Early models. Since plants on Earth evolved under broad-spectrum solar radiation, anytime they are grown exclusively under electric lighting that does not contain all wavelengths in similar proportion to those in sunlight, plant appearance and size could be uniquely different. Nevertheless, plants have been grown for decades under fluorescent (FL) + incandescent (IN) lamps as a sole source of lighting (SSL), and researchers have become comfortable that, in certain proportions of FL + IN for a given species, plants can appear “normal” relative to their growth outdoors. The problem with using such traditional SSLs for commercial production typically is short lamp lifespans and not obtaining enough photosynthetically active radiation (PAR, 400-700 nm) when desired. These limitations led to supplementation of FL + IN lamp outputs with longer-lived, high-intensity discharge (HID) lamps in growth chambers (3). As researchers became comfortable that mixes of orange-biased high-pressure sodium (HPS) and blue-biased metal halide (MH) HIDs together also could give normal plant growth at higher intensities, growth chambers and phytotrons subsequently were equipped mainly with HID lamps, with their intense thermal output filtered out by ventilated light caps or thermal-controlled water barriers. For the most part, IN and HID lamps have found a home in commercial protected horticulture, usually for night-break photoperiod lighting (IN) or for seasonal supplemental lighting (mostly HPS) in greenhouses. However, lack of economically viable options for SSL have held back aspects of year-round indoor agriculture from taking off commercially.

An early SSL commercial model. An early attempt to use HIDs for commercial SSL was Phytofarms of America, which started as an experimental facility of General Mills in Dekalb, Illinois during the late 1970s, and became a private enterprise in the 1980s (4). Phytofarms was a warehouse-based hydroponic production facility specializing in leafy greens and herbs. Although SSL was provided by 1000-watt HID lamps, they were mounted only 4 feet (122 cm) above crop surfaces because their radiant emissions (PAR + heat) were filtered through a jacket of water flowing around each lamp to remove the heat. Another innovation was conveyor movement of hydroponic vegetables along benches, with automated respacing of plants to keep pace with their growth rate so that they would not become overcrowded but also so that photons would not fall on empty spaces between plants (Fig.1). Such innovations plus negotiation of off-peak power rates kept Phytofarms in business for more than a decade, when high electrical consumption, increasing power costs, aging lamps, and other factors finally led them to close in the early 1990s.

The multi-tiered plant factory. In Japan, where the commercial plant-factory movement started in the 1990s, multi-tiered warehouse facilities growing leafy
vegetables used moderate-output FLs for SSL (5). However, FLs decline gradually in light output with cumulative use and have to be replaced frequently, adding to the cost burden of indoor lighting. With a standard separation distance up to 40 cm between shelves in a multi-tiered plant factory (vertical farm in recent vernacular), high-power HID lighting would be too intense for greens production. If the shelf-separation distance were increased to lower incident photosynthetic photon flux (PPF) and increase crop-coverage area per lamp, then the volume-based productivity advantage of vertically stacked shelving would be compromised. HID lamps have not found a major application for greens production in contemporary plant factories, perhaps for similar economic and thermal-management reasons that Phytofarms did not stay in business.

**Improved light sources needed.** Clearly, the field of commercial indoor agriculture is in need of improved sources of plant-growth SSL. What is needed are light sources that are neither too dim nor too bright for specific applications, are not too hot, not too large or fragile, can provide the right wavelengths of light for the particular crop or application, have a long lifespan, and can be used in ways that save considerable energy for SSL.

**Induction lighting.** One source of light that may satisfy some of those criteria is induction lighting, which is a form of electrodeless or non-filament lighting using an electromagnetic field that does not cause the light-emitting fluorescent tube to get overly hot and therefore can be placed close to crop surfaces. It also is a very long-lived light source. It does require a ballast, however, which may fail before the lamp *per se* does. Induction lighting gives off broad-spectrum light, the coolness or warmness of which depends on the particular phosphor blend used to coat the inside of the fluorescent tube.

**Light-emitting diodes.** The light-emitting diode (LED) possesses the most desired SSL characteristics for plant growth (6), does not require a ballast, and can be manufactured and selected to provide monochromatic light of many different colors, which can be blended together on arrays to create a range of hues. Hue also can be controlled by varying the intensity of individual colors of LEDs making up a given blend. Because waste heat is removed remote from photon-emitting surfaces, LEDs also can be placed close to crop surfaces. To achieve high-irradiance lighting with LEDs, a high population density of high-output LEDs must be mounted on arrays, and the arrays need to be actively heat-sinked with flowing air or water cooling electronic components behind photon-emitting surfaces. Another important factor is that LED technology continues to improve in electrical efficiency, and production costs are decreasing. All of these attributes combine to make LEDs a most promising candidate for a range of SSL and indoor-agriculture applications, now and in the future.

**History of LEDs and plant growth.** Initial testing of LEDs for plant growth was conducted at the University of Wisconsin and the Wisconsin Center for Space Automation and Robotics with funding from NASA in the late 1980s, and patents were awarded for this application in 1991 (7) and 1996 (8). The narrow-waveband nature
of LEDs prompted researchers to use them as sources of single-color light to improve study of photobiology, photosynthesis, and plant physiology that previously required cumbersome arrays of broad-band light sources, cutoff filters, flowing-water heat sinks, and small-scale diffraction gratings in dark rooms. Early LED SSL findings at Wisconsin and the Kennedy Space Center (KSC) in Florida indicated that lettuce, wheat, spinach, and radish plants would grow and complete their life cycles under red light alone, but growth and development were significantly better when a small amount of blue light was added to the red. Red and blue light have the best quantum efficiencies for driving photosynthesis, but, along with other wavelengths, also play important roles in plant development, sometimes in opposite directions to each other, so determining spectral balances becomes very important (9). There is no single red:blue ratio of light ideal for all species and for every stage of plant growth. However, for SSL, red and blue light in some proportion are the wavebands of choice for driving photosynthesis and regulating vegetative growth. Because of this, many first-generation LED arrays have been equipped with red + blue LEDs.

**NASA goals for LEDs.** NASA capitalized on these important early findings by funding development of several LED-equipped plant-growth units, first the ASTROCULTURE™ flight chamber for Space Shuttle, which supported five flight experiments with wheat, brassica, and potato from 1995 to 2003, and then the Advanced ASTROCULTURE™ unit for Space Station, which supported the first seed-to-seed experiments with arabidopsis and soybean from 2001 to 2002. NASA has continued to support the development of LEDs for SSL space-flight systems, including the Advanced Biological Research System, the Vegetable Production System, and the Plant Habitat, all for the International Space Station. Green LEDs have been added to arrays currently flying on Space Station, and zinnia and nasturtium have been added to the list of plant species flown in space with SSL. While the historical work at Wisconsin focused on LED hardware development for flight experiments, effort at KSC has emphasized development of technology for long-duration space missions and future colonies on the Moon and Mars (10).

**Red light.** The most staple waveband of light that anchors SSL LED arrays for plant growth is red. Broad-band red (600-700 nm) light has, by far, the highest quantum efficiency for driving photosynthesis, with a broad peak from about 620 to 660 nm (11). As well, red has numerous photomorphogenic effects on plant development mediated by the photoreversible pigment phytochrome. In general, red light promotes stem elongation, leaf expansion, biomass accumulation, and contributes to a phytochrome photostationary state (PPS) that can determine flowering, dormancy, and other important photomorphogenic responses of plants, including seed germination.

**Blue light.** There do not seem to be any simple answers regarding how little or how much blue light is required in an SSL prescription for any given plant species, or even when to apply it during a given plant life cycle. Even though approximately one-third of sunlight PAR emissions consist of broad-band blue (400-500 nm), plants grown outdoors seem to be not particularly sensitive to blue light, at least at outdoor light
intensities (12). Under SSL conditions, however, which tend to involve much lower PPFs than outdoors, the intensity of blue light seems to be a critical factor. Sometimes only a few percent of blue are needed for a particular plant response, above which blue is inhibitory, but that may change during the course of a plant’s life cycle. Plant-growth functions that seem to be particularly sensitive to blue light in SSL situations include stem elongation and leaf expansion, with “too much” blue inhibiting growth in both cases (13). Other plant responses having an absolute requirement for blue light include phototropism, stomatal aperture, leaf thickness, and chlorophyll content. Effects of blue light on secondary product metabolism are mentioned in the section on value-added for SSL.

Green light. Green light (500-600 nm) falls between broad-band blue and red light along the PAR energy spectrum. Green often is disregarded as an unimportant waveband in photosynthesis because absorption spectra of extracted leaf chlorophyll pigments indicate very weak absorption in the green region of the PAR. Because chlorophyll has major absorption peaks only in the red and blue regions, researchers initially selected first red, later blue, LEDs for first-generation LED arrays to support plant growth. However, intact leaves do absorb considerable green light, and in a relative quantum-efficiency curve for photosynthesis vs. PAR wavelengths, some wavelengths of broad-band green actually are more efficient than certain wavelengths of the blue band. Overall, however, broadband green is slightly less efficient than broadband blue. However, when leaf canopies close, red and blue light are absorbed strongly by upper or outer leaf layers, whereas green light penetrates to interior leaf layers, where it subsequently is absorbed and drives photosynthesis of the inner canopy (14). Thus, light sources containing some green can be more effective in stimulating crop growth than are red + blue sources alone, such as when foliar canopies are closed. When applied together with blue light, green has effects opposite to blue on stomatal aperture (15). Yet another useful feature of green light is that the human eye perceives red + green + blue (RGB) light as white light, so if all three wavebands are present simultaneously in plant-growth light, researchers and growers are able to visually evaluate the stress status of crops, the incidence of physiological disorders, and “true” leaf color (the way it looks outdoors), whereas if only red + blue are present, green tissue looks purple, grey, or black, and physiological stress or disease diagnosis is difficult.

White light. The often-confusing issue regarding which colors or proportions of colors to select for SSL applications with LEDs can depend on species, cultivar, stage of development, and intensity of available light. In some ways, the use of LEDs for SSL is causing us to rediscover the value of white light for plant growth and development. Because of all the complications involving LED color selection and the range of possible plant responses, the question often is asked regarding whether white should be the LED color of choice for plant growth. It turns out that white LEDs actually are blue LEDs with a phosphor coating the inside of the light-focusing lens mounted over and around the diode. Energy losses associated with the secondary broad-band photon emissions of the excited phosphor make white LEDs significantly less electrically efficient than emissions from pure monochromatic blue LEDs (16). As
well, the proportions of red, green, and blue wavebands in white LED light vary widely among cool-white, neutral-white, and warm-white LED types, none of which are a close match for the RGB distribution of midday solar light. It actually would be more electrically efficient to make white light from monochromatic RGB LEDs than to use white ones. Nevertheless, inclusion of a few white LEDs on an array may have utility in terms of achieving certain proportions of broad-band color in case green LEDs are not included.

**Far-red light.** The recent availability of far-red (FR, 700-800 nm) LEDs presents opportunities to control plant functions in SSL related to photoperiodism and photomorphogenesis involving the phytochrome pigment system. Plant species with a long-day requirement for flowering are hastened to flower when FR is present simultaneously with R light (17) rather than using red light alone, and a lower phytochrome photostationary state (PPS) is established either during end-of-day lighting or as night-interruption lighting in the middle of the dark period (18). In that sense, photoperiod lighting is SSL, even in the greenhouse. Far-red wavelengths also have photomorphogenic effects on stem elongation, with a low R/FR ratio favoring the “shade-avoidance” syndrome involving internode elongation (19). Leaves developing in a light environment including FR radiation tend to expand to become larger and thinner. Although FR and blue wavelengths can have opposite effects on stem elongation and leaf expansion (20), they both lower PPS, which may trigger accumulation of desirable phytonutrients in leafy greens (21). Like green light, FR wavelengths pass through upper layers of a closed leaf canopy. Unlike green light, FR wavelengths have mostly photomorphogenic effects.

**Ultraviolet and other wavelengths.** Solar light contains both UV-A (320-400 nm) and UV-B (280-320 nm) wavelengths that plants are adapted to, so indoor agriculture scenarios providing electrical sources of SSL, especially of the narrow-spectrum type, may encounter situations in which produce quality and/or appearance may reflect a lack of UV radiation. Certain cultivars within some plant species, especially solanaceous crops, develop callus-like intumescence growth on leaves and shoot tissues in dim light and/or in the absence of UV light (22). Such physiological disorders then, are a consequence of narrow-band SSL radiation leading to a wavelength deficiency. In some cases, the presence of elevated blue and/or the presence of some far-red light can prevent intumescence formation. In other cases, elevated blue does not work (23). There is a reluctance to introduce UV-B into indoor commercial growth environments for worker-safety reasons, but it may be possible to use UV-A if certain worker precautions are taken. It certainly would be preferable to find solutions to physiological disorders caused by SSL within the PAR spectrum per se, although RGB imbalances also can lead to adverse effects on productivity and crop yield as well. These are open, ongoing issues of SSL.

**Commercial propagation using SSL.** Rooting of cuttings and propagation of seedling or grafted stock previously has been done in greenhouses for both ornamental as well as vegetable transplants. When this occurs during low-light seasons, as it often does, supplemental lighting (SL) typically is required. To achieve
target daily light integrals (DLIs) for high population densities of propagules competing for available space and light, SL sources need to be positioned appropriately to deliver minimal DLI and not overheat transplants. Regardless of the SL source, close, dense placement of SL fixtures above the propagules tends to block considerable sunlight if done in greenhouses. Because of the high intrinsic value of the transplant crop, providing SSL as opposed to SL could be economically justified in many cases. The goal of transplant production could very well determine the most appropriate choice of light source for SSL. If the goal is to root cuttings and provide supplemental heat, HPS lamps may be the logical choice for SSL. However, if the goal is to elongate seedling hypocotyls to be used as root stocks for grafted transplants (24), then a mix of red and far-red LEDs may be most appropriate. Another question that could have a bearing on the choice of SSL for transplant production may have to do with the nature of the grow-out environment and how well SSL-grown transplants will tolerate or adapt to it.

**Commercial production using SSL.** The presently most obvious application for SSL in commercial grow out or production is for high-value, rapidly turning specialty crops such as leafy greens, microgreens, and herbs grown in warehouses. These vegetative crops do not require as much light (PPF, DLI) as reproductive crops requiring flowering and fruiting, such as tomato. Greens also are grown in greenhouses using ambient solar light plus SL during low-light seasons. The advantage of growing greens in greenhouses is that some solar light always is present. However, energy is required for heating during cold seasons and cooling during hot seasons, whereas waste heat from SSL in insulated warehouses has to be ventilated year round. So, the seasonal energy tradeoffs weigh on temperature in a greenhouse and on lighting in a warehouse. Given the disadvantages of FL and HID sources mentioned previously, energy-efficient, long-lived, relatively cool light sources such as induction lighting or LED lighting are quite promising for indoor greens production. LEDs are rapidly becoming the SSL fixture of choice for warehouse-based vertical farming (Fig. 2).

**Light-distribution issues of LEDs.** In addition to being able to manipulate and control the spectral quality of light under which plants are grown, the relative coolness of LED light-emitting surfaces allows them to be located in close proximity to plant tissues because waste heat is removed remotely from the actual diode (25). Thus, much-reduced electrical current is needed to achieve target photon flux at plant level than if a (hot) light source is located farther away from the crop surface. Obviously, this unique thermal property of LEDs opens the door for significant energy savings not shared by HID lamps. In the case of upright-growing, branching plants with upper leaves shading lower leaves, or when the foliar canopy of a crop stand closes with respect to overhead lighting, “intracanopy” LED lighting has been shown to prevent loss of chlorophyll fluorescence, premature senescence of leaves, and abscission of flowers and young fruits (26). Vertical LED “lightsicle” strips switched on as needed from the bottom up to keep pace with the top of a growing crop not only enhance stand productivity in SSL situations, but save considerable electrical energy for lighting because photons do not light empty spaces above plants (27). In an
analogous manner, low-stature leafy-green crops typically are overhead lighted with separation distances of 30 to 40 cm between shelves in a multi-tiered plant factory (vertical farm). The same relative coolness properties of LEDs that enable intracanopy lighting also enable "close-canopy" overhead lighting, with separation distances being ≤ 10 cm, the actual distance dictated by spectral blending of light from individual LEDs in the array and the need for unrestricted air movement across crop surfaces (Fig.3). Analogous to the sequential vertical switching of intracanopy LEDs would be close-canopy, “targeted” lighting of low-stature greens (Fig.4) (28), with automated detection of position and size of plants below a horizontal LED array, and selective switching of LED clusters on that array. The demonstrated energy savings of such approaches, enabled by the relative coolness of LEDs, will be highly relevant to sustainable, profitable crop production using SSL.

Value added with SSL. One commercial perk for SSL in general and for the use of LEDs in particular is the potential enhancement of product quality by light-spectrum regulation of secondary metabolism (29). If quality attributes related to appearance, flavor and aroma, and nutritional well being can be manipulated and controlled by the spectrum of growth light, specialty crops produced with specific light prescriptions may have competitive advantage in the marketplace with field-grown produce shipped from afar. This form of value added goes beyond “local grown” and “freshness” and is an area of intense research interest. For strawberry grown under SSL, for example, red + blue LEDs increased fructose and anthocyanin contents, whereas antioxidant contents were enhanced by red or blue light alone. Blue LEDs alone also hastened fruit ripening, while red alone boosted overall production (30). Thus, light prescriptions in SSL production scenarios might be developed depending on desired outcomes. In the absence of outdoor UV, blue LEDs enhanced the purple color of ‘Outredgeous’ leaf lettuce by promoting the accumulation of phenolic compounds in the leaves (Figs. 4A,B) (31). Blue light also enhanced the glucosinilate and β-carotene contents of microgreens, and of antioxidants in multiple leafy species (32). Because green light has a tendency to prevent or reverse the purpling effect of blue light on leaves (33), selective use of LED colors could have great value for manipulation and control of produce or product quality. In some cases, red light alone can enhance pigmentation and secondary metabolite accumulation. The timing of specific SSL treatments during a production cycle could prove important for achieving desired product quality without compromising productivity or yield. Future research will elucidate what kinds of narrow-spectrum light choices need to be combined and in what order for specific product outcomes. This SSL approach appears to be quite promising for indoor agriculture.

Literature Cited


