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Light quality regulates plant architecture in different genotypes of *Chrysanthemum morifolium* Ramat

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ABSTRACT

Specific light spectra play an important role in plant photomorphogenic responses. Plants are sensitive to light ranging from UV (280–400 nm) to far-red light (700–800 nm). The shoot architecture or plant shape is an important quality trait in ornamental plants and can be altered under specific light spectra. The shade avoidance syndrome is a well-documented response of plants to canopy shading and low R:FR conditions, characterized by shoot elongation and inhibited branching. Treatments with LED light combinations to obtain different spectral compositions were tested on rooted cuttings of 3 chrysanthemum genotypes (a pot chrysanthemum, a cut flower and a disbud chrysanthemum genotype) to assess the effect on shoot architecture. Red light treatment generally showed increased bud outgrowth and increased average bud length while blue + far-red light treatment resulted in decreased bud outgrowth and bud length. Some effects were genotype dependent, such as plant height, which increased under blue + far-red light treatments compared to red light treatment, only for the pot chrysanthemum genotype.

Treatment with blue + far-red light in 25 decapitated cuttings showed a strong elongation of the topmost axillary bud and inhibition of underlying buds for the pot chrysanthemum and cut flower genotypes. This effect also persisted in greenhouse conditions.

1. Introduction

The morphological response to light quality in plants is part of a strategy to adapt to a changing light environment. This is regulated by the interaction between plant photoreceptors sensitive to particular wavelengths and their downstream signaling pathways. The most striking effect of light composition on shoot architecture is the shade avoidance syndrome. This phenomenon describes the elongated growth of plants, growing in high density, to escape canopy shading (Pierik and de Wit, 2014). The shade avoidance response includes increased internode elongation, inhibited axillary bud outgrowth, petiole elongation and upward bending of leaves (hyponasty). This response to shading is caused by changes in the red (R) to far-red (FR) light ratio, resulting in a FR enhancement that is perceived by the plant photoreceptors. In a dense canopy, the surrounding foliage absorbs red light, while much more far-red light reaches the lower canopy. The R:FR ratio is calculated by dividing the photon irradiance between 655 and 665 nm (R) with the photon irradiance between 725 and 735 (FR). This R:FR ratio ranges from 1.2 in daylight to 0.1 under canopy shading (Franklin, 2008). Blue (B) and UV light are also known to be involved in plant photomorphogenic responses and are perceived by a number of photoreceptors, including phytochromes, cryptochromes, and phototropins. Blue light and UV light generally show reduced plant height and effects on shoot branching are species dependent (for review see Huché-Thélier et al., 2016). Stem elongation in chrysanthemum is also inhibited by blue light treatment (Shimizu et al., 2006).

The shade avoidance response includes involvement of cryptochrome and phytochrome A (Casal, 2013) but the phytochrome B (PHYB) photoreceptor predominantly regulates the response to red and far-red light (Pierik and de Wit, 2014). Phytochrome B is present in two forms: the inactive Pr and the active Pfr form. The Pr form absorbs red light and gets converted to the Pfr form. The Pfr form absorbs far-red light, which reverts the receptor to the Pr form. In this way a changing red to far-red ratio results in a changing equilibrium between phytochrome B in the inactive Pr or the active Pfr form. This relationship is quantified by the phytochrome

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photostationary state (PSS) or photoequilibrium, quantified by the ϕ-value as the ratio of the Pfr form to the total phytochrome B. Using spectroradiometric data and phytochrome absorbance, the ϕ-value can be estimated (Sager et al., 1988). This value is considered to be more closely correlated to plant responses than the R:FR ratio because the phytochrome photo-conversion involves interacting wavelengths between 350 and 850 nm (Kelly and Lagarias, 1985; Sager et al., 1988). Daylight conditions have a ϕ-value of around 0.81 while single source red and far-red light have ϕ-values of 0.89 and 0.2, respectively.

A low red to far-red ratio, characterized by a low ϕ-value, has been linked to an increased biosynthesis of auxin, associated with the shade avoidance response (Halliday et al., 2009). In this response, auxin is responsible for shoot elongation and also influences the axillary bud outgrowth through the mechanism of auxin in apical dominance, where growth of the shoot apex inhibit outgrowth of underlying axillary buds (Cline, 1991). This interaction of light and auxin has been demonstrated in *Arabidopsis*, where auxin responsive genes were found to be upregulated in *phyB* mutants, which have a reduced branching phenotype (Krishna Reddy and Finlayson, 2014). This indicates a promotion of branching through repression of auxin signaling by PHYB activation with a high R:FR ratio. Inactivation of PHYB by a low R:FR (or in the *phyB* mutant) upregulates auxin responsive genes and inhibits branching. Phytochrome interacting factors PIF4 and PIF5 have been shown to be involved in this interaction of PHYB and auxin signaling (Hornitschek et al., 2012). Furthermore, also auxin biosynthesis plays a role, as increased accumulation of IAA has been shown in *Arabidopsis* seedlings under low R:FR conditions (Keuskamp et al., 2010). A low R:FR ratio has also been shown in *Sorghum* and *Arabidopsis* to promote the expression of the *BRC1* transcription factor, associated with inhibition of bud outgrowth, through PHYB signaling (Kebrom et al., 2006; Finlayson et al., 2010). In addition, involvement of strigolactones has also been shown in *Sorghum*, where the strigolactone signaling gene *MAX2* was required for the effect of PHYB on shoot branching (Kebrom et al., 2006, 2010).

The effect of light quality could be applied to control shoot architecture and the outgrowth of axillary buds. Some studies have made use of spectral filters with a $CuSO_4$ solution or a far-red absorbing dye, to block out far-red light and increase the compactness of plants. This was reported to result in reduced plant height and internode length in chrysanthemum (Rajapakse et al., 1992; Li et al., 2003; Khattak et al., 2004) as well as in other species (reviewed by Rajapakse et al., 1999).

Another way to adjust the R:FR ratio is to use R and FR light sources. In many plants, using FR light (or low R:FR) results in increased plant height and decreased bud outgrowth and bud length (Demotes-Mainard et al., 2016). R and FR LED light sources have been examined in chrysanthemum for flower bud induction (Singh, 2013; Jeong et al., 2014), rooting and biomass (Kurilčik et al., 2008; Christiaens et al., 2015; Hong et al., 2015) as well as plant height (Lund et al., 2007).

In cut flower chrysanthemum, the final shape of the plant is required to be elongated and unbranched, except for some branches with flowers near the apex. In the production of cut flowers with a single top flower (disbud types), axillary buds have to be removed manually. In general though, the early production phase of these types still requires a compact growth for better shoot quality, for which growth retardants are used. Only rarely, if plants would reach insufficient length through natural growth, gibberellic acid (GA) is used to stimulate elongation. In that case, a light treatment could present a non-chemical alternative to control growth. The production of pot and garden chrysanthemums requires a highly branched, bushy plant habit.

In this study, we tested different LED combinations to find a light recipe to stimulate axillary bud outgrowth and a bushy architecture for pot and garden chrysanthemums, as well as a light treatment that inhibits outgrowth of axillary buds for disbud type chrysanthemums. Hereto, we investigated the effect of different combinations of red, blue and far-red LED light, compared to fluorescent light on shoot architecture (plant height and bud outgrowth) in chrysanthemum. Treatments with far-red LED light were always given in combination with other light spectra (in this case blue), since far-red light does not contribute to the photosynthetic active radiation (McCree, 1971).

2. Materials and methods

2.1. Plant material

Unrooted cuttings of different chrysanthemum genotypes were obtained from companies in Belgium (Gediflora for genotype C9; Dataflor for genotype C13) and the Netherlands (Dekker Chrysanten for genotype C17). Genotype C9 is a pot chrysanthemum type, characterized by a short growth habit and spontaneous branching. C13 is a special type of disbud chrysanthemum from which unwanted lateral buds are being removed during growth in order to obtain large flowers. C17 is a cut flower chrysanthemum with an elongated growth habit and strong apical dominance. Cuttings were rooted in a standard greenhouse at 20 °C under long day light (16 h High Pressure Sodium (HPS) 100 μmol m^{-2} s^{-1}) conditions for 3 weeks before start of the experiment in the LED growth chamber. In all experiments, rooted cuttings were randomly placed in a 56-cell tray for each treatment.

2.2. Experimental set-up

Light conditions in the growth chamber (MAIS AUTOMATISERING NV, St. Katelijne Waver Belgium) were set by adjusting the fluence rate of red, far-red and blue light (Koninklijke Philips N.V., Amsterdam, Green Power LED research modules) with a total fluence rate of 60 μmol m^{-2} s^{-1} PAR light. Fluorescent light (FL: cool white Philips Master TLD 36W/840) of 60 μmol m^{-2} s^{-1} served as a control condition in a separate growth chamber for the second and third experiment. The light spectra of the blue, red, far-red and fluorescent light sources is found in Supplementary Fig. 1. In the first experiment, fluence rates of 30 and 90 μmol m^{-2} s^{-1} were also tested. The temperature was set at a constant temperature of 20 °C with a relative humidity of 70% and 19 h photoperiod. The spectral distribution of light intensity between 200 and 900 nm was measured with a JAZ spectrophotometer (Ocean Optics Inc., Dunedin, FL, USA) and converted with Spectrasuite (Ocean Optics) and Excel to μmol m^{-2} s^{-1} values. Fluence rate of FR light is also expressed as μmol m^{-2} s^{-1} but does not contribute to the total PAR (total fluence rate between 300 and 700 nm). The ϕ-value was calculated using phytochrome absorbance data from Sager et al. (1988). Rooted cuttings were kept in the growth chamber for 6 weeks.

1. In the first experiment, 25 rooted cuttings of cut flower chrysanthemum genotype C17 were tested per light treatment. Ten of these cuttings were decapitated at the start of the experiment and 15 were left intact. The used light qualities and fluence rates are in Table 1. The treatments with R and BFR represented an extremely high ϕ-value of 0.89 and an extremely low ϕ-value of 0.2 respectively. These treatments were also given at a fluence rate of 30 μmol m^{-2} s^{-1} and 90 μmol m^{-2} s^{-1}. Treatment with 60 μmol m^{-2} s^{-1} FL was used as a control. 60 μmol m^{-2} s^{-1} blue light and other combinations of blue and red light were added to include intermediate ϕ-values for 60 μmol m^{-2} s^{-1}.