Plant Physiology: Manipulating Plant Growth with Solar Radiation

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Introduction
The importance of light in the growth of plants is a well-established phenomenon. A common observation is that plants grown in the dark are yellow (chlorotic), taller (etiolated), have thinner stems, and in general, are not so healthy looking.

Greenhouse plant producers also know the importance of light for proper plant production. They often grow plants with artificial lights, if sunshine is inadequate; or in a shaded area, if sunshine appears to be too plentiful (and hot) or if the plant producers are trying to slow the growth of the plants.

During this session the discussion will focus on (1) basic principles of light and plant development, (2) principles on light regulation of plant development in the emerging field of photomorphogenesis, and (3) alternative methods of regulating plant development that modifies the wavelengths of light that surrounds the plant.

Light – Radiant Energy
All light is made up of energy. 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 infrared light).

Light for the plant is used 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 (colored cells of the plant). This information affects the morphological development (size/proportion of root and shoots) of the plant.

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". Note that this definition is based on human vision. For our purposes, a more appropriate *definition of color would be the distribution of wavelengths coming from a radiation source, or reflected from a reflective object*.

Perception Of Light And Color By Humans And Animals
Light sensitive cells exist in almost all organisms. For example, some protozoa (single-celled organisms) 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.

Photons of light striking the rods or cones (photoreceptor cells) of the eye trigger the emission of a nerve impulse by the cell. 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 colors of 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 transform light energy into chemical energy for production of carbon molecules (sugars) that are then used to construct more complex compounds, and ultimately plant cells and organs (root, leaf, stem, flower, fruit).

Plants also monitor radiant energy within their environment for the purpose of adjusting their growth appearance. This monitoring of the light environment ("plant vision") and subsequent response is termed photomorphogenesis. Photomorphogenesis is more properly 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 (distance between leaves on stem), chlorophyll development, flowering, abscission (deleafing), lateral bud outgrowth, and root and shoot growth.

If photosynthesis is the "engine" providing the energy for plant growth, photomorphogenesis is the "steering wheel" to influence the direction and final plant appearance.

Photomorphogenesis involves the activation of several photoreceptor (pigment) systems (Senger and Schmidt, 1994). These systems include phytochrome, which absorbs red (R) light (wavelengths 660-680 nm) and far-red (FR) light (730-740 nm), "cryptochrome", which absorbs ultra-violet (UV-A) (320-380 nm) and blue light (400-500 nm), and a UV-B receptor (290 nm). These receptors detect the light environment and subsequently influence plant growth and development.

Plants monitor the environment by sensing changes in the quality (wavelength(s)), quantity (intensity), duration (length of exposure), and direction of light. Light perception in plants is a sequential process. Light must first be absorbed by the photoreceptor, and then the photoreceptor is transformed to either its Red (Pr) or Far Red (Pfr) form. Depending on the distribution of the wavelengths of the light, a specific proportion (ratio) of the two forms of the photoreceptor (Pr and Pfr) is established within the plant. This ratio becomes a "message" to the plant, and causes the production of plant growth regulators to stimulate a plant growth response.

Light Energy Capture By Plants - Photosynthesis
One of the main roles of light in the life of plants is to serve as an energy source through the process of photosynthesis. Using water and carbon dioxide, plants produce the "foodstuffs" necessary for growth and survival. Carbohydrates (starches and sugar) for plant components and stored chemical energy are produced during this biochemical process in plants.

Plants capture the energy in light using a green photoreceptor pigment called chlorophyll. In the research laboratory, chlorophyll can easily be extracted from plant tissue using chemical solvents. Chlorophyll can also be extracted by abrasion, as anyone who has ever pruned tomato plants by hand, or has gotten grass stains on their clothes, can attest.

Photosynthetic Radiation
Photosynthetically active radiation is well established as the primary measurement for quantifying radiation of the plant light environment. The action spectra (the wavelengths which activate photosynthesis) of 22 crop plants are presented in Figure 1.

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

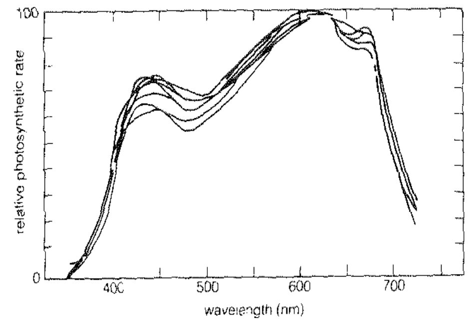

Figure 1. Action spectra for photosynthesis of 22 crop plants (from Salisbury and Ross, 1992).

Units
The mole is the unit for a very large number of photons. It equals 6.02×10^{23} photons (602 sextillion, or about a billion billion photons), and it is also designated as an Avogadro's number of photons.

Terminology
Photosynthetically Active Radiation (PAR) is defined as the photons of radiation in the 400 to 700 nm waveband. PAR is a general term that can describe either the photosynthetic photon flux density (PPF), or the photosynthetic irradiance (PI).

Photosynthetic Photon Flux Density (PPF, or sometimes written as PPFD) is defined as the photon flux density of PAR. This is the number of photons in the 400 to 700 nm (PAR) waveband contacting a unit surface area over a given time period. The appropriate unit is (micromol per square meter per second), or abbreviated as μmol m^{-2} s^{-1}.

Photosynthetic Irradiance (PI) is defined as the radiant energy flux density of PAR. This is the energy of the radiation in the 400-700 nm waveband, which is contacting a unit surface area over a given period of time. The appropriate unit is Watts per square meter, or abbreviated as W m^{-2}.

Light Regulated Plant Development - 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 differs from photosynthesis in several major ways. The plant pigment responsible for light-regulated growth responses is phytochrome, not chlorophyll. 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 important to influence the phytochrome pigments. The wavelengths, which affect photosynthesis, are broader (400 to 700 nm) and less specific.

Photomorphogenesis requires very little light energy (light intensity) to get a growth-regulating response. Plants generally require a greater amount of energy for photosynthesis to occur.

Photomorphogenic Radiation

Phytochrome Wavelengths (Red and Far-red Light Responses)

The second most discussed effect of radiation, after photosynthesis and its subsequent effect on plant growth rates, is photomorphogenesis and its specific effects on plant development. The wavelengths specific for phytochrome responses are Red and Far-red light. The plant light environment must be characterized according to the absorption spectra or action spectra of phytochrome, since phytochrome is the pigment involved in the regulation of plant development. The action or response spectrum is indicated by the wavelengths that will cause a plant response. The action spectra for various plant physiological processes are presented in Figure 2 (Salisbury and Ross, 1992).

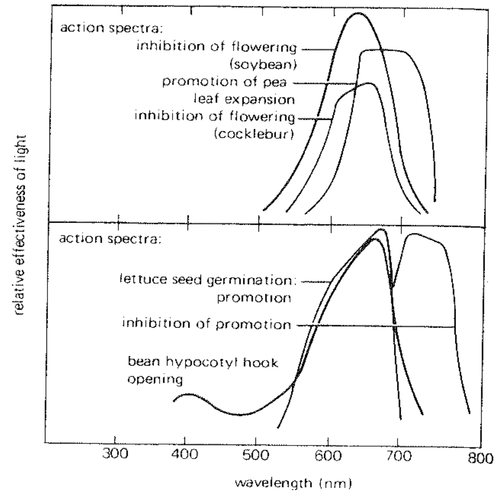

Figure 2. Action spectra for various physiological processes (from Salisbury and Ross, 1992).

Phytochrome is found in both active (Pfr) and inactive (Pr) forms. The relative proportion of each form is beneficial to know, since it is this proportion, which determines the type of plant response. Unfortunately it is not easy to measure the proportion of active and inactive forms of phytochrome directly. However, separately measuring photon flux densities at 660 nm and 730 nm offers an indication of the proportion of Pfr to Ptotal in the plant (Smith, 1994), and provides (Pfr/Ptot) which is the proportion of Far-red "active" form to the total phytochrome in green leaves.

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 and reporting. He suggested that certain parts of the radiation spectrum were identified with specific physiological plant responses, and that simplified measures of the quantity of radiation available to plants in those spectral regions should be reported.

It is unrealistic to expect complete spectroradiometric data (the intensity of light at each wavelength) for all experiments, and specifically for those, which 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, because the action spectra for various plant responses are not universally known.

"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 the location of this hypothesized plant pigment ("cryptochrome") is not known. 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

Current Methods To Regulate The Growth Of Plants

The ability to control plant development is important for many plant producers. Current methods used for growth regulation of plants include the use of plant growth regulators, temperature regulation of day and night temperatures in a relatively new method called "DIF", or applying mechanical (seismic) stress. Other than chemical growth regulators, none of these alternative methods has been completely acceptable for widespread use by commercial plant producers.

The use of chemicals in agriculture is continuously being scrutinized for deleterious effects on the plants, humans, and the environment; and no chemical growth retardant is registered for use on vegetable transplants. The use of regulation of temperature has shown some promise in regulation of plant development but it is potentially expensive to implement since it often requires the cooling of day temperatures to that below night temperatures. Mechanical stress may offer some control in plant growth but this requires the potentially abrasive touching or agitation of the plants. An alternative method of growth control is needed by the industry.

Using Light To Regulate Plant Growth In The Greenhouse
It has been shown in a wide variety of experiments that plant growth and development could be regulated by modifying the relative amounts of wavelengths of light reaching the plant.

<u>Exposing the Plants to Red and Far-red Light</u>
Transplants of tomatoes and peppers were exposed to either End-of-Day (EOD) red (R) light or far red (FR) light, each day, for four weeks in a controlled environment room. A treatment for comparison received no EOD R or FR light. R and FR wavelengths were generated by filtering light from fluorescent and incandescent light sources, respectively. After four weeks of light treatments, the transplants were then placed in large pots in the greenhouse under ambient light conditions to evaluate subsequent growth and yield. The plants treated with EOD FR were taller and had longer total leaf lengths or larger leaf areas than plants either treated with EOD R or plants not treated with EOD light (Table 1). For example, tomatoes treated with Far red light were 44% taller than the control, but tomatoes treated with Red light were 10% shorter than the control. EOD light during transplant production had no effect on subsequent fruit production.

Table 1. Effect of End-of-Day (EOD) treatment of tomato and pepper transplants on plant height and leaf lengths or leaf area.

EOD	Tomato		Peppers	
Light	Plant height (cm)	Total Leaf Lengths (cm)	Plant height (cm)	Leaf area (cm^2)
Red	9.1	88.7	43.7	2524
Far red	14.5	115.2	51.8	3170
Control	10.1	102.0	43.8	2357
Significance	*	*	*	NS

NS, *: Not significant or statistically insignificant.

<u>Supplementing the Greenhouse Light Environment with Fluorescent Light</u>
In another experiment, tomato and pepper transplants grown in a glass greenhouse were treated with supplemental cool-white fluorescent light each day for one hour before sundown for a period of six weeks. Fluorescent lamps enrich the environment with Red wavelengths, and they have been used is in previous photomorphogenesis research as a Red light source. A control treatment consisted of no supplemental fluorescent light. Transplants were then placed in the field at Clemson, SC to evaluate subsequent growth and yield.

Prior to transplanting to the field, tomato and pepper plant height and leaf areas were reduced in plants treated with supplemental fluorescent light (enriched Red light) (Table 2). Plant height was reduced by 16% compared to the control for both tomato and pepper. Subsequently, this supplemental fluorescent light treatment reduced plant height, leaf area, and fruit weight and number prior to first fruit harvest in the field. Total fruit production of tomatoes and peppers was not affected by fluorescent light treatment.

Table 2. Tomato and pepper plant growth as affected by EOD supplemental fluorescent light prior to transplant.

EOD treatment of transplant	Before transplanting	
	Height (cm)	Leaf area (cm^2)
Tomatoes		
EOD	18.6	75.3
Control	22.1	90.3
Significance	*	*
Peppers		
EOD	12.3	99.11
Control	14.6	113.87
Significance	*	*

NS, *: Not significant or statistically insignificant.

Filtering out FR Light Using the Greenhouse Covering

As an alternative to adding more Red light, a similar effect can be obtained by removal of Far-red light, as a means to modify the R:FR ratio from the natural solar radiation. Using liquid copper sulfate ($CuSO_4$) filters, reduced plant height in *Rosa x hybrid* 'Meirutral' (McMahon and Kelly, 1990) and chrysanthemum (*Dendranthema* x *grandiflorum* (Ramat.) (Rajapakse and Kelly, 1992). However, the use of $CuSO_4$ filters is not practical in commercial horticulture due to the difficulty in handling, maintenance, as well as the phytotoxicity of $CuSO_4$ if leakage occurred.

Several formulations of photoselective plastic panels which contained poly-methyl methacylate resin (PMMA) and a FR intercepting dye have been developed (Mitsui Chemicals Inc., Japan) and are under investigation for use as a plant growth control method in commercial horticulture (Ranwalla et al., 1999). The objective of the research was to evaluate the effects of these photoselective panels on watermelon plant growth.

Four experimental formulations of treatment panels, a control (no dye), and a liquid CuSO4 filter were evaluated as greenhouse covers. The resulting R:FR ratios of transmitted solar radiation for the control (no dye) was 1.1 and for the CuSo4 filter was 12.7. The resulting R:FR ratios for the four experimental formulations were 1.6, 2.7, 4.1, and 6.6. The various formulations of treatment panels had no effect on seed germination. With a R:FR of 1.6, seedling height was reduced by 21% and shoot dry mass was reduced by 26%, while the leaf chlorophyll was increased by 21%, when compared to control. However, the R:FR of 2.7 treatment was more effective than the R:FR of 1.6 treatment in reducing seedling height and increasing leaf chlorophyll (46% and 36%, respectively, when compared to control). The effects of the other treatment panels with R:FR ratios of 4.1 and 6.6 were similar to those of 2.7. Although CuSO4 reduced seedling height by 64%, the seedlings were not visually healthy and had the lowest shoot dry mass (76% lower compared to control). These results indicate that the R:FR ratio of 2.7 in the plant environment was effective in producing compact and more green watermelon seedlings which may have potential advantages in transplant production.

Definitions

Chlorophyll *-- green pigment photoreceptor cells that capture light energy for use in photosynthesis.*

Color *-- distribution of wavelengths of light coming from a radiation source, or reflected from a reflective object.*

EOD treatment *-- End-of-Day application of red (R) or far red (FR) wavelengths of light.*
Red light wavelength (R) *-- 600 to 660 nm wavelengths of the radiation spectrum.*
Far red light wavelength (FR) *-- 700 to 740 nm wavelengths of the radiation spectrum.*

Morphology of the plant *-- physical size, shape and distribution of the plant architecture.*

nm or nanometer *-- unit of measure of the wavelength of light; one billionth of a meter.*

Photosynthetically Active Radiation (PAR) -- *the photons of radiation in the 400 to 700 nm waveband. PAR is a general term that can describe either the photosynthetic photon flux density (PPFD), or the photosynthetic irradiance (PI).*

Photosynthetic Photon Flux Density (PPFD) *-- the number of photons in the 400 to 700 nm (PAR) waveband contacting a unit surface area over a given time period. Units:* $\mu mol\ m^{-2}\ s^{-1}$.

Photosynthetic Irradiance (PI) *-- the energy of the radiation in the 400-700 nm waveband that is contacting a unit surface area over a given period of time. Units:* $W\ m^{-2}$.

Photomorphogenesis *-- the ability of the plant to monitor light and regulate its growth and development (shape, size, proportion of the plant), independently of photosynthesis.*

Photons or Quanta *-- packets of energy associated with a wavelength of light.*
Photosynthetic wavelengths (PAR) *-- 400-700 nm.*

Photosynthesis *-- plant process where light is transformed into carbon molecules (plant matter); carbon dioxide is consumed, oxygen is given off, water is required, and energy is stored.*

Photoreceptors *-- plant cells that can sense light and or capture light energy.*

Photoreceptors Pr and Pfr *-- red and far red forms of the photoreceptor that influence photomorphogenesis.*

R:FR *-- the ratio of the measured intensity of red wavelength of light to the far red wavelength.*

Spectroradiometric data *-- the measured energy intensity of each wavelength of light.*

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