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Blue light associated with low phytochrome activity can promote elongation growth as shade-avoidance response: A comparison with red light in four bedding plant species

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ABSTRACT

To explore the action mode of blue light on elongation growth of bedding plants, the plant growth and morphology traits of petunia (*Petunia* × *hybrida*, 'Duvet Red'), calibrachoa (*Calibrachoa* × *hybrida*, 'Kabloom Deep Blue'), geranium (*Pelargonium* × *hortorum*, 'Pinto Premium Salmon'), and marigold (*Tagetes erecta*, 'Antigua Orange') were compared under four light quality treatments: (1) R, "pure" red light (660 nm); (2) B, "pure" blue light (450 nm); (3) BR, "unpure" blue light created by mixing B with a low level of R to provide B/R ≈ 9; (4) BRF, "unpure" blue light created by adding a low level of far red light to BR with red/far red ≈ 1. Continuous (24-h) light-emitting diode lighting with either 100 or 50 μmol m^{-2} s^{-1} photosynthetic photon flux density at ≈ 23°C was used with the above treatments. After 14–20 day of lighting treatment, B promoted elongation growth compared to R, as demonstrated by a greater canopy height, main stem length, internode length, and daily main stem extension rate. However, BR showed similar or inhibitory effects on these traits relative to R, while BRF exhibited similar promotion effects as B. The calculated phytochrome photoequilibrium, an indication of phytochrome activity, was higher for R (0.89) and BR (0.74) than for B (0.49) and BRF (0.63). Adding red (or far red) light reversed the effects of B (or BR) on elongation growth and the phytochrome photoequilibrium, suggesting that blue light promotion of elongation growth is related to the lower phytochrome activity. Also, B and BRF, when compared to R or BR, promoted elongation growth to a greater degree at 50 than 100 μmol m^{-2} s^{-1} for petunia and calibrachoa. In addition to the promoted elongation growth, B and BRF reduced side branch number, biomass allocation to side branches, leaf epinasty, leaf angle, and/or leaf chlorophyll content relative to R or BR, but increased individual leaf area, petiole length, and/or biomass allocation to main stem, which varied with different species. It suggests that the promoted elongation growth by blue light associated with lower phytochrome activity is one of shade-avoidance responses with varying sensitivity among species.

1. Introduction

Compact growth is one of the ideal marketable morphological characteristics of ornamental plants, especially bedding plants (Wollaeger and Runkle, 2015; Mah et al., 2018). Light adjustment technology has been adopted as one of the environmentally friendly ways to modify crop morphology in greenhouse production (Demotes-Mainard et al., 2016). Plants require light not only for photosynthesis, but also for regulation of their growth and development (Folta and Childers, 2008). Previous studies have clearly indicated that at least two photoreceptor systems, i.e., phytochromes, activated by red light and deactivated by far red light, and blue light receptors, cryptochromes, are involved in mediation of elongation growth by light (Cosgrove, 1981). Although both red and blue light can mediate stem elongation (Laskowski and Briggs, 1989; Hoenecke et al., 1992; Huche-Thelier et al., 2016), many previous studies have shown that blue light was more effective than red light in suppressing shoot/leaf elongation in a range of plant species (Cosgrove, 1981; Appelgren, 1991; Wheeler et al., 1991; Hoenecke et al., 1992; Cosgrove, 1994; Brown et al., 1995; Kong et al., 2012). However, in these studies, blue light sources may not have provided "pure", but rather "contaminated" blue light, i.e., blue light mixed with small amount of other spectral bands (Bergstrand et al., 2014).

Studies using light-emitting diode (LED) in recent decades have reported contradictory morphological responses to blue vs. red light in different species, and even in the same species; and, the effect of blue vs. red LED light on stem elongation is species- and even variety-dependent (Huche-Thelier et al., 2016). The emission of narrow-

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waveband light by LEDs provides the opportunity to re-evaluate the effects of "pure" blue light on plant growth and development and its relationship with other wavelengths such as red and far red (Tarakanov et al., 2012; Wollaeger and Runkle, 2013). Further study on blue light using LEDs will certainly contribute to a more in-depth understanding of the mode of action of blue light, and a more precise control of plant morphology using LED technologies in the near future (Tarakanov et al., 2012; Huche-Thelier et al., 2016).

Petunia, geranium, calibrachoa, and marigold are popular and economically important bedding plant species. However, limited information is available on the effects of blue vs. red light on these species, especially the effect of narrow-band LED light on plant morphology including elongation growth, even though a number of LED studies have been carried out on agronomic crops over the past decades (Massa et al., 2008). Also, the previous results of blue vs. red light effects on stem elongation of these bedding plants are not consistent and are often contradictory. Some studies have shown blue light to increase shoot elongation compared with red light. For example, in calibrachoa, propagated cuttings showed greater shoot elongation under monochromatic blue vs. red LED light with photosynthetic photon flux density (PPFD) of 40 or 80 $\mu mol\, m^{-2}\, s^{-1}$ and 16-h photoperiod (Olschowski et al., 2016). For marigold, monochromatic blue vs. red LED light (90 ± 10 $\mu mol\, m^{-2}\, s^{-1}$ PPFD and 16-h photoperiod) increased stem length (Heo et al., 2002). For petunia ('Baccarat Blue'), monochromatic blue vs. red LED light promoted stem elongation under 100 $\mu mol\, m^{-2}\, s^{-1}$ PPFD and 14-h photoperiod (Fukuda et al., 2011), as well as under 70 or 150 $\mu mol\, m^{-2}\, s^{-1}$ PPFD and 12-h photoperiod (Fukuda et al., 2016). Similar results were also observed in petunia ('Dwarf varieties mix') during early seedling stage, where a 12-h photoperiod was used but PPFD information was not mentioned (Akbarian et al., 2016). By contrast, for petunia ('Wave Pink'), monochromatic blue vs. red LED light (160 $\mu mol\, m^{-2}\, s^{-1}$ PPFD and 18-h photoperiod) inhibited leaf and stem expansion (Wollaeger and Runkle, 2014, 2015). In these two studies, higher light intensity, longer photoperiod, and different petunia varieties were used compared to the previously mentioned studies. For geranium, strong inhibitory effects on stem elongation were observed in shoot cultures under blue vs. red light (30 $\mu mol\, m^{-2}\, s^{-1}$ PPFD and 18-h photoperiod), but fluorescent light sources rather than LEDs were used for this study (Appelgren, 1991). It appears that the inconsistent results that have been reported may be due to the differences in lighting source, light intensity, genotype, and/or photoperiod.

Taking into account the increasing evidence of elongation growth promotion by blue light from LED lighting rather than broad-band lighting sources, it may indicate that "pure" blue light needs to act together with other wavelength(s) to inhibit elongation growth, at least in some species under a certain range of light levels. Previous study using non-LED lighting on de-etiolated seedlings of *Arabidopsis* indicated that blue light mediated inhibition of hypocotyl elongation was enhanced by its co-action with a low level of red light, but this effect was reversed by an equally low-level far red light, suggesting the involvement of phytochrome in this process (Ahmad and Cashmore, 1997). However, it is not clear whether blue light action on other plant species would have the same effect as with *Arabidopsis* if using LED lighting. In a previous LED study on petunia, the combination of 50% red and 50% blue light inhibited stem elongation when compared to 100% blue light, but was not different from 100% red light (Fukuda et al., 2016). Similarly, the combination of red and blue LED light (34–85% red light) induced more compact plants when compared to 100% blue LED light in petunia and geranium (Davis et al., 2015). However, in the above two studies, the effects of adding far red light were not tested, and a higher proportion (more than 30%) of red light was used for the red and blue LED combination treatment. The question that remains to be answered is whether "unpure" blue light, created by mixing "pure" blue light with a small amount (e.g., 10%) of monochromatic red light to activate phytochrome, can inhibit elongation growth when compared to monochromatic red light, and whether this response can be reversed by adding a small amount of far red light (e.g., red/far red ≈ 1) to de-active phytochrome in these bedding plants.

PPFD level of around 100 $\mu mol\, m^{-2}\, s^{-1}$ has been commonly used for LED lighting studies in the past decades, and at this light level inconsistent effects of "pure" blue vs. red light on elongation growth have been reported in different species, and even in the same species (Huche-Thelier et al., 2016). Surprisingly, under light levels < 100 $\mu mol\, m^{-2}\, s^{-1}$ and even as low as 30 $\mu mol\, m^{-2}\, s^{-1}$, many LED studies on tissue cultured plantlets have consistently reported elongation growth inhibition by "pure" blue when compared to red light in a wide range of species such as chrysanthemum (Kim et al., 2004), strawberry (Nhut et al., 2003), grape (Poudel et al., 2008; Li et al., 2017), banana (Nhut et al., 2002), *Cymbidium* (Tanaka et al., 1998), and *Doritaenopsis* (Shin et al., 2008). Nevertheless, it is difficult to compare these previous results about blue light effects under different light levels due to different environment conditions and plant materials. Different from tissue cultured plantlets, seedlings from seeds do not have rooting and/or differential induction stages. So, for the seedlings of these four bedding plant species, further study is required to determine how plant growth and morphology responds to blue vs. red light under decreased light levels, e.g., PPFD of 50 vs. 100 $\mu mol\, m^{-2}\, s^{-1}$.

For different ornamental plant species, blue light has been suggested to play an equal or greater role than red light in mediating inhibition of stem extension in long-day plants, such as *Campanula carpatica* 'Blue Clips', *Coreopsis* × *grandiflora* 'Early Sunrise', *Lobelia* × *speciosa* 'Sompliment Scarlet', *Pisum sativum* 'Utrillo', and *Viola* × *wittrockiana* 'Crystal Bowl Yellow' (Runkle and Heins, 2001; Kim et al., 2002; Shimizu et al., 2005). Petunia and calibrachoa are long-day plants, but marigold and geranium are short-day and day-neutral plants, respectively. In the commercial production of bedding plants, marigolds appear to be less susceptible to stretching than the other three bedding plant species based on the information provided by local greenhouse growers. It is not known if there are some differences among the four species in their morphological responses to blue vs. red LED light under the same environment conditions.

Previous studies have indicated that blue light inhibits plant elongation within seconds, while the inhibition by red light begins 15–90 min after the onset of irradiation, and in some species, blue light inhibition persisted only during the period of irradiation, after which elongation growth quickly returned to the high rate during the dark period (Gaba and Black, 1979; Cosgrove, 1981; Kigel and Cosgrove, 1991). The dark period in the previous studies using periodic lighting may have reduced the difference in blue vs. red light effects on elongation growth to a varied degree. Continuous lighting (no dark period) may be able to remove the effects of different photoperiod on elongation growth response to blue vs. red light. However, no studies using continuous (i.e., 24-h) blue or red LED lighting have so far been reported on bedding plants, and to our best knowledge, just one study has been performed on a non-bedding plant species, sesame (Hata et al., 2013).

Based on the above information, the following three hypotheses were formed for the four bedding plant species under continuous lighting using LEDs: (1) co-action with a low level of red light is required for "pure" (or monochromatic) blue light to inhibit elongation growth at least in some species under a certain range of light levels (e.g., ≤100 $\mu mol\, m^{-2}\, s^{-1}$ PPFD), but this inhibition effect can be reversed by addition of far red with an amount equal to red light; in other words, blue light effect on elongation growth is related to phytochrome activity at least in some cases; (2) the effects of blue vs. red light on plant elongation as well as other morphological traits differ under lower (e.g., ≈50 $\mu mol\, m^{-2}\, s^{-1}$ PPFD) and higher (e.g., ≈100 $\mu mol\, m^{-2}\, s^{-1}$ PPFD) light intensity; alternatively, there are interaction effects between light intensity and light quality; (3) blue vs. red light effects on plant growth and morphology vary with different species, especially those with different photoperiod flowering responses.