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Advanced Light Control Technologies in Protected Horticulture: A Review of Morphological and Physiological Responses in Plants to Light Quality and its Application

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Plants use light as both a primary energy source and a signal for morphogenesis. Plant growth and morphogenesis are strongly affected by light intensity, photoperiod, and quality. Light quality studies have shown, for example, that plants receiving low levels of red light, in shaded locations (e.g., under dense plant canopies), exhibit rapid stem elongation and flowering. Photoreceptors-complexes of proteins and pigments in plant cells-act as "antennae" to absorb particular light spectra and generate signals to change gene expression through signal transduction systems in plant cells. By modifying gene expression, light signals control not only plant growth, but also flowering time, fruit color, or the functional chemical content of crops. Artificial light sources have now achieved long life, good energy efficiency, and increased luminance. Today, we can use various types of artificial lamps (e.g., fluorescent, metal halide, or high-pressure sodium) to suit the lighting aims in horticultural crop production, but light-emitting diodes (LEDs) are now the most advanced artificial light sources available. Their energy efficiency is projected to overcome that of fluorescent lamps within 5 years. In addition, because LEDs can radiate narrow spectra, specific lights can be used to control specific plant growth responses, such as plant shape or flowering time, without the need for chemical growth regulators. We can also use new photo-selective filters to modify sunlight and thus control plant growth and insect and disease activity. These new light technologies are still expensive, but expected cost reductions will make the technologies available for protected horticultural production.

Key words: gene expression, light quality, photomorphogenesis, photoreceptors, phytohormone

Introduction

The involvement of light in plant growth is complex. The characteristics of light change with wavelength. There are dangerous electromagnetic waves, such as cosmic and γ rays, that can injure living organisms. Nevertheless, living organisms can use most of the electromagnetic spectrum that reaches the surface of the Earth, notably the visible part of this spectrum, which we call "light". It is generally known that the visible light is a approximately same wave length range with photosynthetic active radiation.

Light has two major roles in plant growth. The first is as an energy source for photosynthesis: without light, higher plants cannot grow. The second is as a signal to, for example, control plant growth, regulate flowering time or morphogenesis. Plant growth and development are sometimes changed by changes in color of the radiated light (Eskins, 1992). For example, the shape of geranium leaves can be modified by changes in light color (Fukuda *et al*., 2008). Light color is the difference in wavelength distribution known as "light quality". Light signals are received by the photoreceptors in plant cells (Lin, 2000). Plant photomorphogenesis is mediated by photoreceptors and the signal from photoreceptors can control the

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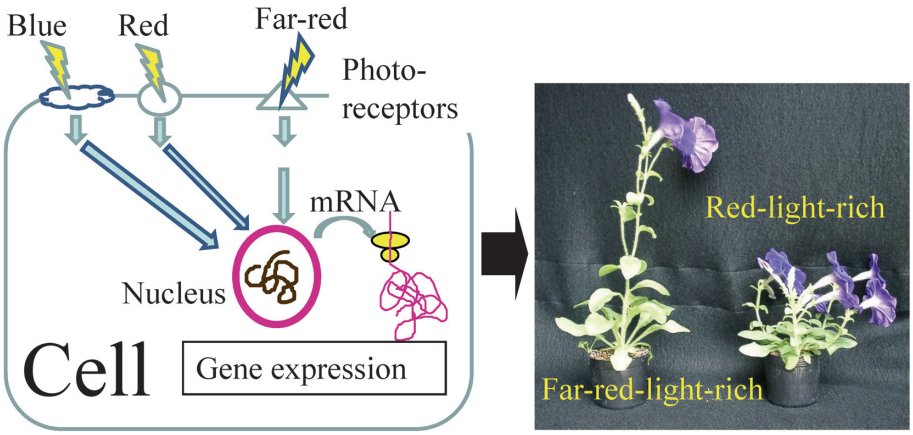

Fig. 1. Light quality and plant photomorphogenesis. Petunia plants shown at right were grown under metal halide lamps (far-red-light-rich) or high-pressure sodium lamps (red-light-rich) for 60 days (Ubukawa *et al*., 2004).

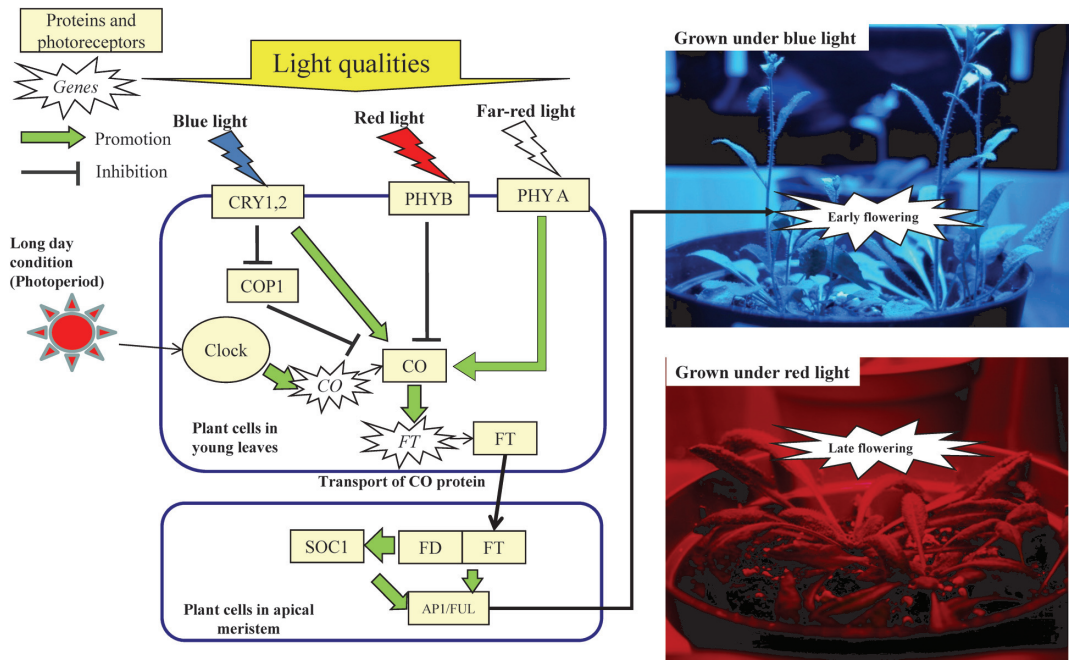

Fig. 2. Light quality and signal transduction systems in *Arabidopsis thaliana*.

genes expression concerned with cell division and enlargement (Fig. 1). Photoreceptor signals can thus induce floral bud formation and change plant shape. For example, petunia plant shape can be changed with changes in the ratio of red to far-red (a kind of infrared) light (Fig. 1; Fukuda *et al*., 2002; Ubukawa *et al*., 2004). Moreover, increasing the far-red percentage can induce petiole elongation in *A. thaliana* (Hisamatsu *et al*., 2005).

Light signals control floral induction genes via photoreceptor stimulation (Lin, 2000; Cerdan and Chory, 2003; Adams *et al*., 2009). When light of a specific quality turns on the "gene switch" associated with floral bud initiation, early blooming is induced.

Signal transduction from photoreceptors to control plant growth

Some researchers have suggested that the signals

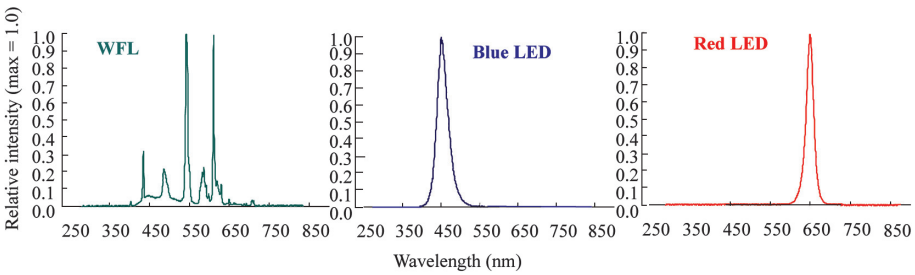

Fig. 3. Light qualities of white fluorescent lamp (WFL), red LED, and blue LED.

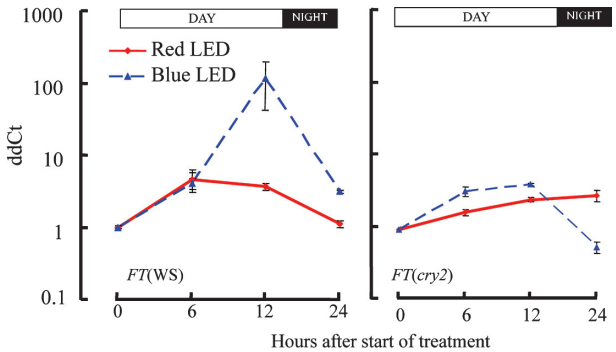

Fig. 4. Relative expression of *FT* in *Arabidopsis thaliana* under blue and red light treatments. The expression levels are shown in wild type (WS: Wassilewskija) and *cryptochrome2* mutant (*cry2*). Expression level data are normalized against the level of expression of *ACTIN2*. The expression level at 0 h is set at a delta-delta Ct (ddCt) in RT-PCR value of 1. Error bars show standard error (n=3).

from two different types of photoreceptor, cryptochrome (CRY) and phytochrome (PHY), control floral induction genes such as *FT* (*Flowering Locus T*) and *SOC1* (*Suppression of Overexpression of Constans 1*) and the stability of CO (CONSTANS) protein (Fig. 2; Lin, 2000; Cerdan and Chory, 2003; Adams *et al*., 2009). A blue light signal from CRY1 or 2 stimulates *FT* and *SOC1* expression via increased CO protein stabilization, which leads to activation of *AP1*; this in turn induces meristematic tissue differentiation and can induce early flowering in *A. thaliana*. In contrast, a red light signal from PHYB inhibits CO protein stability and can thus cause late flowering (Srikanth and Schmid, 2011). Far-red light can independently promote *FT* expression in *A. thaliana* (King *et al*., 2008). The main light qualities that control flowering timing are blue, red, and far-red (Bernier and Perilleux, 2005).

General light sources such as white fluorescent lamps emit broad spectra, from blue to far-red light (Fig. 3). In contrast, light-emitting diodes (LEDs) can radiate monochromatic light (e.g., blue or red). Blue light can be absorbed by CRY, which can then put out a signal for floral induction (Lin, 2000). We have demonstrated that changes in the relative expression of *FT* in *A. thaliana* after light treatment (Fig. 4). Monochromatic blue light provided by blue LEDs greatly increased *FT* expression—by about 100 times 12 h after the start of blue irradiation—in wild-type of *A. thaliana cv.* Wassilewskija (WS). However, mutant *cry2* of *A. thaliana* that had lost the *CRY 2* gene did not respond to blue light. Monochromatic blue light stimulated CRY, its signal acting to switch on floral induction genes such as *FT*. The signal from CRY can inhibit the expression of *COP1* (*Constitutively Photomorphogenic 1*), which depresses CO protein accumulation (Srikanth and Schmid, 2011). The increased level of CO under blue light can thus induce early flowering in *A. thaliana*. PHYA, which can absorb far-red light, emits a signal to induce floral bud initiation (Fig. 2) (King *et al*., 2008). These genetic systems for the control of flowering operate mainly in the responses of short-day and long-day plants to changes in photoperiod. Details of the mechanism of flowering control by light in a model plant, *A. thaliana* have already been reported (Srikanth and Schmid, 2011).

Many researchers have reported the effects of light quality in other plant species, including chrysanthemum, petunia, and geranium and so on (Rajapakse and Kelly, 1992; Kubota *et al*., 2000; Maki *et al*., 2002; Fukuda *et al*., 2008; Haliapas *et al*., 2008). We, too, have studied the effects of light quality on petunia growth (Ubukawa *et al*., 2004; Fukuda *et al*., 2008, 2011, 2012). In general, most commercial cultivars of petunia grow many lateral shoots and flowers (Fig. 5) under a white fluorescent lamp (WFL). Under WFL,

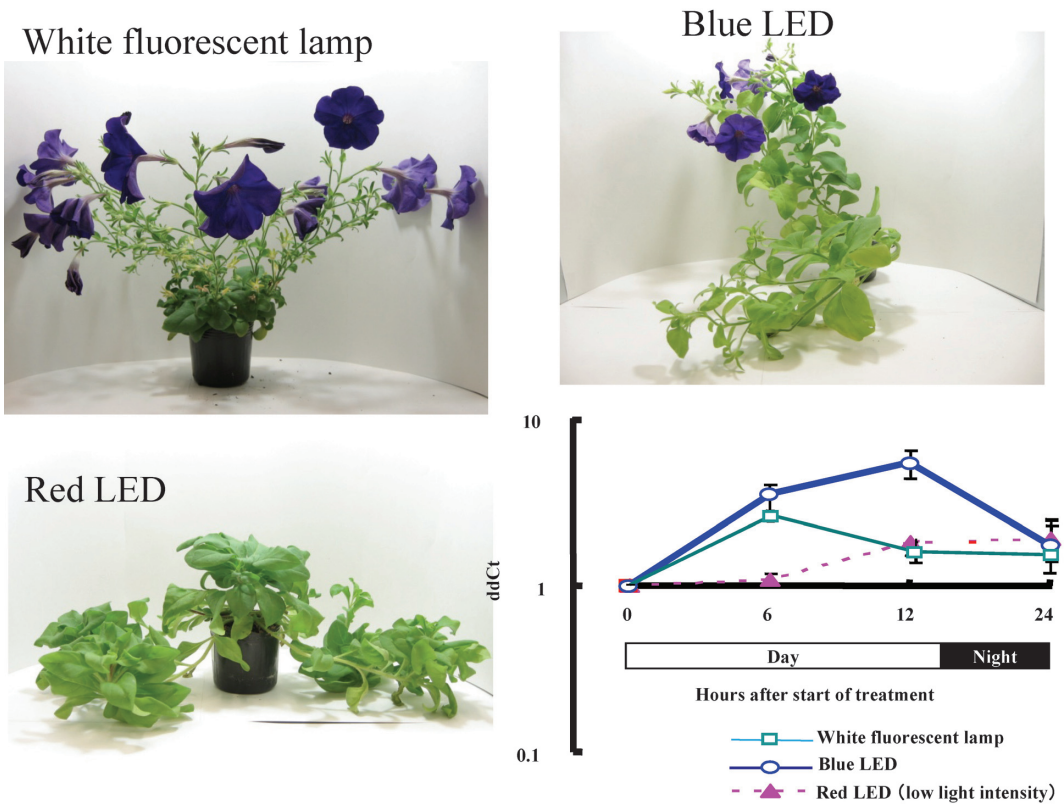

Fig. 5. Changes in petunia plant shape under white fluorescent lamp, blue LED, and red LED treatment. Relative expression of *FBP28* in petunia under each light treatment is also shown (Fukuda *et al.*, 2011). Expression level data are normalized against the expression level of *ACTIN8*. The expression level at 0 h is set at a ddCt value of 1. Error bars show standard errors ($n=2$).

the main shoot is short, but under blue LED, main shoot elongation is dramatic and flowering is observed on the main shoot (Fukuda *et al*., 2011). In contrast, under red LEDs, petunia plants have short main shoots and long and abundant lateral shoots, without flowering. Ferrario *et al*. (2004) reported that the petunia MADS box gene *FBP* (*Flavin Binding Protein*) sequence was similar to that of the *A. thaliana* flowering gene *SOC1*. Under blue LEDs, the floral induction gene *FBP28* (*Flavin Binding Protein 28*), which is a homologe gene of *SOC1* in *A. thaliana*, is expressed more highly than under red or white LEDs (Fig. 5; Fukuda *et al*., 2011). In petunia, as in *A. thaliana*, the signal transduction system for floral bud formation is excited by blue light via CRY, but how can we explain the differences in petunia plant shape under different light treatments?

In general, changes in plant shape are induced by phytohormones, and some types of phytohormone are regulated by changes in light quality (Xiaoying *et al*., 2007). In the case of petunia, red light without blue and far-red light (Ubukawa *et al*., 2004) during the daytime can be a strong inhibitor of the biosynthesis of active GA and can thus induce dwarfism. In addition to that study, we sampled shoot tips of petunia at the end of the 1st, 2nd, and 3rd weeks of red or blue light treatment and measured phytohormone levels. The auxin content under blue LEDs was slightly higher than that under red treatment (Fukuda *et al*., 2012). The abscisic acid (ABA) content of the petunia shoot tips showed a sudden increase at the 3rd week of treatment, but this increase was the same in both treatments. Levels of the cytokinins *trans*-zeatin and *iso*-pentenyl riboside were low under both light treatments, and there were no clear trends between both light treatments. However, the content of active gibberellic acid (GA) varied markedly among light treatments. On day 14 of treatment, under red LEDs, GA_4 was detected in trace amounts only and the level of GA_1 was 1.14 pg g FW^{-1}, whereas under blue

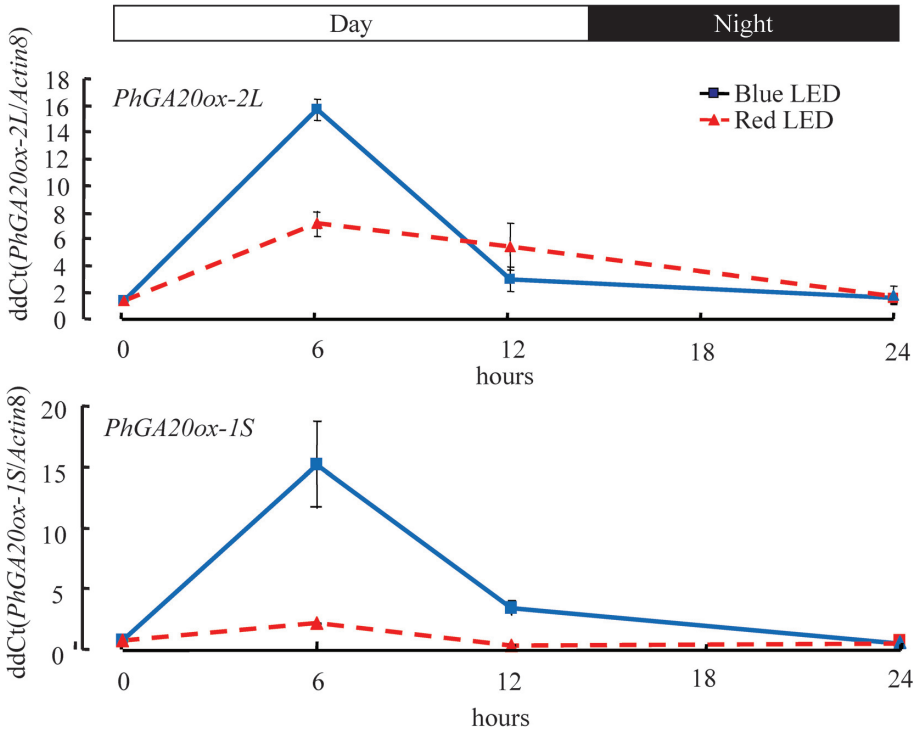

Fig. 6. Changes in levels of expression of *PhGA20ox-1L* and *PhGA20ox-1S* in petunia under blue and red LEDs (Fukuda *et al*., 2012). Error bars show standard errors (n=3).

LEDs, the levels were around 9 and 10 pg g FW^{-1}, respectively. Under red light without GA application, plants were dwarfed, with an increase in the number of lateral shoots. However, after GA_3 application under red LEDs, plant height increased, and responsiveness to GA in terms of main shoot elongation remained. From those results, we concluded that the change in plant shape under different monochromatic light is mediated by phytohormones, mainly GA (Fukuda *et al*, 2012). Under blue LEDs, production of GA 20-oxidase—one of the key enzymes in the synthesis of active GAs—increased in the shoot tips during the daytime (Fukuda *et al*., 2012). Expression of *PhGA 20ox-1S* and *PhGA20ox-2L*, two homologous genes for that encoding GA 20-oxidase in *A. thaliana*, under blue LED treatment was about two to five times that under red LED treatment by 6 h after the start of illumination (Fig. 6). Under blue light, synthesis of active GA is thus promoted and the GA content in plant body increases (Fukuda *et al*., 2012). Upon red-light stimulation of PHY signaling in petunia, the transcript levels of the GA 20-oxidase genes were inhibited, resulting in a low content of active GA (Fukuda *et al*., 2012). In *A. thaliana*, red light also inhibits the GA 20-oxidase gene and induces shortening of petioles (Hisamatsu, 2005). *GASA4* is down- and up-regulated by far-red and red light, respectively, in *A. thaliana* (Chen *et al*., 2007); *GASA4* activity decreases GA synthesis.

GA is also an important factor in control of flowering time. Chen *et al*. (2007) reported that a *gasa4* mutant showed early flowering, and that the phenotype was similar to that of plants under far-red light. The low level of active GA in petunia grown under red light could be an indirect factor in the inhibition of floral bud development.

When blue light stimulates CRY, the expression of floral induction genes such as *FT* and *SOC1* in petunia increases; this activates flower bud differentiation and development (Fig. 7). In contrast, the signal from PHYB stimulated by red light inhibits the expression of these genes. The signal from PHYB also inhibits GA 20-oxidase genes and can thus reduce the content of active GA and cause dwarfism. However, under blue light, there are no, or few, signals from PHYB; the content of active GA can thus increase and promote floral bud formation.

As we showed here, light quality signals can modify the expression of genes involved in plant development,

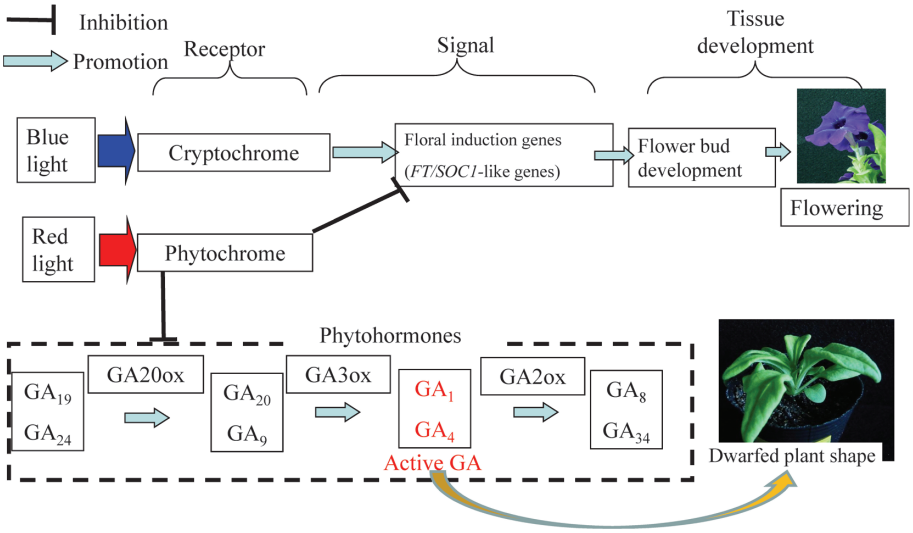

Fig. 7. Schematic diagram of light quality and signal transduction systems in flowering time and plant shape regulation in petunia.

phytohormone synthesis, and cell division, and these changes can induce changes in morphogenesis. If we can understand the mechanisms by which changes in light quality control plant development, then we can apply lighting control technology to practical plant production.

Application of lighting technology to plant production

Crop production can be enhanced by supplemental lighting. Supplemental lighting can be turned on or off according to changes in irradiance of solar radiation (MaCavoy and Janes, 1988). We can also extend day-length for photosynthesis by using supplemental lighting at night (Fukuda *et al*., 2004, 2006). In short-day plants such as chrysanthemum (*Chrysanthemum*× *morifolium* Ramat.) and beefsteak (*Perilla frutescens)* plants, floral bud formation is inhibited by lighting during the middle of the night. In strawberry, lighting for night break is used to inhibit the dormancy of flower buds (Yanagi *et al*., 2006). For such purposes, the light source needs to suit the purpose. Metal halide (MH), high-pressure sodium (HPS), and incandescent lamps have been used for lighting in agricultural production (Table 1). To irradiate the enough level of light intensity for promotion of photosynthesis, MH or HPS have been used (Grimstad, 1987). Today, new lighting technologies such as LEDs are also being used to promote plant growth and control plant shape.

We irradiated petunia transplants with light of different qualities for different periods of time, namely continuous red LED light; red light irradiation for 3 weeks followed by blue LED light irradiation for 1 week; red LED light irradiation for 2 weeks and then followed by blue LED light irradiation for same 2 weeks; red LED light irradiation for 1 week and followed by blue LED light irradiation for 3 weeks; and continuous blue LED light irradiation. Plant height increased with increasing duration of blue light irradiation (data not shown). In addition, application of the plant growth regulator CPPU (forchlorfenuron) to increase the cytokinin content in the plant body induced early flowering and a dwarfed plant shape under red LED light (Fukuda *et al*., 2012). Artificial monochromatic lighting of transplants with LEDs could be used to change characteristics such as plant height, number of lateral shoots, and flowering time to meet consumer demand.

Pigmentation is also modified by light quality. In tomato, the redness of the skin comes from the carotenoid and lycopene contents. The enzyme phytoene synthase is a key mediator of the pathway for synthesis of these pigments. Schofield and Paliyath (2005) showed that phytoene synthase activity is modified by irradiated light qualities, and that red light promotes it via the PHY signal. We think that not only the content of pigment, but also that of other secondary metabolites such as ascorbic acid, is affected by irradiance level and light quality, and that lighting technology could therefore be used to control phytochemical

Table 1. Aritificial light sources for crop production.

	Incandecent lamp	White fluorescent lamp	Metal halide lamp	High pressure sodium lamp	Light emitting diode (LED)
Electicity consumption (W/lamp)	75	40	400	360	0.04
PAR* efficience (mW/W)	71	151	197	287	224
Spectrum	Warm white	White	White	Orange	White, Monochromatic
Life (hrs)	1,000–2,000	3,000–10,000	8,000–10,000	10,000–12,000	3,000–100,000
Facility cost	Low	Low	High	High	High
Main applications in agriculture	Lighting for night break (Chysanthemum, Beefsteak plant)	Lighting for night break, Supplemental lighting. Plant factory system	Supplemental lighting	Supplemental lighting	?

*PAR: Photosynthetic active radiation

content.

The activity of insects and microorganisms is also influenced by light (Fig. 8). The coupling behavior of moths can be confused by night time lighting of 500 to 600 nm wavelength in greenhouse and so on (Yase, 2011) (e.g., from a yellow fluorescent lamp or HPS vapor lamp). Moreover, mildew resistance in strawberry can be strengthened by exposure to ultraviolet (UV) light (Kanto *et al*., 2009). UV-B irradiation can induce expression of the genes involved in disease resistance, such as the gene encoding PR (pathogenesis-related) protein (Kanto *et al*., 2009). Details of the mechanism of light-inducible disease resistance are still not clear, but UV-B radiation may induce disease resistance in some types of plants by causing a kind of environmental stress response.

Application of covering material technology to plant production in greenhouses

Shading is used to control lighting conditions in greenhouses. More specifically, however, morphogenesis can be controlled by using optical-selection covering materials that decrease specific light qualities (e.g., UV rays).

Temperature control by shading is also important. Thermal screens such as infra-red reflective films are now being used in commercial crop production. Insect control with nettings and covering films that prevent the ingress of near-UV rays is also being used in greenhouse systems (Shahak, 2008). In addition, plant shape (e.g., height) can be controlled by using photoselective covering materials that absorb the red or far-red components of sunlight (McMahon *et al*., 1991; Ilias and Rajapakse, 2005). Reducing the ingress of infra-red in greenhouse can inhibit air temperature rises inside in sub- and tropical area (Kumar *et al*., 2009). However, it also changes the light quality and thus the red to far-red light ratio (McMahon *et al*., 1991; Ilias and Rajapakse, 2005). Such changes in light quality can signal PHY and thus mediate shoot elongation. In Israel, photoselective nettings are being used to modify light quality; they could be of practical use in agricultural production without the need for chemical plant growth regulators (Shahak, 2008).

Conclusions

Light is a signal for plant growth control, and sunlight modulated by photoselective screens, or irradiation with monochromatic light, can be a stimulus for the switching on of specific genes. Changes in gene expression can induce the development of various phenotypes such as fruit skin color, plant shape, and disease resistance. Light-control technologies have great potential for use in smart and cool plant-production systems. LEDs or advanced fluorescent lamps can be used to supply monochromatic light; LEDs have

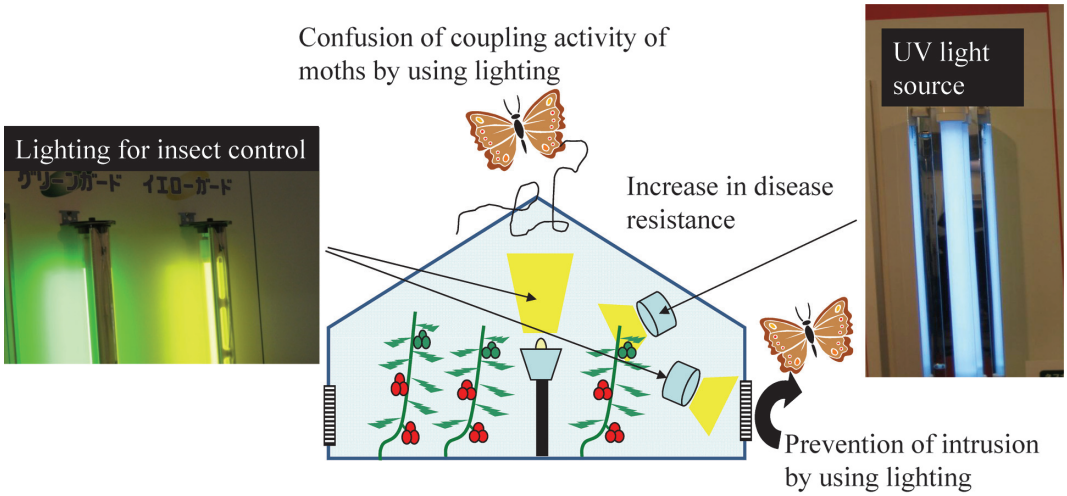

Fig. 8. Pest and insect management with lighting.

the advantage of high energy efficiency (Table 1) and thus low electricity consumption. In general, chemical plant growth regulators are still used in horticultural crops. However, monochromatic light from LEDs and sunlight modulated by photoselective screens have the potential for use as chemical-free ways of controlling plant growth. These new and advanced light technologies are still costly. However, in the near future, their use in all kinds of crop production should become common.

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