytochrome have received extensive investigation: phytochrome A (phyA) and phytochrome B (phyB).

In darkness, phyB exists in its inactive state (Pr form) and absorbs red light most strongly (peak absorbance = 666nm). When the Pr form absorbs light, it changes to the active form (Pfr form) and its absorption spectrum is red-shifted so the maximal absorbance is in the far-red (730nm) region of the spectrum. The active form of phytochrome (Pfr) reverts back to the inactive form if left in darkness, but can also be converted back to the inactive Pr form by absorption of light. In natural light environments, phytochrome B continuously cycles between its active and inactive states and the spectral mix of light controls whether the Pr or Pfr form of the molecule dominates. A short pulse of red light is sufficient to induce some phytochrome responses but if the red pulse is followed by a far-red pulse the response does not occur: this is referred to as far-red reversibility. This phenomenon underpins the importance of end-of-day light quality for plant morphology and influences how effective night break lighting is at influencing plant responses.

The function of phyA differs from that of phyB in two key ways. First, phyA is activated by far-red light as well as red light and, second, phyA primarily accumulates in plant tissues in darkness (phyA is down-regulated both transcriptionally and post-transcriptionally in the light).

While generally discussed in reference to their ability to detect red:far-red ratio of light, phytochromes absorb light of wavelengths across the whole spectrum, including blue light. For example, green light is capable of driving both phyA- and phyB-induced germination (Shinomura *et al*, 1996). Each wavelength or mixture of wavelengths of light will create a slightly different Pr:Pfr mixture, providing the plant with a sensitive mechanism for sensing light quality.

2.8 Hormones and light

The combined influence of the different photoreceptors provides plants with an extremely sensitive and plastic ability to optimise morphology and physiology to match their environment. Many of the changes in morphology and development seen in plants in response to light are mediated via plant hormones (Lau & Deng 2010). Auxin is a major regulator of cell division, cell expansion, and plant morphology and is itself highly regulated by light (Halliday *et al*, 2009). Auxin levels are found to increase in the presence of light (Bhalerao *et al*, 2002). Auxin moves through plants both passively via the phloem and actively from one cell to another through the process of polar auxin transport. Polar auxin transport is highly regulated by light and auxin is moved through the plant in different directions, allowing phototropism (Wan *et al*, 2012) and, at different rates, allowing changes in root to shoot development (Reed *et al*, 1998) and lateral root development (Bhalerao *et al*, 2002). Light also plays an important role in regulating other important plant hormones including gibberellin (García-Martínez & Gil, 2002), abscisic acid (ABA), and cytokinin (Lau & Deng 2010). The complex network of molecular pathways linking light and hormone signalling is gradually being elucidated and this knowledge will help optimise light treatments to maximise plant quality.





SECTION THREE

LEDs in horticulture

A major goal of all plant producers is to maximise or increase yield while minimising or reducing inputs. LED top lights are already able to reduce energy inputs compared to HPS lighting by 40+% (Fionia FL300 technical specifications) and ongoing development will continue to reduce the energy requirements of LEDs. Energy saving is a major force behind the push to switch to LED lighting but in this section we will examine the range of additional benefits that LEDs bring to horticulture via spectral manipulation of the plant light responses outlined in section two.

LEDs provide the potential for optimisation of light treatments that allow the enhancement of specific plant qualities or control over plant morphology and flowering time. It is often thought that the spectrum must be optimised for plants to be grown under LEDs but this is not necessarily the case, especially if LEDs are used as a source of supplemental lighting in glasshouses. Using commercially available LEDs, high-quality plants can be produced that are in many cases better than those produced with conventional HPS lighting (Randall & Lopez 2014). Furthermore, ongoing development of light spectra and an improved understanding of species-specific light requirements will aid further improvements in crop production systems.

3.1 Crop growth under red and blue LEDs

LEDs were first examined as potential light sources for plant photosynthesis and growth in the late 1980s and early 1990s (Bula *et al*, 1991, Barta *et al*, 1992, Tennessen *et al*, 1994). Initially, only red LEDs were sufficiently bright and when blue light was included, it was provided with fluorescence tubes. LED technology has developed rapidly since then, they have become brighter and more colours have become available. These developments have been tracked by horticultural scientists and, especially since commercial LED systems have become available in the last couple of years, a growing range of applications for LEDs in horticulture has been examined.

Many species of plants have been grown using LED lighting and a great deal of knowledge has been gained regarding plant light requirements and techniques for altering crop performance, though there are still many questions regarding the best use of LEDs. To produce healthy plants both, red and blue light are required. Red light is most effectively used to drive

photosynthesis (see section 2.1) but plants are generally found to grow more effectively when some blue light is contained within the light spectrum (Kim *et al*, 2004a and 2004b, Johkan *et al*, 2010). Wheat and Arabidopsis plants produce more seeds (Goins *et al*, 1998; Goins *et al*, 1997); lettuce, radish and spinach produced more biomass (Yorio *et al*, 2001) and Frigo strawberries produce more fruit with higher sugar contents (Samuoliene *et al*, 2010) when grown with both red and blue light compared to red alone and there are many more examples of similar crop improvements. One of the main reasons for this is that the blue light helps open the stomata-promoting CO₂ uptake. When exposed to only LED light, stomatal conductance is greater in plants exposed to red:blue mixtures of light than those exposed to 100% red light (Hogewoning *et al*, 2010; Nanya *et al*, 2012; Savvides *et al*, 2012; van Leperen *et al*, 2012). Stomatal responses to light do, however, differ between species so not all species will benefit equally following the addition of blue light. In roses and chrysanthemums stomatal conductance was found to be greater in plants grown in glasshouses under supplemental LED lighting containing more blue light. However, campanulas showed little increase in stomatal conductance to supplemental blue light (Ouzounis *et al*, 2014). Not only can light quality and quantity affect whether stomata open or not, it can also alter the number and density of stomata that develop on a leaf. Stomatal development was found to be lower under monochromatic light compared to mixtures of light in *Withania somnifera* L.) Dunal. Plantlets (Lee *et al*, 2007). UVB light causes soybean to produce fewer stomata, which could increase drought tolerance, but decreases photosynthetic performance (Gitz *et al*, 2005). While stomatal opening and closing in response to light causes reversible changes in water use, any influence light quality has on the development and density of stomata will have a long-term influence on stomatal conductance, photosynthetic performance and water use efficiency. In addition to its effects on stomata, light quality has many other important functions for maintaining healthy plant growth through regulation of plant metabolism and morphology. Cucumber plants grown under blue and UVA light were found to have both higher photosynthetic potential and transcription of the genes required for carbon fixation than plants grown under red green or yellow light (Wang *et al*, 2009). In rice leaves, addition of blue light in a red background caused higher photosynthetic and stomatal conductance rates and were associated with higher chlorophyll and rubisco contents (Matsuda *et al*, 2004).



Figure 8. The influence of changing the red:blue percentage of growth light on the morphology of lettuce plants. The blue light percentage changes from 0% on the left of the image to 100% on the right of the image

While the need for both red and blue light is well established there is less consensus on the appropriate red:blue ratio. In lettuce plants, growth rates (measured as biomass accumulation) decreased as UVA and blue light was increased (Li & Kudota 2009, Son & Oh 2013). In contrast, an increase in rapeseed growth rate was observed as blue light percentage increased from 0 to 75% (in a red:blue mix; Li, Tang & Xu 2013). Folta & Childers (2008) observed the greatest growth of strawberry plants when grown under 34% blue light. However, Yoshida *et al.*, (2012) observed the greatest strawberry yield in plants grown under continuous blue light and suggested that red light inhibited flowering.

There are several reasons for the wide range of optimal red:blue ratios cited in the literature: 1) different light requirements between species and varieties of the same species; 2) different opinions on the optimal plant; 3) different stages of crop development benefit from different light spectra; 4) the background light conditions (presence or absence of sunlight in particular can alter the results); 5) an insufficient range of red:blue ratios having been tested. These different factors are expected to result in a wide selection of light recipes for growth of different crops and as a wider range of applications (tissue culture, propagation, breeding and post-harvest light treatments) are considered, the differences in light treatments may become even more extreme. For example, cutting rooting was most successful under 100% red light (see section 3.5) and for storage of large numbers of strawberry plants for use in breeding and research projects 100% blue may be helpful as it keeps the plants compact (Folta & Childers 2008).

Any experiment that tests plant light responses can only examine a finite range of spectra. This limits the speed at which a light recipe can be optimised, though well-designed experiments will help point towards the optimal light treatment. High-quality plants can be grown under just red and blue light and given that red and blue LEDs are the most energy efficient many commercial lighting systems have focused on these colours. However, there are many instances where additional colours of light may provide additional benefits. The complexity of developing light recipes will also increase as more colours of light are included in the mixture. Even if the best red:blue ratio is first determined, the addition of a third colour in the mixture is likely to change the optimal balance between the red and blue light in the new spectra.

3.2 The influences of other colours of light on crop growth

The inclusion of green light, provided by LEDs, has been shown to increase fresh and dry weight biomass accumulation in lettuce plants when the green light replaces some of the blue or red light in the mixture (Stutte *et al.*, 2009, Kim *et al.*, 2004a). There may be two reasons for the observed increases in growth rate. First, green light can penetrate deeper into the plant canopy and, therefore, drive more photosynthesis, and, second, reducing the blue or red light reduces the growth restriction imposed by plant photoreceptors. Not all instances where green light has been added to the spectrum have resulted in enhanced crop performance. Li and Kubota (2009) found that in lettuce, while addition of green light caused no increase in biomass, plant morphology was affected, and increased stem and leaf elongation was observed. Early in crop development, larger

leaves may benefit crop performance by allowing greater light capture; however, larger leaves later in the crop cycle may reduce plant quality, especially if combined with stem extension. Some of the discrepancies between the different sets of published results may be due to differences in the total amount of light provided as well as the proportion of green light provided. Kim *et al.*, (2004b) found that 24% green light boosted yields; however, reduced yields were produced when greater than 50% green light was used, probably as a result of lower overall photosynthetic rates. Kim *et al.*, (2004a) also found that green light could cause stomatal closure and that stomatal opening was greatest under broad spectrum lighting (suggesting that white light may be better in this case). In tomato transplants, the addition of small amounts of green (520nm), orange (622nm), and yellow (595nm) LED light was found to reduce plant growth rate (Brazaityte *et al.*, 2010) and some of the negative impacts on the plant growth could still be observed one month after exposure to the different light treatments (Brazaityte *et al.*, 2009). Yellow light has also been found to suppress the growth of lettuce plants (Dougher & Bugbee 2001); however, it should be noted that these experiments were not performed with LED lighting and spectral assessments were, therefore, complex and may have been misleading. Lu *et al.*, (2012) examined the effect of supplemental LED light on tomato production on the single truss system and concluded that white light would be more effective at driving canopy photosynthesis in dense canopies than red or blue light, because the green light component of the white light spectrum penetrates further into the canopy than red or blue.



Far-red light is important for plant development and performance throughout the life of the crop. For example, while far-red light can inhibit germination of lettuce seeds (Brothwick *et al.*, 1952, Shinomura *et al.*, 1996), it can nevertheless increase leaf area in lettuce (Li & Kubota 2009, Stutte *et al.*, 2009) potentially allowing greater light capture and growth rates. While far-red light can increase leaf area, it will also cause stretching or bolting if provided during the later stages of crop development. Far-red light can also have negative impacts on pigmentation by reducing chlorophyll (Li & Kubota 2009), which, in addition to affecting the appearance of crops, could reduce photosynthetic rates. The area where far-red light can perhaps be used to greatest effect is for controlling flowering time. Runkle and Heins (2001) demonstrated that far-red light promotes flowering in several long-day ornamental species and that an absence of far-red light can even prevent flowering. This work examined plant light responses using spectral filters. With the use of LED light treatments, plants can be grown using even more extreme ranges of red:far-red ratios, providing the potential for either delaying or advancing flowering still further than is possible with spectral filters.

Many factors will provide constraints when developing lighting systems and in nurseries producing multiple plant species some compromises will be required. There will also likely be some trade-offs between the requirements of the plants and the cost of lamps that can provide the desired light. If optimised light treatments are not available or are too expensive to implement, LEDs are still expected to benefit crop production. Plant light responses are highly variable and this diversity is related to the range of ecological niches that different plants are adapted to. Shade plants are, therefore, expected to respond differently to sun plants and long-day plants will respond differently to short-day plants. It is unlikely that one light spectrum will be sufficient to grow all plants at optimal quality. A greater understanding of the diversity of plant light responses is, however, expected to allow us to develop light treatments for particular groups of plants.

While there is general agreement about what makes a healthy or unhealthy plant, there is less consensus regarding how a plant should appear at sale, in part this is because different customers will have different preferences. This means that different growers may require different light spectra to grow the same crop. The optimal plant will also differ according to the specific needs of the particular crop. In many scientific reports described here, the optimal conditions were regarded as those that grew plants most rapidly. In commercial horticulture, however, the plant must also maintain the desired specifications.

3.3 End of day, day extension and night interruption lighting

End of day (EOD) red or far-red lighting treatments can be used to manipulate plant height. For example, EOD-far-red treatments are effective in encouraging tomato plants to grow taller, such as for production of optimal plants for grafting, and EOD-red treatments can improve plant compactness (Kubota *et al*, 2012). Incandescent lighting in glasshouses has been used to manipulate day length flowering responses to either promote or delay flowering, using either day-length-extension (DE) or night-break (NB) light treatments. As with EOD light treatments, these methods can be cost-effective as even low light intensities ($1\text{--}5\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$) can provide strong influences on crop responses. The role of LEDs as replacements to incandescent lights has been investigated as they provide considerable energy savings, but also because incandescent lights are becoming more difficult to acquire.

AHDB Horticulture project PC 296 (Adams *et al*, 2012) investigated the use of several types of LED with different spectra for use in NB and DE lighting to promote and delay flowering in several long- and short-day species. Spectral quality of the lights was found to have a significant role on their effectiveness in controlling flowering. Far-red-only and red+white+far-red lamps promoted flowering at levels similar to incandescent lamps, while red+white lamps were less effective than incandescent light. For example, chrysanthemum flowering was delayed in short days by NB and DE illumination with red+white and red+white+far-red lamps. Far-red-only lamps had no effect on any of the short-day plants. None of the LED light combinations were found to be as effective as incandescent lamps at delaying flowering in Christmas cactus. Begonia and poinsettia flowering times were advanced in response to red+white+far-red light treatments. LED treatments affected plant morphology as well as flowering time. Plants tended to grow taller as the amount of far-red in the treatments increased.

While chrysanthemums normally flower when days are shorter than 13.5 hours, Jeong *et al*, (2012) observed that a four hour day DE blue light treatment allowed them to flower during a 16-hour day. These experiments demonstrate that LEDs can be used effectively to control plant flowering and also highlight the importance of the spectral composition of lights used for this application. Further trials may be required to assess which model of lamp should be used with each species.

3.4 Interlighting

Manipulation of the spectrum provides the possibility of improving crop production, but LEDs also provide the opportunity to light crops in non-traditional ways. LEDs are cool light sources and, as such, can be placed close to crops or within a canopy to light leaves that would normally receive little natural or supplemental light. By adding light to leaves normally in the shaded region of the canopy, plants are able to use the light more efficiently. This means that interlighting has the potential to increase yields more than the same amount of light added at the top of the canopy. LEDs provided within the canopy were able to improve biomass production of Cowpea (*Vigna unguiculata L. Walp.*) as well as reducing the senescence of older leaves within the canopy (Massa *et al*, 2008). More recent interlighting trials have investigated different mixtures of red and blue light. The addition of increasing amounts of blue light within the canopy was found to increase yields of cucumber but not tomato plants, though the blue light reduced the internode lengths of both species (Menard *et al*, 2006). Trouwborst *et al*, 2010 found that interlighting in cucumber crops increased leaf photosynthetic rate and photosynthetic potential of leaves lower in the canopy. However, the interlighting treatments caused extensive leaf curling. This reduced light interception of the canopy and prevented the interlighting treatment from increasing crop yields. Hao *et al*, 2012 also had mixed results when using interlighting with cucumber. Over the first two weeks of their experiment, quality and yield increased by more than the increase in total photon irradiance; however, these gains declined as the experiment progressed, especially in the blue interlighting treatment where some leaf curling was observed. Interlighting in tomato crops has proved more successful and there is now a growing number of commercial installations, all of which are reporting significant increases in yields through the summer period when light levels are not traditionally thought to be limiting. One potential negative impact of LED lighting in glasshouses is the lack of radiative heat that is produced by LEDs. In experiments where the energy consumption of glasshouses has been monitored, LED-lit compartments have required higher air temperatures to counteract the loss of radiative heat. This reduced the overall energy saving as there was a greater heating demand. Dueck *et al*, (2011) reported that the use of LEDs for tomato production increased energy consumption; however, this was attributed to the energy demands of the water cooling systems of the LEDs used in that system. Current commercially available LEDs do not require water cooling systems. Gomez and Mitchell (2013) examined the use of LED towers in comparison to standard HPS lighting for tomato production. Their results indicated that the LEDs provided a significant energy saving but provided similar yields as the HPS lighting systems. In a more detailed analysis of the system, Gomez *et al*, 2013 measured the efficiency of electrical conversion into fruit biomass to be 75% greater for the LED

lights compared to sodium lamps; however, this did not take heating requirements into consideration. In all experiments that compare HPS and LED light there is a need to assess the differences in plant temperature to ensure that any effect of temperature can be separated from the effects of light in the plant's responses. HPS light can increase leaf temperature by several degrees and this can greatly increase plant growth rates. While the drop in crop temperature may have negative effects on crops in the colder months of the year, the lower temperature will benefit crops on warm days with low light levels. As with any significant change in crop environment, the switch from HPS to LED lighting will require a period of learning how to correctly manage plant irrigation and growth in the new conditions.



Figure 10. Tomato LED lighting trial at the LED4CROPS high-wire facility at Stockbridge Technology Centre

3.5 Propagation

Many important horticultural crops are propagated by taking cuttings or using micropropagation techniques. As with other areas of horticulture, there is a growing interest in using LEDs to create light mixtures that promote rooting and improve strike rates. This is of particular interest for high-value crops that are challenging to root or which take long periods to root. One of the challenges of taking cuttings is preventing dehydration. Plastic sheeting and fogging help to reduce transpiration, but this can also be reduced by the light spectrum used. Blue light drives stomatal opening, so removing blue light from the spectrum will help reduce transpiration. As well as reducing blue light to help cuttings remain hydrated, the use of red light treatments has been shown to directly promote root development in several species. Rooting was improved in two of three varieties of Grape (*Vitis ficifolia*) when illuminated with red light compared to fluorescent or blue light. In the third variety, rooting levels were high and similar in all light treatments examined (Poudel *et al*, 2008). This suggests that red light can improve rooting in more difficult-to-root varieties but may not further improve rooting in easier-to-root varieties. When Wu & Lin (2012) propagated *Protea cynaroides* plantlets under red LED light, 67% rooted compared to 7% under conventional fluorescent tubes, and 13% rooted under blue light or a red:blue (50:50%) combination of LED light. Root development was also found to be more extensive under the red light treatments. In *Protea cynaroides* cuttings, Wu (2006) observed that the concentration of phenolic compounds increased over time and that root development only occurred after their concentration attained a certain level. Further investigation demonstrated that the phenolic compound 3,4-dihydroxybenzoic acid could promote root formation up to 100 mg l⁻¹ but inhibited root formation at higher concentrations (Wu *et al*, 2007). The use of red light in the propagation phase caused the plants to generate phenolic compound

concentrations favourable to rooting, while the inclusion of blue light raised the concentrations to high levels and caused inhibition of rooting. Similar effects may be occurring in other species, but the active compounds are likely to vary between different species.

While the rooting performance of the plants highlighted above was best in 100% red light, the range of red:blue mixtures tested was limited and further development of the light spectra may be expected to further improve plant quality. Red:blue mixtures of light have been found to drive the best rooting in several species. In vitro propagation of banana plantlets and subsequent transfer to a soil growing substrate was found to be best when performed under 80% red and 20% blue light (Nhut *et al*, 2002). A 50% blue light treatment was most effective for the propagation of Cotton plants (Li *et al*, 2010). Strawberry plantlets performed best when propagated under 70% red: 30% blue light (Nhut *et al*, 2003). In climbing Gentian, red light was found to promote rooting while blue light inhibited rooting. However, the optimal rooting was observed using a 70% red: 30% blue mixture (Moon *et al*, 2006). If 100% red light treatments provide the best rooting in certain species, even after further recipe development, it will be important to ensure that the plants are moved to a different light treatment containing some blue light after the critical stage of root initiation in order to prevent etiolation of the young plants and help ongoing root development: blue light enhances both root and shoot development (Nhut *et al* 2003).

The light spectrum provided to cuttings during propagation appears to have a big influence on the rate and quality of root development, but the light treatment prior to cutting may also influence strike rates. Eucalyptus grandis cuttings were found to have a greater rooting success when the stock plants were grown under low red:far-red ratios (Hoad & Leakey 1996). As cutting success is closely linked to cutting quality, improving the quality of stock plants through changes to lighting or with spectral filters is expected to provide significant benefits, especially if combined with optimal post-cutting light treatments.

3.6 Improving crop quality

In many sectors of horticulture, the greatest benefits resulting from LEDs are likely to be an improvement in crop quality and consistency. In this section, we will examine how LEDs can improve three key attributes of crops: morphology, pigmentation, and flavour/aroma.

3.6.1 Improving crop morphology and reducing the use of plant growth regulators

Spectral manipulation can maximise biomass production but, depending on the particular conditions and crop, larger plants may not be desirable. Morphology and quality may be negatively affected if plants are grown 'too soft'. In this section, we will examine the use of LEDs to improve crop quality. Several methods are used in the industry to control plant morphology during crop production. These include altering irrigation, increasing EC of irrigation solutions, application of plant growth regulators (PGRs), and altering temperature profiles (eg negative DIF). The use of PGRs in the ornamentals sectors is particularly widely used to help maintain crop quality during periods of low light. The ability to control the light spectrum with LEDs, or

with spectral filters, provides the potential to manipulate plant morphology. This may reduce or remove the need for plant growth regulators. Poinsettia plants grown under 80% red: 20% blue supplemental LED lighting were 20–34% shorter than those grown under HPS (5% blue) lamps (Islam *et al*, 2012). Although leaves were smaller and plants achieved a lower dry matter accumulation, there was no delay in bract colour formation or post-production performance, indicating that LEDs could be useful for reducing the use of PGRs for poinsettia production. An increase in the blue light proportion of supplemental light was also found to cause roses and chrysanthemum to remain more compact during production: the most compact roses were observed under 40% supplemental blue light (the highest proportion examined in this study; Ouzounis *et al*, 2014). The quality of the supplemental light was also found to strongly influence leaf morphology, with 100% red light treatments causing rose leaves to become curled. In many species, stem elongation decreases as the proportion of blue light increases (Folta 2005, Moon *et al*, 2006, Nanya *et al*, 2012). While higher percentages of blue light reduce plant height, the reduced leaf size may also have negative influences on growth and development, which may influence production periods. The red:blue ratio, while important, is not solely sufficient to control plant morphology: light intensity is also critical. In tomato plants, it was the absolute intensity of the blue light that controlled the length of hypocotyl and stem extension rather than the % of blue light in the light recipe (Nanya *et al*, 2012). While stem elongation was controlled by blue light, the position of the first flower truss was proportional to the total photosynthetic rate of the plant (more photosynthesis = earlier truss development). In principle, this would mean a plant grown in 75% blue light of $100\mu\text{mol m}^{-2} \text{s}^{-1}$ would have the same internode size as a plant grown in 38% blue light at $200\mu\text{mol m}^{-2} \text{s}^{-1}$, though it should be noted that plants grown at the higher light intensity would grow more quickly and flower earlier. Higher light intensities will reduce crop production time, which has the potential to reduce production costs albeit after an initial capital investment in lamps.

Other colours of light also influence plant morphologies. In chrysanthemums, blue light reduced leaf mass, green light reduced stem mass, and red and far-red light caused a reduction in root mass (Jeong *et al*, 2012). Red:far-red ratio of light is important for controlling plant morphology. In contrast to roses and chrysanthemums, campanula height was unaffected by supplemental blue light, and the addition of red light provided the greatest effect on reducing plant height in this case (Ouzounis *et al*, 2014). The addition of red light likely reduced plant height by changing the red:far-ratio of light and reducing far-red light with spectral filters could have a similar influence on plant morphology. Differences between plant morphological responses to red/far-red and blue light will be associated with differences in the relative contributions of phytochromes and blue-sensitive photoreceptors (cryptochromes and phototropins) to inhibition of stem extension. A better understanding of the regulatory responses between species will help further improve lighting strategies and help us predict how other species are likely to respond to different light treatments.

3.6.2 Improving pigmentation

Primary metabolites are the chemicals that are directly involved in normal growth, development and reproduction, and loss of these compounds results in death. Plants also produce many other compounds, known as secondary metabolites, that act

to improve the fitness of an organism and help it acclimatise to a changeable environment. Many of these compounds convey qualities that are desirable by humans such as colour, flavour, and aroma. The production of many secondary metabolites is regulated by light. In this section we will examine the influence of light on the secondary metabolites apparent to the human eye: pigments.

Red, far-red, and blue light have all been implicated in driving synthesis of the pigments required for photosynthesis (Tripathy and Brown 1995; Miyashita *et al*, 1997; Tanaka *et al*, 1998; Kim *et al*, 2004a; Huq *et al*, 2004; Moon *et al*, 2006; Li *et al*, 2010). Blue and red light cause an increase in chlorophyll levels, whereas far-red results in lower levels. As well as influencing the appearance of plants, these changes can also alter the rate of photosynthesis and therefore impact plant growth rates. The link between secondary metabolites and photosynthesis comprises an additional layer of complexity that should be considered when designing light recipes. When a light recipe is designed to enhance the production of pigments such as anthocyanins, the pigments filter out some of the light that would be used for photosynthesis, thus reducing photosynthetic and growth rates. In experiments where light recipes are changed to increase pigmentation, there will be a reduction in the photosynthetic rates (Hogewoning *et al*, 2012) which may result in a subsequent decrease in pigmentation. Maintaining the desired pigment concentration would almost certainly require a higher intensity of light.



Figure 11. Light quality can greatly alter the anthocyanin concentration of lettuce plants

Many crops have red-coloured leaves or flowers that are distinctive and desirable. Maximising pigmentation is important to retain quality for customers. Red pigmentation is mainly provided by two types of compound: anthocyanins and betacyanins. Anthocyanin synthesis is regulated by many different biochemical pathways, but blue-light via the cryptochromes (Ninu *et al*, 1999) is an important signal for driving synthesis. In lettuce, supplying supplemental LED lighting of different colours against a background of fluorescent white light resulted in increases in leaf anthocyanin, xanthophyll, and β -carotene concentrations (Li *et al*, 2009). UV-A and blue light both increased the anthocyanin concentration, with blue light prompting the largest increase. By contrast, far-red light and green light reduced anthocyanin concentration, and far-red light also reduced chlorophyll, xanthophyll and β -carotene content. UVB was also shown to be a potent stimulator of anthocyanin production in lettuce (Park *et al*, 2007) and UV transparent spectral filters have been demonstrated to increase plant and flower pigmentation (Paul *et al*, 2006).

Betacyanins have replaced anthocyanins as red pigments in the Caryophyllales Order (excluding the families Caryophyllaceae,

the family that contains *Dianthus*, and Molluginaceae; Sakuta 2014). The Caryophyllales contains 6% of all eudicots (~11,155 species) and includes the Amaranthaceae, (the family that contains spinach, swiss chard, and beetroot). Unlike with anthocyanins, betacyanins have not been shown to increase in concentration in response to blue/UVB light. These pigments instead appear to accumulate in response to red light and their synthesis is thought to be controlled by the phytochromes (Elliott 1979). This means that, while the red pigmentation of many species could be improved by increasing the amount of blue light, it is probable that plants in the Caryophyllales Order will improve their red pigmentation on provision of more red light. This is one example of how understanding the biology of plants can help direct light recipe design.

Other pigments are also influenced by light quality. Carotenoid concentration was found to be greater in Buckwheat seedlings grown under white compared to 100% blue or red light (Tuan *et al*, 2013). It should be noted that few plants perform well under 100% red or blue light, and a combination of red and blue may produce as many carotenoids as white light. Polyphenols in chrysanthemum were at their highest levels when grown with red or green supplemental lighting and at their lowest levels when grown with blue supplemental lighting. However, the plants grown under blue light flowered and this flowering may have influenced the production of secondary metabolites.

3.6.3 Improving flavour and aroma

As described above, spectral manipulation has been shown to alter the production of pigments in a wide range of species. Large differences in pigment contents can alter the flavour of crops, but light is also important in regulating the biosynthesis of many of the compounds that function to directly alter the flavour and aroma of leaves, fruits, and flowers. UVB light exposure has also been linked to increased oil and volatile contents in a range of herb species including sweet flag (*Acorus calamus* L.; Kumari *et al*, 2009), Japanese mint (*Metha arvensis* L var. *piperascens*; Hikoaka *et al*, 2010), lemon balm, sage, lemon catmint (Manukyan 2013), *Cymbopogon citratus* (Kumari & Agrwal 2010), and basil (Bertoli *et al*, 2013). Other regions of the spectrum are also of importance in influencing the flavour and aroma of crops.

In basil plants, blue light was found to increase the oil content of leaves in comparison to white light treatments (Amaki *et al*, 2011). In the same study, green and red light were found to have little effect on oil contents, although green light was shown to increase crop biomass production compared to other light treatments. While more blue light can increase oil and other secondary metabolite contents, it is not always sufficient to simply provide more blue light. In basil plants grown under 100% blue light, Rosmaric acid (RA) levels were 3 mg l⁻¹; however, under 100% red or white light the RA concentration reached 6mg l⁻¹ (Shiga *et al*, 2009). A possible reason for the lower level of secondary metabolite production observed in this study was that the photosynthetic rate under blue light was lower than under red or white light. Data from Manukyan (2012) indicated that increasing PAR led to an increased production of secondary metabolites. It is important to provide plants with sufficient light to drive enough photosynthesis as this provides the metabolic building blocks for the various biosynthetic pathways as well as stimulating the biosynthetic pathways to maximise production of desirable compounds. As with the other aspects of plant growth under LEDs, some light

recipe development will be required to optimise crop flavour as increasing the production of some compounds may reduce the concentrations of others and this will impact flavour.

In the majority of research, the influence of light quality on crop quality is considered during the period of crop growth. More recently, the effect of post-harvest light treatments has been considered. Post-harvest light treatments provide the potential to enhance crop qualities during transport or prior to sale or to delay the onset of senescence thus extending shelf life. Costa *et al*, (2013) found that exposure to two hours of low intensity red light (30-37 μmol m⁻² s) delayed senescence of basil leaves for two days during storage at 20°C in the dark. The authors concluded that the effects were due to changes in gene expression mediated by phytochromes, which mediate cell senescence in low light conditions, rather than via photosynthetic carbon gain. Colquhoun *et al*, (2013) showed that post-harvest light treatments of petunia, tomatoes, blueberries, and strawberries could alter the volatile compounds produced by the different crops. Red and far-red light treatments of eight hours were found to increase several volatile compounds in petunia that are known to be important components of flower scent. Fewer compounds were examined in strawberries and tomatoes, but both large increases and decreases were observed in volatile compounds in these crops following exposure to different light treatments.

Changing the light spectrum can cause some compounds to increase while others may decrease. While it is apparent that light treatments increase the concentration of certain compounds, it is not always understood how these changes may impact crop flavour. Many of the studies focus on just one or two compounds, but flavour is influenced by a large range of compounds. Due to the limits of our understanding regarding the ways in which secondary metabolites are influenced by light and how these influence flavour, it is currently more efficient to develop light treatments for improved flavour by trial-and-error. The compounds of importance, and their synthesis in response to light, can subsequently be elucidated.

3.7 Lighting strategies

Light recipe design will be affected by different aspects of plant quality as, for example, optimal flavour may be found in plants with poor morphology. In these cases, the best light treatment may require a compromise to achieve the best balance of different desirable qualities. However, with the flexibility of LED lighting there is the possibility to develop lighting programmes that change through crop development to optimise different qualities at different stages of development. For example, enhancing red pigmentation just prior to harvest could reduce the growth rate/yield penalty that those pigments impose while still maximising plant appearance at sale.

LEDs also provide the opportunity to implement dynamic lighting systems for use in glasshouses. Dynamic lighting systems that turn off the lamps when the solar light intensity is above a certain intensity or if the desired daily light integral has been exceeded are not restricted to only LEDs and are already widely implemented across the industry. However, LEDs could allow the refinement of such systems to increase the frequency at which the lamps can be turned on and off, such as to match passing clouds, or to change the spectrum through the day to maintain the control of morphology while minimising energy inputs. For instance, to maintain control of crop morphology

it may only be necessary to provide blue light at dawn and dusk when the natural light intensities are low. Such lighting strategies will require further research to identify the optimal ways of implementing such systems, but these strategies provide the potential to greatly reduce energy inputs while improving plant quality.

3.8 Other lighting techniques

Unlike traditional lighting systems, LEDs can be turned on and off rapidly (hundreds of times per second). This creates the opportunity to potentially maximise the photosynthetic performance of crops while minimising the energy inputs. In theory, it would be possible to pulse the light in such a way as to deliver the correct amount of light energy to excite every photosystem in a leaf without inducing the array of energy dissipation mechanisms that help protect plants from damage under natural conditions. This would help maximise the light use efficiency of plants. Tennessen *et al.*, (1995) demonstrated that, so long as the intervals between light pulses was less than 200 μ s, the amount of photosynthesis was proportional to the total amount of light provided to the plants. Jao & Fang (2004) observed that potato plantlets grew fastest when light was pulsed at 720Hz. They also noted that, if energy consumption reduction was the main aim, pulsing the light at 180Hz provided the most energy-efficient system. Shimada & Taniguchi (2011) found that pulsing red and blue light out of phase affected both the photosynthetic rate and the morphology of the plants compared to providing the light pulses in phase. While these experiments provide interesting results from the perspective of how plants sense and use light, the most pronounced physiological effect on the plants was an increased shade avoidance response, which is of no benefit for most horticulture applications. Currently, the additional costs associated with designing LED lighting systems with these capabilities would make them impractical. Finally, pulsed light would not function as desired in a glasshouse setting where natural light is present. Several research groups are attempting to develop lighting systems that are controlled by sensors to modulate the light regime to match the current needs of the plants. In the near to medium term these systems are expected to remain in the research laboratory as they are likely to be prohibitively expensive for commercial applications.

Mobile lighting systems can be used to light crops. This implies that fewer lamps could be needed to light a given area, which would greatly reduce installation costs. There are no technical reasons for mobile systems to require LED lamps rather than other types of lamp; however, the increased robustness of LED lamps lowers the risk of lamp damage and injury to crop workers. Mobile systems have two major limitations: the amount of light supplied to plants is lower, and maintenance of the systems for moving the lamps is needed. Maintenance and installation costs could be low if existing mobile irrigation booms were used to mount lamps. Li *et al.*, (2014) showed that lettuce plants could be grown under mobile lights; however, in their system, only half as many lamps were used as with the fixed LED treatment. For substantial savings in light installation costs to be achieved, the lamps would need to cover a much greater area of crop and this necessarily reduces the amount of light that can be supplied to the plants. In addition, to provide a large amount of light to the plants as is required to maintain plant growth, light intensity would need to be high as the lamps pass the plants.

Plants, however, can take up to 45 minutes to achieve maximum photosynthetic rates (Kirschbaum & Percy 1988) meaning that much of the light provided by a mobile lamp passes may not be used for photosynthesis. In instances where only low doses of light are required (for example, end-of-day light treatments or UVC/UVB treatments), mobile lights mounted on irrigation booms may provide an economically viable way of installing lamps.

3.9 Insect management under LEDs

Light is a highly important environmental cue for all insect species. Several aspects of the light environment influence insects, such as daylength, intensity, direction, polarisation, spectrums, and contrast. These environmental cues influence many insect biological and behavioural responses including the circadian rhythm, host identification, take off and landing frequency, reproductive success, phototaxis (movement towards or away from light), and feeding frequency. Improving our understanding of insect light responses will be important to ensure both pollination and pest control can be maintained under LED light sources. There are two main aspects to consider: 1) the direct effect of light quality on insect responses, and 2) the effect of the host species' responses to light quality on the insect of interest.

Our knowledge of the spectral sensitivity of insect vision is limited to a few species, but the diversity between species is considerable. For example, bees are able to see UV (peak absorbance ~350nm), blue (peak absorbance ~450nm) and green (peak absorbance ~550nm) light but have low sensitivity for red light (Backhaus 1993). Many insects are also able to detect the polarisation of light and use this information to navigate (Rossel 1993, Reppert *et al.*, 2004). The pest *Caliothrips phaseoli*, a thrip species that attacks soy, has one photoreceptor that can only detect UV (UVA and UVB) light, and these insects are, therefore, blind to PAR. However, spectral sensitivity in this species is enhanced: some of the eyes also contain pigments that fluoresce under UVA light, and this acts as a UVA filter so those eyes only detect UVB light. This allows the insects to distinguish UVB from UVA even though they only have one photoreceptor (Mazza *et al.*, 2010). Western flower thrips (*Frankliniella occidentalis*) see both visible and UV light. Males and females have similar visual responses but have different swarming behaviours, with males more likely to gather on flowers than females (Matterson *et al.*, 1992). Behavioural responses to light, both innate and learned, provide added complexity to insect light responses that will provide added challenges to understanding and manipulating insect light responses.

A better understanding of pest light responses can be used to improve traps for monitoring insect populations. Making traps more attractive to insects can render them more effective, which enables earlier identification of pest issues. Green LEDs have been used to increase trap effectiveness for West Indian sweet potato weevils (*Euscepes postfasciatus*; Nakamoto & Kuba 2004), Whitefly (*Bemisia tabaci*), Greenhouse whitefly (*Trialeurodes vaporariorum*), Fungus gnats (*Bradysia coprophila*), and Aphids (*Aphis gossypii*; Chu *et al.*, 2003; Chu *et al.*, 2004). In environments with no natural light, trap effectiveness will be far more strongly influenced by the colour of the traps and the colour of the LEDs than in glasshouses where natural light dominates.

Indirect effects of light quality on pests are caused by plant responses to light. In a species of wild tomato (*Lycopersicon hirsutum*), seasonal changes in day length and quantity cause large changes in synthesis of 2-tridecanone resulting in much greater concentrations in June than in January (Kennedy *et al.*, 1981). When caterpillars of *M. sexta* were fed on tissue from plants grown in January, 8% died, while 87% perished when fed on plants grown in June. More subtle effects are likely to influence pest performance on crops grown in different light conditions. Plants produce a range of volatile organic compounds (VOCs) that act as attractants to both pests and beneficial insects. Changes in light quantity (Pare & Tumlinson 1999) and quality (Kegge *et al.*, 2013) alter the production of VOCs and spectral manipulation may help enhance VOC production to maximise crop protection.

3.10 Plant pathogens and their interactions with light

The interactions between plants and their pathogens are also influenced by the light environment. Light affects many aspects of plant biology and many of these responses influence plant resistance to disease. The red:far-red ratio in particular has been shown to influence the expression of many genes, via the phytochromes, that are involved in disease resistance (Greibel & Zeier 2008). Low red:far-red ratios decrease the production of many secondary metabolites involved in disease resistance and thus reduce resistance (Ballaré *et al.*, 2012). Salicylic acid (SA) and jasmonic acid (JA) both play important roles in mediating defences against pathogens and low red:far-red ratios have been shown to reduce the response of both pathways to disease attack (de Wit *et al.*, 2013).

Light will also have direct effects on fungal pathogens as they also possess an array of photoreceptors than modulate their gene expression (Corrochano 2007). Fungi have circadian rhythms (Liu & Bell-Pedersen 2006) and certain species sporulate at specific times of day to coincide with events that enable them to infect plants, such as during times when leaves are likely to be wet. Rose powdery mildew (*Podosphaera pannosa*) was found to release spores during the day and more spores were released with brighter light (Suthaparan *et al.*, 2010). Colour of the light was also important: compared to white light, more spores were released under blue and far-red light and fewer spores were released under red light. Both day-extension and nightbreak light treatments with red light were also found to greatly reduce the release of mildew conidia and this may provide a good method for reducing the intensity and spread of mildew in crops. As powdery mildews are obligate pathogens, it is not possible to determine if the effect of the light treatments occurs as a direct effect on the pathogen or a result of the plant responses. However, red light treatments have also been found to increase disease occurrence in two broad bean diseases: *Alternaria tenuissima* and *Botrytis cinerea* (Islam *et al.*, 1998). Spore germination rates were also affected by light colour, with blue light reducing germination by 16.5% compared to other treatments. The spores of many plant pathogens are killed by exposure to solar radiation (Kanetis *et al.*, 2010). The UVB component of solar radiation is the most likely region of light to be causing spore death. Models of spore germination could be used to define the best time of day to provide a pulse of UV light that would maximise effectiveness. It may also be possible to use novel light strategies to increase disease control. Blue light

inhibits spore germination, so if red light only is provided early in the day, spores will germinate and they can then be more easily killed with a UV pulse before the blue light is again turned on. UVC light has also been trialled for the control of plant diseases. For these treatments to be effective, it is important to make sure that treatments are applied when the pathogens are vulnerable. If the UV light is provided before sporulation or after infection then it will be ineffective at providing protection. If applied during the germination of the spores, UVC can be effective at preventing infection. Designing the light scheme to co-ordinate UVC application with spore release may be an effective method for controlling disease in controlled environment chambers. Care should be made when using UVC light as it can easily damage plant tissues if exposure is too high and this wavelength can pose a health hazard for staff.

Just as different plant species have different light responses, the light responses of different pathogens vary, as do the interactions between different plant/pathogen systems in response to light. Schuerger & Brown (1997) observed that in tomatoes infected with bacterial wilt (*Pseudomonas solanacearum*) and cucumber plants infected with powdery mildew (*Sphaerotheca fuliginea*) disease symptoms were at their lowest in plants grown under 100% red light. By contrast, for tomato mosaic virus (ToMV) on pepper plants, disease symptoms were slower to develop and less severe in plants grown in the presence of blue/UVA light. These data indicate that spectral modification could be used as part of an integrated disease management system as long as the correct light treatments can be selected and/or achieved.

3.11 Conclusions

LED lights are more energy efficient than other types of lighting system and provide the potential to reduce energy consumption of lit crop production. LEDs, however, provide many additional benefits to horticulture through spectral manipulation of crops. Red and blue mixtures of light provide the most energy efficient method of producing light for crops. Red and blue can effectively drive photosynthesis and control plant morphology. Both red and blue light are required in most cases to produce healthy plants but the optimal red:blue mix differs greatly between species and application. While red and blue light are often sufficient to produce healthy crops, other colours can improve crop performance and far-red light may be required for flower production in certain species. For all light combinations, some development of light spectra may be required to optimise crop performance. However, currently available LED lighting systems can produce crops that are equal or higher quality than traditional lighting systems and, while spectral optimisation may provide additional benefits, optimisation may not always be necessary. The benefits of LEDs span all areas of crop production and crop qualities. Spectral manipulation can effectively improve propagation, crop morphology, pigmentation, flavour and aroma. The benefits of LEDs can even be applied post-harvest to improve crop quality prior to sale. LED lighting systems for horticultural purposes are new but have already demonstrated many benefits to the industry. The speed at which this technology is developing is expected to result in further improvements in energy efficiency and also lead to additional applications.



SECTION FOUR

Other information

4.1 References

A

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