# A PLANT PHYSIOLOGIST'S VIEW OF THE PERCEPTION OF LIGHT AND COLOR BY PLANTS

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Abstract: The accurate reporting of the light (radiant energy) environment in plant-related plasticulture research is important to help further our understanding of light and color effects on plants and in the development of new and effective plastic materials to use in the plant industries. Unfortunately, some of the measurements used in reporting the light environment in plant research is directed toward human vision quantification using units such as lux or foot candles. The pigment systems of human eyes and plants are different and as a result the light parameters reported for human and plant systems should also be different. The plant light environment must be quantified using the wavelengths important for the pigment systems of photosynthesis (PAR wavelengths) and, when appropriate and possible, photomophogenesis (red, far-red, and blue light wavelengths).

Keywords: Light, radiant energy, measuring, reporting.

## Introduction

In recent years there has been an increase in research devoted to light (radiant energy) and, in particular, color perception by plants. Included among this research in the plasticulture field is the effect of reflective mulches on plant growth and development (e.g. Brown et al., 1992; Decoteau et al, 1990). In some cases (more often in popular press articles), the reporting and interpretation of color perception effects on plants is according to human vision characteristics. While human vision characteristics may be easier to report and understand, it does not give a good indication of the physiological effects of light wavelengths on plant development. In this paper we will discuss light, color, perception of light and color by humans and plants, and make some recommendations for reporting the plant light environment, especially as it applies to research in the plasticulture field.

## Light - Radiant Energy

All light is made up of energy. Light to humans is the wavelengths of radiant energy in the electromagnetic spectrum that activates the light receptors in our eyes. When these light receptors are activated, the impulses are interpreted by our brain and we experience vision.

Light to plants is all the wavelengths of the electromagnetic spectrum including the wavelengths that humans can see (visible light) and the wavelengths that humans can't see (such as microwaves and infra-red light).

Light in human or animal vision typically acts only as a medium for transferring information about position and movement, shape and color of material objects. The human and animal interest in light perception is mainly centered on food, enemies, seeking other members of the same species for reproduction, etc. (Bjorn, 1994).

Light for the plant is not only used as an informational medium, but also for producing food through the process of photosynthesis. The characteristics of direction and spectral composition of light in the plant's environment is transferred to the plant through the interception and activation of pigment systems. This information affects the morphological development (root and shoots) of the plant, hopefully imparting to the plant some type of ecological or physiological advantage for survival. Plants also use light for sensing and detecting competitors and keeping track of time.

## Color - The Wavelength Distribution of Radiant Energy

According to the *Random House Webster's College Dictionary* (1992 edition), color is "the quality of an object or object with respect to light reflected by it, usually determined visually by measurement of hue, saturation, and brightness of the reflected light". This definition of color contributes to some of the inconsistencies in reporting radiant color characteristics in plant research, since the definition's criteria is set to human vision. In plant physiological research, a more appropriate definition of color would be the relative distribution of wavelengths from a radiation or reflective source.

## Perception of Light and Color by Humans and Animals

Light sensitive cells exist in almost all organisms. For example, some protozoa have "eye spots", which are more sensitive to radiant energy than the rest of the cell. Even what may be considered more primitive are the evolutionary scales of the flatworm. These scales are bowl shaped structures containing black pigments, at the bottom of which are clusters of light sensitive cells.

The development of eyes appears to have come later in evolution. The necessary first step was the development of lenses to concentrate light on a group of photoreceptors. As better lens systems evolved, the photoreceptors became able to form images, and an eye was formed.

Quanta of light striking the rods or cones of the eye trigger the emission of a nerve impulse by the receptor cell. These nerve structures are ready to discharge, having been charged with requisite energy by internal chemical reactions.

The prime function of the cones of the eye is to perceive colors. There appears to be three different types of cones in the eye, which respond respectively to blue, green , and red light. Intermediate colors other than blue, green, and red are perceived by simultaneous stimulation of two or more types of cones (Villee, 1977).

## Plant Uses of Radiant Energy and Plant "Vision"

Plants utilize specialized pigments to intercept and capture radiant energy. For example, plants capture the energy in light during the process of photosynthesis. Photosynthetic wavelengths (400-700 nm) activate the chlorophyll pigments, which transforms light energy into chemical energy for production of carbon metabolites that are then used to synthesize plant cellular components.

Plants also monitor radiant energy as an indication about the environment in which they are growing in and for adjusting plant growth. This monitoring of the light environment may be considered plant "vision" and would be more correctly termed photomorphogenesis.

Photomorphogenesis is defined as the ability of light to regulate plant growth and development, independent of photosynthesis. Plant processes that appear to be photomorphogenic include internode elongation, chlorophyll development, flowering, abscission, lateral bud outgrowth, and root and shoot growth.

Photomorphogenesis involves the activation of several receptor (pigment) systems (Senger and Schmidt, 1994). These pigment systems include phytochrome, which absorbs red (R) light (660-680 nm) and far-red (FR) light (730-740 nm), "cryptochrome", which absorbs UV-A and blue light (400-500 nm), and a UV-B receptor (290 nm). These receptors detect the light environment and subsequently influences plant growth and development.

The process of photomorphogenesis differs from photosynthesis in several major ways. The primary plant pigment responsible for light-regulated growth responses is phytochrome. Phytochrome is a colorless pigment that is in plants in very small amounts. Only the red (600 to 660 nm) and far-red (700 to 740 nm) wavelengths of the electromagnetic spectrum appear to be the most important in the light-regulated growth of plants. The wavelengths involved in generating photosynthesis are generally broader (400 to 700 nm) and less specific.

Photomorphogenesis is also considered a low energy response - meaning that it requires very little light energy to get a growth-regulating response. Plants generally require greater amount of energy for photosynthesis to occur.

Plants monitor the environment by sensing changes in the quality, quantity, duration, and direction of light. Light perception in plants is a sequential process. Light is absorbed by the phytochrome photoreceptor, and the photoreceptor is transformed to the Pr or Pfr form. A ratio of the two forms of phytochrome (Pr and Pfr) is established depending on the spectral characteristics of the light. A message is then perceived by the plant which influences the balance of endogenous growth regulators and stimulates a plant growth response.

## Measuring Radiant Energy

There are several ways to measure and characterize radiant energy. These include radiometry, photometry (including photosynthetic active radiation), colorimetry, spectroradiometry, and spectrophotometry.

*Radiometry* is the measurement of energy flow in a broad band of wavelengths. Typical units for the radiometer include W $m^{-2}$ (irradiance), W $ster^{-1}m^{-2}$ (radiance) and W $ster^{-1}$ (intensity).

*Photometry* is the measurement of energy by the human eye. An ideal photometer has a spectral response as defined by the Commission Internationale de l'Eclairage (C.I.E.) "standard observer". Lux is the integrated spectral irradiance weighted by a special weighing function. The weighing function is precisely defined (Figure 1), but can be thought of as the average (photopic) eye sensitivity for a large number of people. The photopic curve indicates the areas of wavelength sensitivity for human vision. Typical units for the photometry include lux (illuminance), foot-candle (illuminance), candela m-2 (luminance), and candela (luminous intensity).

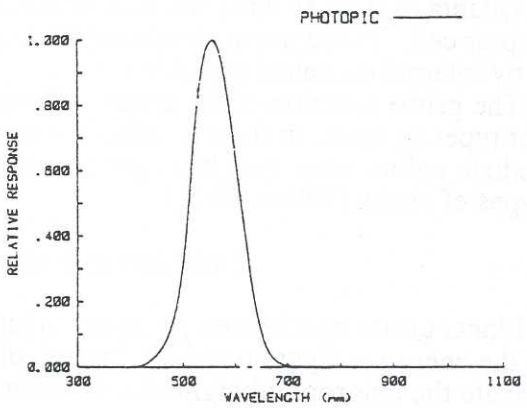


**Figure 1. CIE Standard Observer spectral response for human vision (from LI-COR, 1982)**

*Colorimetry* is the measurement of color in the 1932 CIE standard colormetric system. Typically, chromaticity coordinates (x,y,z) are reported.

*Photosynthetically Active Radiation (PAR)* is the measurement of energy utilized by plants for photosynthesis. A quantum sensor is used to measure PAR and has a uniform response in the wavelength region from 400-700 nm. Typical units for the quantum sensor include photon $s^{-1}m^{-2}$ (photon flux density), microeinstein $s^{-1}$ $m^{-2}$ (photon flux density), and mircomole $s^{-1}m^{-2}$ (photon flux density).

*Spectroradiometry* is the measurement and analysis of the energy emitted by a radiation source or incident on a surface, at different wavelengths. Typical units include W $m^{-2}$ ($nm^{-1}$) (spectral irradiance), Watts $ster^{-1}$ $m^{-2}$ ($nm^{-1}$) (spectral radiance), Watts $ster^{-1}$ ($nm^{-1}$) spectral intensity. In addition, if we convert to quantum measurements we have micromoles $m^{-2}$ $s^{-1}$ ($nm^{-1}$).

*Spectrophotometry* is the measurement and analysis of the specular or diffuse reflective, adsorptive, or transmissive qualities of a gas, liquid, or a solid as different wavelengths. Typical units used in

spectrophotometry are dimensionless and include percent R,T or T (as a function of wavelength or optical density).

Note: The publication *Radiation Measurements and Interpretation* (LI-COR, 1982) served as the primary reference source for the above section.

## Reporting the Light Environment in Plant Research: Problems

Strictly speaking the use of the word "light" is improper to use in plant research (since light defines the electromagnetic radiation as sensed by the human eye), but it is still conventionally used. Early measuring devices used filters to simulate the same response as the human eye and were termed light meters, with units of lux or foot-candles. Since most plant responses are stimulated by the same wavelengths of radiation as those we see, many light readings were taken and reported in the early literature.

In plants, several different light absorbing pigments exist, each with its own absorption and action spectrum. Therefore, various plant functions respond to different spectral bands of light with different efficiencies. It is obvious that plant pigments are not similar to the pigments responsible for vision; therefore, photometric measurement of light for plant studies is not appropriate.

## Reporting the Light Environment in Plant Research: Recommendations

Guidelines exist for measuring and reporting environmental parameters, including the light environment, in growth chamber and greenhouse research (ASAE, 1986, Krizek and McFarlane, 1983; Spomer, 1981). For most types of field research, such guidelines are not available. Regardless, consistent reporting of the light environment in plant research must be followed, including accurate and descriptive reporting of photosynthetic radiation and photomorphogenic radiation.

## PHOTOSYNTHETIC RADIATION

Photosynthetically active radiation is well established as the primary measurement for quantifying radiation of the plant light environment. The action spectra for photosynthesis of 22 crop plants is presented in Figure 2.

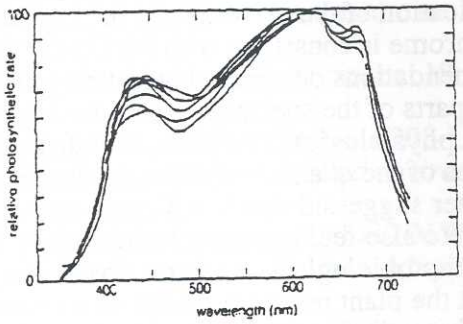


**Figure 2. Action spectra for photosynthesis of 22 crop plants (from Salisbury and Ross, 1992).**

The following guidelines put forth by LI-COR (1979) and generally accepted by most plant science journals should be followed in the reporting of photosynthetic radiation:

*Units*

The mole (instead of the Einstein) should be used as the unit to designate Avogadro's number of photons. In general, the quantity of photons in a mole is equal to the quantity of photons in an Einstein (i.e., 1 Einstein = 1 mole = $6.02 \times 10^{23}$ photons).

*Terminology*

Photosynthetically Active Radiation (PAR) is defined as the radiation in the 400 to 700 nm waveband. PAR is a general term that covers both photon terms (photosynthetic photon flux density) and energy terms (photosynthetic irradiance).

1. Photosynthetic Photon Flux Density (PPF or PPFD) is defined as the photon flux density of PAR. This is the number of photons in the 400 to 700 nm waveband incident per time on a unit surface. The appropriate unit is umol $m^{-2}$ $s^{-1}$

2. Photosynthetic Irradiance (PI) is defined as the radiant energy flux density of PAR. The is the radiant energy (400-700 nm) incident per unit time on a unit surface. The appropriate unit is Watts $m^{-2}$.

PHOTOMORPHOGENIC RADIATION

The second most discussed action of radiation on plants is its effects on plant development.

*Phytochrome Wavelengths (Red and Far-red Light Responses)*- Since phytochrome is the most implicated pigment involved in the regulation of plant development, the plant light environment must be characterized according to the absorption spectra or action spectra of phytochrome. The action spectra for various physiological processes is presented in Figure 3 (Salisbury and Ross, 1992).

Since phytochrome is found in both active (Pfr) and inactive (Pr) forms, the relative proportion of each form would be beneficial to know. Unfortunately it is not easily possible to measure the equilibrium (termed Pfr/Ptot) of phytochrome in green leaves. But reporting of the light environment in which phytochrome is implicated can take advantage of the close relationship of the hard to measure Pfr/Ptot and the more easier to measure ratio of photon flux densities at 660 and 730 nm (Smith, 1994).

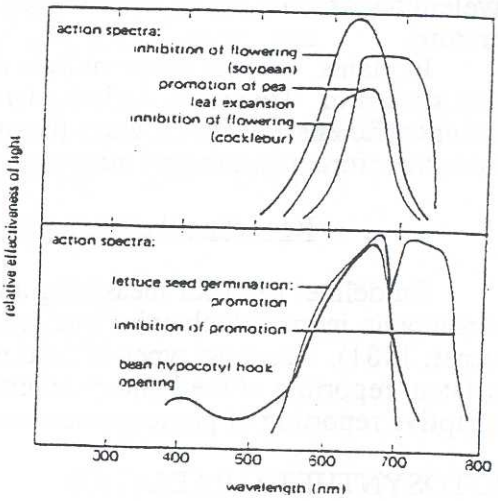


**Figure 3. Action Spectra for Various Physiological Processes (from Salisbury and Ross, 1992)**

The reporting specific wavelength ratios for the quantification of the wavelengths of light important to phytochrome is consistent with McCree's (1979) recommendations on spectral measuring. He suggested that certain parts of the spectrum should be identified with specific physiological responses, and that simplified measures of the quantity of radiation available to plants in these spectral regions should be developed. He further suggested that it was important to limit the number of wavebands to be specified.

We also feel it is unrealistic to expect complete spectroradiometric data for all experiments that are not photobiological in nature. Even if such data were available, the data would be hard to use to interpret the plant response results of an experiment unless action spectra for various plant responses were universally known.

In our experiments (which may be considered photobiological), we typically measure reflected light from a color of mulch (see Decoteau et al., 1990). We measure upwardly reflected light at a defined distance above the mulch surface (e.g. 10 cm) on a representative clear day at about solar noon light with a spectroradiometer. Our reflected light readings are then expressed as a percentage of direct sunlight at each measured wavelength (for a complete spectral scan) to determine shifts in spectral balance due to mulch color. If phytochrome is being implicated in our results then spectral irradiances corresponding to absorption and action maxima of phytochrome in the red and far-red (or conversely the far-red and red was done in many of our manuscripts) regions of the spectrum are reported. We use 645 and 735 nm to calculate the R:FR light ratios. Others have used broader band measurements (for an excellent review see Rajapakse and Kelly, 1994).

*"Cryptochrome" Wavelengths (Blue Light Responses)* - There are a series of well documented plant responses that have been attributed to radiation in the blue portion (400 to 500 nm) of the electromagnetic spectrum. Unfortunately, our knowledge on the action or even isolation of this

hypothesized pigment ("cryptochrome") is not as advanced as it is for phytochrome. In addition some of the plant's responsiveness to blue light may be attributed to perception and activation of phytochrome in these wavelengths (Mohr et al., 1984).

In research where light effects on plant development are not considered to be directly implicated to phytochrome but may be due to activity of the blue light receptor system ("cryptochrome"), the amount of blue light in the plant environment must be quantified and reported. In our research we have reported the quantum amount of radiation in the 400 to 500 nm wavebands. In addition, others have reported various ratios of red:blue and far-red:blue.

*Alternatives to Reporting the Plant Light Environment When a Spectroradiometer is not Available* - For experiments in plasticulture research where phytochrome (or any other photomophological pigment system) may be implicated in affecting plant growth and a spectroradiometer is not available for precisely measuring the light environment, an alternative to reporting integrated spectral measurements would be to provide a detailed explanation of the materials used in the study. This was recently done effectively by Brown et al (1992) in a mulch color evaluation. This reporting should include brand and type of plastic used, and material(s) used to modify the reflective, absorptive or transmissive properties of the plastic. The purpose of such a detailed listing would be to allow researchers in the future to reproduce the experimental design if more detailed radiation measurements were needed.

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