How far-red photons affect plant growth and development:
a guide to optimize the amount and proportion of far-red under sole-source electric lights.

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How far-red photons affect plant growth and development

Part 1: How does far-red radiation (701-750nm) affect plant growth and development?

1.1 – Photosynthetically active radiation (400-700nm), is that all plants care about?

McCree demonstrated that for a wide variety of plants grown outside and in growth chambers, radiation from 400-700nm (visible light) drove CO₂ assimilation. CO₂ assimilation was measured as the relative quantum yield of photosynthesis (mol CO₂ assimilated mol absorbed photons⁻¹) and showed two broad peaks at 440nm and 620nm, similar to the absorption peaks of chlorophyll a and b. This 400-700nm range became known as photosynthetically active radiation (PAR) and formed the basis of defining light intensity for plant growth (Photosynthetic Photon Flux Density, PPFD, µmol photons (400-700nm) m⁻² s⁻¹). Apart from the photoreceptors directly involved in photosynthesis, plants have evolved other photoreceptors that sense changes in light quality and respond to different wavelengths. Light quality refers to the colours or wavelengths that your light source emits and in what proportion to one another. The photoreceptors that perceive light quality regulate hormones that can affect almost every aspect of plant growth and development. Light quality and intensity also interact with each other to regulate plant morphology, growth, and development. Outside 400-700nm, photoreceptors also detect ultra-violet (UV, 280-400nm) and far-red (FR, 701-750nm) radiation. Far-red interacts with red (R, 600-700nm) light and the following sections discuss their effects on plants. We have chosen to define FR for plant growth as radiation from 701-750nm. This range directly stimulates CO₂ assimilation and most plant leaves do not absorb above approximately 750nm. Some plants with purple leaves can absorb radiation up to approximately 780nm and here this may contribute to phytochrome effects.

1.2 – The red to far-red ratio (R:FR) and shade avoidance

The ratio of R to FR light (R:FR) is a well-researched aspect of light quality that can have subtle to large effects on plant morphology, growth, and development. Phytochromes are photoreceptors (light receptors) that primarily sense the R:FR and guide plant morphology and development. Phytochromes exist in two photoconvertible forms: Pₗ (R phytochrome) and Pₘ (FR phytochrome). The Pₗ form has an absorption peak at about 660nm and Pₘ at 730nm. Red light drives phytochromes toward the Pₗ form whereas FR light drives phytochromes toward the Pₘ form. Although both forms absorb between 600-700nm, the Pₗ form absorbs almost solely above 700nm. Based on their absorption peaks, the R:FR is often defined as the sum of photon flux density from 655-665nm/725-735nm, and occasionally 660-670nm/725-735nm² or 600-700nm/700-800nm. When plants are fully exposed and not shading each other, the light intensity and intensity they receive are equal to their light source. However, when plants shade each other, the light intensity declines and the light quality changes. The R:FR ratio of direct sunlight is 1.1 to 1.2 but can drop to 0.23 or as low as 0.05 in severe plant shade (Figure 1). Plant leaves block most of the photosynthetic photon flux density (PPFD, 400-700nm), including R light (600-700nm), but reflect or transmit most of the FR light (701-750nm), decreasing the R:FR (Figure 1).
In nature, plants perceive changes in the R:FR and compete with each other to reach for the sun. To mitigate shading from neighbors, plants have evolved the shade avoidance syndrome (SAS). The primary symptoms of the SAS are elongation of stems, internodes, and petioles as well as earlier flowering to hasten development. Consequently, root growth, nodulation of legumes, leaf development, and tolerance of pathogens and herbivory can become impaired, as resources are diverted into elongation and reproduction.11,12 Interestingly, in Arabidopsis thaliana, sub-zero temperature tolerance increases, due to secondary effects of the hormonal changes underlying the SAS.13,14 How much a given plant species will show the SAS reflects whether it has evolved or been bred to require full sun to thrive, or whether it is shade tolerant.15-20 Appreciable shading can occur in any lighting environment where plants grow too close together, including greenhouses, growth chambers, growth rooms, and other sole-source lighting environments such as indoor vertical farms.

Historically, the SAS has been synonymous with phytochrome effects. However green light effects have also been attributed to the SAS.21-26 For this review the “SAS” and “phytochrome effects” are almost interchangeable and are referring to the same processes. Here, the SAS is the result of phytochrome action, which is caused by changes in the amount and/or proportion of far-red from shading, or is emitted from your electric light source itself. Adding some far-red can cause “beneficial” phytochrome effects such as increased leaf expansion and timely flowering, whereas the SAS is likely an “undesirable” phenotype at the far end of phytochrome effects. In reality this is a gradient of effects under phytochrome regulation.

1.3 – Too much far-red (FR) may induce the shade avoidance syndrome (SAS) from your electric light source

If FR is included in sole-source lighting environments, it is important to know how much R is also present to prevent inducing the SAS from your light source itself (unless that is your goal). The R:FR ratio of your light source is one indicator of how much it may induce the SAS. Direct sunlight has a R:FR ratio close to 1.15, and although you may think any light source with a R:FR ≥ 1 is safe from producing a strong SAS phenotype, this is not necessarily the case. Low light intensities and a low R:FR work together to induce the SAS.4 For example, A. thaliana grown at 150 PPFD under 4000K white light emitting diodes (LEDs) with “too much” FR (R:FR = 1.0) can strongly induce a SAS phenotype (Figure 2). Adding FR while keeping the R:FR >3 at light intensities ≤600 PPFD appears to be safe for preventing a strong SAS phenotype, but still promotes timely flowering (Figure 3).23,24

The R:FR is one indicator of how much a given electric light source may induce the SAS. Although the R:FR is robust for assessing sunlight and plant shading for electric light sources, other parameters and approaches may be better indicators.20 The phytochrome photostationary state (PSS) is another indicator of how strongly a sole-source lighting environment may induce the SAS and is potentially better suited for multi-coloured light sources with strong peaks at different wavelengths.9 The PSS is a better biological model than the R:FR for predicting stem elongation, but the R:FR ratio was developed to help predict the PSS in a time before spectroradiometers were readily available. The R:FR ratio has persisted in the field of plant science because it is an intuitive and easy to use metric, unlike the PSS. The lower the R:FR and PSS, the more likely certain aspects of the SAS will be induced. However, changes in the R:FR and PSS do not always correlate with each other, especially when comparing violet, blue, and green light can also strongly affect how a given plant species will show the SAS reflects whether it has evolved or been bred to require full sun to thrive, or whether it is shade tolerant.15-20

1.4 – Importance of far-red (FR) in your light source

Without FR in your light source, which could occur in growth chambers or other sole-source lighting environments, there is little concern about inducing the SAS with most light sources. However, adding some FR may be important or beneficial to your plant growth objectives. Sunlight has a substantial amount of FR and including some FR from halogen bulbs or LEDs in your light source may produce plants that grow more similar to those grown under sunlight. This is especially true regarding the photoperiodic flowering response.22-24 Morphologically, adding FR from halogen bulbs or LEDs to white fluorescent or white LEDs may promote stem elongation compared to plants grown under sunlight, even if the R:FR is greater than sunlight (>1.1 – 1.2). This is because both white fluorescent or white LEDs have almost no UV radiation (specifically UV-B), which reduces stem elongation in plants grown outside under direct sunlight.27

The growing ubiquity and accessibility of FR LEDs is accelerating research on how FR light affects plant growth. Two effects of adding FR may include 1) greater leaf expansion and leaf area, and 2) a direct stimulation of photosynthesis and CO₂ assimilation when combined with PAR (PPFD).28-31,32 These two effects can result in bigger plants, which...
was recorded years ago in tomato supplemented with incandescent light, grown under low light intensities. Across 14 diverse crop species adding FR photons increases net photosynthesis (CO₂ assimilation) equally to adding PAR photons (PPFD). The extent and magnitude of these growth stimulating FR effects across all plant species is an area of active research. Another area of active research is understanding the contribution of phytochromes versus the direct effects of FR on the photosynthetic apparatus, and how the two systems may interact. In light of these findings, some research groups are now advocating FR photon flux be included in PPFD, extending its range from 400-750nm.

1.5.1 – Phytochrome effects on seed germination

Seed germination appears to be under some level of phytochrome influence for the majority of plant species, however phytochromes are more influential in regulating germination for full sun adapted plants with small seeds. During the early stages of seed imbibition, R light stimulates and FR inhibits seed germination, and this effect is fully reversible in lettuce (Lactuca sativa L.). However, FR can actually stimulate seed germination after the initial inhibitory effects have worn off (after a few days of imbibing water). In some domesticated cereal grasses such as barley (Hordeum vulgare L.), the phytochrome influence on seed germination is lacking. The phytochrome influence does occur in Brachypedium distachyon (L. P. Beauv.) however, which is a grass closely related to the cereals. There is speculation that the phytochrome influence has been selected against in some domesticated cereal grasses to improve uniformity of seed germination.

1.5.2 – Phytochrome effects on above-ground morphology and growth

Most conspicuous are the morphological effects of a strong phytochrome response or the SAS. Almost universally across plant species, the SAS increases plant height as stems and internodes extend upward in search of better and brighter light. The sensitivity of plants to exhibiting the SAS ultimately depends on their evolutionary and/or breeding history and whether they are shade avoiding or shade tolerant. In shade tolerant species such as white clover (Trifolium repens L.), snapdragon (Antirrhinum majus L.), petunia (Petunia x hybrida), lettuce, and radish (Raphanus sativus L.), FR light increases leaf area. In this way, FR light stimulates the growth of shade tolerant plants by increasing their leaf area and light interception capacity for carbon gain. In shade avoiding species that are sensitive to the SAS, some FR may still promote leaf expansion and overall growth. However, at some point, if the amount and/or proportion of FR becomes too high, shade avoiding species sensitive to the SAS may invest more into elongation growth and reproduction at the expense of leaf area, potentially reducing productivity and overall biomass. Similarly, in bunch grasses, the SAS results in fewer, taller, tillers, with reduced overall biomass.

1.5.3 – Phytochrome effects on flowering time and phenology

For some plants, day-length is a critical cue to transition from vegetative to reproductive growth. Plants that are sensitive to the length of the photoperiod are classified as either day-neutral or short-day plants. Long-day plants flower in response to the lengthening days (shortening nights) of spring whereas short-day plants respond to the shortening days (lengthening nights) of autumn. Far-red light interacts with day-length to promote flowering in most plants, however in some species FR can delay flowering or have no effect. Knowing how FR will affect the time to flower is important for planning experiments and making reliable comparisons of flowering time and reproductive development with other research.

1.5.4 – Long-day plants

Far-red light almost invariably promotes flowering in long-day plants. Long-day plants that show this effect include A. thaliana, wheat (Triticum aestivum L.), oats (Avena sativa L.), barley (H. vulgare), perennial ryegrass (Lolium perenne L.), lentil (Lens culinaris Medikus), spinach (Spinacia oleracea L.), lettuce, strawberry clover (T. pretense L.), Rudbeckia fulgida Atan., whorled tickseed (Coreopsis verticillata L.), black henbane (Hyoscyamus niger L.), and petunia.

1.5.5 – Short-day plants

In short-day plants, FR light can either promote flowering like in long-day plants or have little to no effect in ornamentals such as Dahlia (Dahlia hortensis Cav.) or African Mangold (Tagetes erecta L.). In the short-day plants rice (Oryza sativa L.), strawberry (Fragaria sp.), Chrysanthemum (Chrysanthemum x morifolium (Ramat.) Hems!), and Xanthium pennsylvanicum L., FR light will shorten the time to flower as in long-day plants. Some lines of soybean (Glycine max L. Merr.) appear to be an exception however, as here FR light can delay flowering, and this effect is stronger under 20 hour compared to inductive 12 hour photoperiods.

1.5.6 – Day-neutral plants

In day-neutral plants, FR light may have little or no effect on the time to flower as in Impatiens or Geranium. However, in some day-neutral plants such as sunflower (Helianthus annuus L.), FR light appears to accelerate flowering as in long-day plants.

1.6 – Phytochrome effects on stress tolerance

Interestingly in Arabidopsis, a low R:FR appears to increase abiotic stress tolerance while decreasing biotic stress tolerance. A low R:FR increases tolerance of sub-zero temperatures in Arabidopsis by upregulating CBF gene expression. Low R:FR also activates pathways involved with innate salt tolerance by increasing pinitol production in Mesembryanthemum crystallinum L.. However, a low R:FR increases susceptibility to both pathogens and herbivory by downregulating both the salicylate and jasmonate responses. Here competition for light is prioritized over pathogen defense.

1.7 – Phytochrome effects on root and nodule development


1.8 – End of day far-red (FR) produces similar effects as including it throughout the day

As the sun sets, the R:FR slightly decreases as the sun drops below 10° elevation toward the horizon. Here increased refraction by the atmosphere preferentially increases FR over R light and plant phytochromes have evolved to sense this change in light quality. As a result, providing FR light at the end of the day in sole-source lighting environments can similarly affect plant morphology and development as adding FR throughout the day. For growth chambers and other sole-source lighting environments, running your FR light fixtures for 30-60 minutes at the end of the day instead of continually throughout the day has the benefit of saving some electricity.
1.9 - Conclusions

Some FR effects may be universal across all plant species. Adding FR to an electric light source may result in a growth stimulus, elongation of stems and/or internodes, and earlier flowering compared to less or no FR. However, with “too much” FR, some plants may begin to show a stronger and stronger SAS phenotype. More research is required to understand the universality of FR effects, especially the optimal beneficial amount of FR for growth and how much this varies between species. In reality, there is a gradient of effects from finding the optimal beneficial amount of FR to SAS effects. For example in wheat, certain aspects of the SAS may appear (eg. stem elongation and earlier flowering) when adding FR, even with a R:FR of 7 (BioChambers, unpublished data). The R:FR, PSS, and %FR give an indication of the potential for a light environment to benefit growth and/or induce aspects of the SAS. These three parameters can be used as relative indicators for changes made to the light environment by adding FR to a given electric light source, or shading from plant leaves. However comparing R:FR, PSS, or %FR values between sunlit and sole-source lighting environments should be done with caution. Other parameters and approaches are being developed that aim to be more robust and comparable between sunlit and sole-source lighting environments. In deciding whether to include FR, or how much, you must ask yourself "what are my goals for plant growth?" Are your goals to perform research on an aspect of plant biology that is comparable to literature of the past, but is affected by adding FR or a lack thereof? Or, are your goals to adjust FR to optimize vegetative plant growth and/or plant growth for flower or seed production? The following section describes how to adjust the amount and proportion of FR in your growth chamber or room to help achieve your plant growth goals.

Part 2: How to adjust the amount and proportion of FR in your growth chamber or room

2.1 - Incandescent lighting

Incandescent lighting was a common source of lighting for many years, but now more efficient forms of lighting have replaced the incandescent light bulb. This has many benefits for indoor lighting applications for human beings. However, in plant growth chambers incandescent lighting was used to provide a source of FR light. Since FR light is weakly or not visible by humans, it is not considered useful and therefore not included in many common lighting sources.

When looking at replacements in a chamber originally designed with incandescent lights, there are a few things to consider:

A - Electrical power

Incandescent lights are often rated by their electrical power consumption. For example, 60W bulbs were commonly used in plant growth chambers. Any replacement for an incandescent bulb must not exceed the electrical power rating of the original bulb. It can however, be replaced by a source with a lower wattage without impacting chamber performance.

B - Light intensity

It is important to note that equivalent electrical power does not indicate equivalent light intensity. Another light source may have the same wattage but emit higher intensities of FR light (PFD of FR, 701-750nm), which can change the %FR (PFD 701-750nm/400-750nm) or R/F (PFD 655-665nm/725-735nm) inside a chamber (Figures 5 & 6). When deciding what to replace incandescent bulbs with, pay careful attention to the intensity of the replacement, the type of plants being grown, and the desired conditions of the experiment.

C - Spectrum

The quality of light must be considered when looking at replacing incandescent bulbs. Different lighting technologies produce different spectra, which may differentially affect plant growth. For example, FR LED fixtures produce a very different spectra compared to incandescent or halogen bulbs (Figure 6).

D - Life rating

Incandescent bulbs have a short life rating and will randomly burn out and shut off completely. Halogens may have a similar life rating to incandescents, while others like FR LED fixtures, can be much longer. Unlike incandescents or halogens that burn out completely, FR LED fixtures will gradually dim over time. The L rating is a useful indicator of how LED fixture output declines over time. An L70 = 50,000 hours indicates the fixture maintains 70% of its initial output after 50,000 hours of being ON. Consider this when looking for an incandescent replacement.

E - Beam angle

Incandescent bulbs project light in all directions. Some replacements do not have the same distribution of lighting. When looking for a replacement, make sure that the light from your source will uniformly radiate on all your plants (Figure 7).

Figure 5: The spectra and intensity of 40W Halogens (H) are a good match for 60W Incandescents (I), while 25W H closely match 40W I. Both H and I contribute photosynthetically active radiation (PAR, Photosynthetic Photon Flux Density, PFD, 400-700nm) as well as far-red radiation (FR Photon Flux Density (PFD) 701-750nm).

<table>
<thead>
<tr>
<th>1) 40W Halogen Bulbs</th>
<th>2) 25W Halogen Bulbs</th>
<th>3) 60W Incandescent Bulbs</th>
<th>4) 40W Halogen Bulbs</th>
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The PFD output of I and H bulbs (and differences between them) can differ between brands. These measurements represent general differences in power consumption versus output between them.

Figure 6: The intensity of far-red (FR Photon Flux Density (PFD) 701-750nm) from FR LEDs is generally greater than that of Halogen (H) bulbs, even at ¼ the wattage. However due to their strong FR peak, FR LEDs generally contribute almost nothing to photosynthetically active radiation (PAR, Photosynthetic Photon Flux Density, PPDF, 400-700nm).

1) 40W H: 41 PPFD/18 FR PFD, 2) 10W FR LEDs: 2 PPFD/51 FR PFD.

These measurements were taken 81cm from the lights inside a TPC-19 (25°C) with either 16 40W H bulbs (blue line), or 16 10W FR LED fixtures (orange line).
Incandescent replacement technologies:

2.2 – Halogens

Halogen lighting differs from incandescent lighting as it uses a halogen gas inside the bulb to extend the life of the bulb and allow for greater efficiency. Often a halogen bulb will have a greater light intensity (often reported in lumens) than an incandescent using the same electrical power. Therefore, when using a halogen bulb as a replacement for an incandescent, it is helpful to refer to the lumen output along with the wattage rating. Although comparing lumen output is useful, the standard unit of light for plant growth is photosynthetic photon flux density (PPFD, µmol photons (400-700nm) m⁻² s⁻¹). Here is a useful spreadsheet to convert lux (lumens m⁻²) to PPFD if you have the spectral output of a given light source: https://www.apogeeinstruments.com/content/PPFD-to-Illuminance-Calculator.xls

Halogen bulbs are a good replacement for incandescent bulbs because they often match the spectrum of the incandescent bulb while using less power (e.g. 43W halogen to replace 60W incandescent). Incandescent and halogen bulbs emit both photosynthetically active (PPFD) and FR radiation (Figure 5). However, halogens still suffer from a short life rating and are less efficient when compared to other modern lighting technologies such as LEDs. BioChambers include four levels of ON/OFF control for incandescent/halogen bulbs, included with our fluorescent + incandescent/halogen lighting option. This provides some control over the amount (%FR) and proportion (R:FR) of FR and PPFD, while providing an appreciable FR light when available. Halogen bulbs have been used in combination with fluorescent lighting for years (Figures 8 & 9). It appears halogens are also safe to use with warm white LEDs (Figure 10). However without a R peak close to 660nm (from R LEDs, common in horticultural LED fixtures, see Figure 3), be careful using FR LEDs. Many FR LEDs have a peak close to 730nm, which can reduce the R:FR to close to 0 and may induce the SAS (see Figure 2). This consideration is valid for both white fluorescent and white LED based lighting systems (Figures 2, 9, & 10). Despite the versatile spectrum of halogens, they are becoming increasingly difficult to find due to their inefficacy at converting electrical energy into light (PPFD). BioChambers is continually evaluating R+ FR LED solutions to act as halogen replacements. These replacements will maintain a similar or higher R:FR than halogens while providing an appreciable amount of FR. The goal of these fixtures is to make them work well with either white fluorescent or white LED tube based systems. Information on how to use these R + FR solutions will be added to this guide or be released as a separate document.

One of our most popular LED lighting options is Fluence Physiospec Indoor with FR. The Physiospec Indoor and FR bars are controlled independently and are dimmable to allow for good control over the amount and proportion of FR (Figure 11).

2.3 – Light Emitting Diodes (LEDs)

LED lights can produce FR light and have greater electrical efficacy than incandescent bulbs. The spectrum of FR LEDs is often a pronounced peak between 720-740nm, which can have greater FR light intensities than halogen bulbs even while using ¼ the electrical power (Figure 6).

2.4 – Combining incandescent replacement technologies with a white fluorescent or white LED dominant lighting environment

White fluorescent or white LED only systems can lack appreciable FR light by themselves (Figures 9 & 10). Growing plants under only white fluorescent or white LED lights may cause differences in plant growth and development relative to including a FR light source. For the majority of plants, the time until flowering may be longer and plant height may be shorter under white fluorescent or white LED light alone, all else being equal. Without appreciable FR light, plants will lack the beneficial aspects of FR on growth and development such as leaf expansion, stimulation of photosynthesis, and timely flowering. Halogen bulbs have been used in combination with fluorescent lighting for years (Figures 8 & 9). It appears halogen bulbs are also safe to use with warm white LEDs (Figure 10). However without a R peak close to 660nm (from R LEDs, common in horticultural LED fixtures, see Figure 3), be careful using FR LEDs. Many FR LEDs have a peak close to 730nm, which can reduce the R:FR to close to 1 or less and may induce the SAS (see Figure 2). This consideration is valid for both white fluorescent and white LED based lighting systems (Figures 2, 9, & 10). Despite the versatile spectrum of halogens, they are becoming increasingly difficult to find due to their inefficacy at converting electrical energy into light (PPFD). BioChambers is continually evaluating R+ FR LED solutions to act as halogen replacements. These replacements will maintain a similar or higher R:FR than halogens while providing an appreciable amount of FR. The goal of these fixtures is to make them work well with either white fluorescent or white LED tube based systems. Information on how to use these R + FR solutions will be added to this guide or be released as a separate document.

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Advantages | Disadvantages | Differences
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**Halogens**
Closely matches the spectral quality of incandescent lights | Life rating is similar to that of incandescent lights | More efficient than incandescent bulbs | May become unavailable in the near future

**Far-red LEDs**
More efficient than halogen bulbs | Beam angle may not cover all plants | Spectrum (light quality) very different from incandescent lights
Long life rating

**No Replacement**
(Only white fluorescent or white LEDs)
Possibility of shade avoidance syndrome effects are low or non-existent | Beneficial aspects of FR on plant growth are minimal or non-existent | Plants may take longer to flower and be shorter relative to adding a source of FR
References


