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Antagonistic action of blue and red light on shoot elongation in petunia depends on gibberellin, but the effects on flowering are not generally linked to gibberellin

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ABSTRACT

Plant morphology and flowering are influenced by light quality, but responses vary between species. Here we investigated effects of irradiance (70 or 150 μmol m^{-2} s^{-1}) of red (R) and blue (B) compared to white (W) light, provided by light emitting diodes, on growth and flowering in petunia. R light inhibited shoot elongation, but opposite to commonly observed, B light greatly enhanced shoot elongation. Consistent with this, bioactive gibberellins (GA_1, GA_4) showed higher and lower levels under B and R light, respectively, and GA_3 application induced elongation in uniconazole-treated plants, although delayed in R. Inhibited shoot elongation under RB treatment in spite of higher GA level compared to R only, supports that R light inhibits elongation growth, and indicates negative effect of R light on GA signaling. Floral bud formation and flowering occurred earlier under B compared to W light. Whereas no floral buds were observed under low R irradiance, high R irradiance and temporal switching to B light during long-term low R irradiance induced floral development. Except slight trends of promoting effect of the highest GA_3 level and delay in uniconazole-response under B light, lack of flowering under low R irradiance was not significantly affected by uniconazole or GA_3 application. In conclusion, B and R light are strong signals enhancing and inhibiting shoot elongation, respectively, through modulation of GA content. B light is a strong signal in floral bud formation, whereas effect of R light depends on irradiance, indicating existence of an energy/photosynthesis-related floral pathway in petunia. Although light quality affects flowering and main shoot elongation, these responses do probably not correlate with each other through GA synthesis.

1. Introduction

Light quality is well known to affect photomorphogenesis in plants. In a range of species stem elongation is influenced by the red (R) to far-red (FR) ratio (R/FR), which is perceived by phytochrome photoreceptors (McMahon et al., 1991; Rajapakse and Kelly, 1992; Maki et al., 2002). In such species, stem elongation is reduced and enhanced by higher and lower R/FR ratio, respectively. Kubota et al., (2000) reported that R light-rich spectra under photo-selective films resulted in short main stems in petunia (*Petunia* × *hybrida*). Reduced stem elongation was also observed in petunia grown under high pressure sodium (HPS) lamps, as compared to metal halide (MH) lamps (Fukuda et al., 2002; Ubukawa et al., 2004). The HPS lamps used provide a higher R/FR ratio (4.4) than the MH lamps (1.1) but also a lower proportion of blue (B) light, with 3.0% in HPS versus 7.5% in MH (Ubukawa et al., 2004). A wide range of species responds to B light with inhibition of shoot elongation (Cosgrove, 1981; Wheeler et al., 1991; Honecke et al., 1992). In bean (*Phaseolus vulgaris*) the reduced shoot elongation under a low B light proportion was shown to be associated with reduced dry matter portioning to the stem (Maas et al., 1995). However, the effect of B light varies between species, and increased stem elongation under B light has been reported in petunia and a few other species like *Salvia* and marigold (*Tagetes*) (Fukuda et al., 2012; Heo et al., 2002).

The transition to flowering in plants is also well known to be regulated by the light conditions. Generally, the photoperiod controls the transition to flowering in long day (LD) plants such as *Arabidopsis thaliana* and spinach (*Spinacia oleracea*) and short day

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(SD) plants like *Chrysanthemum* and rice. Not only photoperiod, but also the light quality affects induction of flowering in a number of species. In *A. thaliana*, R-FR light-sensing phytochromes (phy) and the B light receptors cryptochromes (cry), specifically phyA, phyB and cry2, have important roles in floral induction (Cerdan and Chory, 2003; Bernie and Perilleux, 2005). In this species, B and FR light stimulate signal transduction resulting in floral induction (Bernie and Perilleux, 2005), whereas low-intensity R light inhibits the signal from phyA and cry2, and thus delays floral bud formation (Cerdan and Chory, 2003). Petunia, like *A. thaliana,* is a quantitative LD plant and the timing of transition to flowering is a complex function of temperature, light integral and photoperiod (Adams et al., 2009). Haliapas et al. (2008) reported that high irradiance and FR end-of-day (EOD) treatment induced floral bud formation in petunia.

In LD plants such as *A. thaliana* and spinach, gibberellin (GA) is an important factor in transition to flowering (Bernie and Perilleux, 2005). Izhaki et al. (2001) suggested that GA regulates transition to flowering in petunia, and Ben-Nissan et al. (2004) reported that GA might induce transition to flowering through the GA-induced protein (GIP2). Treatment of petunia with the biosynthesis inhibitor prohexadione-Ca delayed anthesis under a photo-selective film absorbing FR light, suggesting an interaction between GA and light quality in control of flowering (Ilias and Rajapakse, 2005). Furthermore, GA is well known to control shoot elongation (Yamaguchi, 2008). Kurepin et al., (2012a,b) showed that shoot elongation in *A. thaliana* is promoted by the bioactive GA_4 and auxin under a low R/FR ratio. It has also been shown that the levels of GA, i.e., GA_{20} and the bioactive GA_1, are lower in petunia grown under HPS compared to MH lamps, and this was suggested to be mediated at least partly by the phytochrome system since these light sources differ in R/FR ratio (Ubukawa et al., 2004). However, since these broad-band light sources differ also in other parts of the spectrum such as with respect to the B light proportion (Ubukawa et al., 2004), the relationship between light quality and GA in shoot elongation and floral bud formation in petunia is still unclear.

The recent progress in the development of light emitting diodes (LEDs) of defined wavelengths has attracted considerable attention by facilitating research on light quality responses in plants. Also, since greenhouse production of plants at the northern hemisphere often depends on artificial lighting, the potential of using LED as light sources in greenhouses is of great interest due to the potential of exploiting light quality responses in control of growth and development. For example, Islam et al., (2012) suggested practical use of blue LED in addition to HPS lamps to control shoot elongation in poinsettia.

The objectives of the present study were (1) to investigate the effects of light-quality provided by monochromatic B or R LED on morphology and flowering in petunia; (2) to determine the interaction between light quality and irradiance; and (3) to study the effects of different lighting periods of B light. In addition, the interaction between light treatment and GA was studied by quantification of GA and application of the GA-biosynthesis inhibitor uniconazole and GA_3.

2. Materials and methods

2.1. Plant material and pre-cultivation

Seeds of *Petunia* × *hybrida* Vilm. 'Baccarat Blue' (Sakata Seed Corporation, Yokohama, Kanagawa, Japan) were sown in a cell tray filled with a commercial growth medium (Metromix350, Sun Gro Horticulture, Vancouver, British Columbia, Canada). The seeds were germinated at 25 °C under a 12 h photoperiod at a photosynthetic photon flux (PPF) of 70 μmol m^{-2} s^{-1} at 400–700 nm in a growth cabinet (LH-60FL12-DT, Nippon Medical & chemical instrument Co., Ltd., Osaka, Osaka, Japan) equipped with fluorescent lamps (FL10-B, Hitachi Appliances, Tokyo, Japan) as light source. After germination, the seedlings were transplanted individually to 10 cm pots filled with the same commercial growth medium used for germination. The seedlings were fertilized with a commercial fertilizer (Hyponex, N:P:K = 6:10:5, Hyponex, Osaka, Japan).

2.2. Experimental growth conditions

When four true leaves had emerged at 21 days after sowing (experiment 1–3), the seedlings were transferred to growth cabinets at 25 °C with 12 h photoperiods of different light qualities provided by panels of light emitting diodes (LED); White (W) LED (NSPW510BS, Nichia, Anan, Tokushima, Japan), red (R) LED (F4F,

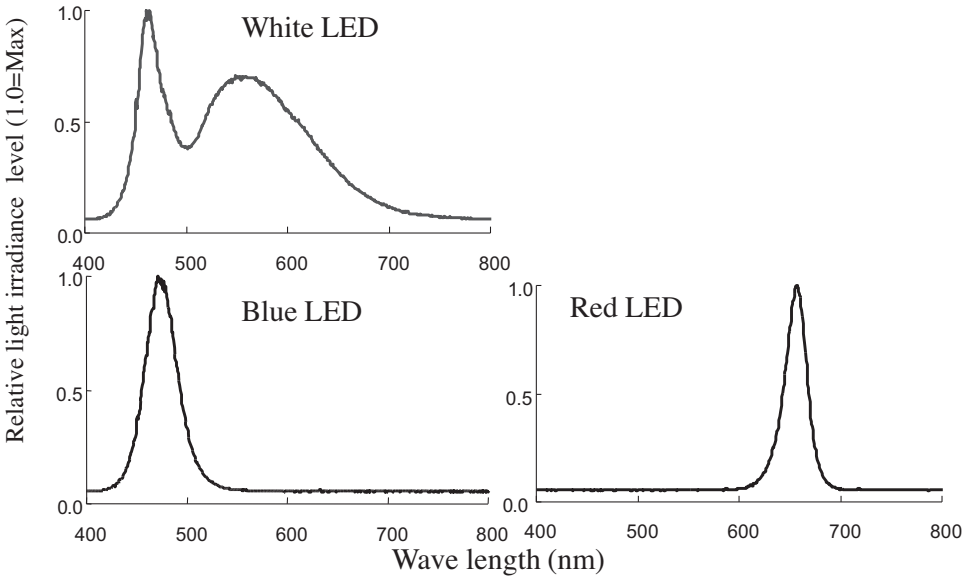

Fig. 1. Spectra of the light from the light emitting diodes (LED) used in this study. The peak wavelengths are 470 nm in white LED, 470 nm in blue LED and 660 nm in red LED. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)