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An intermediate phytochrome photoequilibria from night-interruption lighting optimally promotes flowering of several long-day plants

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ABSTRACT

Flowering of long-day (LD) plants is promoted by low-intensity (photoperiodic) lighting during an otherwise long night. Conventional lamps that emit a relatively low red (R; 600–700 nm) to far-red (FR; 700–800 nm) light ratio (e.g., incandescent lamps) create an intermediate phytochrome photoequilibria (PPE) and are sometimes more effective at promoting flowering of LD plants (LDP) than lamps that emit a higher R:FR (e.g., fluorescent lamps) and establish a higher PPE. Thus, we postulated that flowering of several LDPs would be increasingly promoted as the fraction of FR radiation increased relative to R light and the established PPE decreased. *Rudbeckia* (*Rudbeckia hirta*), snapdragon (*Antirrhinum majus*), *Fuchsia* (*Fuchsia* × *hybrida*), and three cultivars of *Petunia* (*Petunia* × *hybrida*) were grown at 20 °C under a truncated 9-h ambient photoperiod with or without 4-h NI lighting by incandescent lamps or light-emitting diodes that emitted seven different R:FR and created estimated PPE from 0.16 to 0.89. For all three *Petunia* cultivars and snapdragon, flowering was earliest under an NI with an intermediate PPE and delayed under short days (SDs) or an NI that elicited the highest or lowest PPE. For *Rudbeckia* and *Fuchsia*, all NI treatments promoted flowering except for the highest PPE NI, which was perceived as an SD. There were relatively subtle effects of the NI treatments on extension growth except in *Petunia*, in which all three cultivars showed a quadratic response to the PPE under the NI treatments, where plants were tallest at flowering under intermediate PPE. We conclude that an NI that establishes an intermediate PPE optimally promotes flowering of a variety of LDPs. These results are not consistent with the established paradigm for how light quality regulates flowering of LDPs, particularly in *Arabidopsis*, suggesting that the paradigm is not necessarily applicable to plants outside of the Brassicaceae.

1. Introduction

The flowering of many horticultural crops – especially ornamentals – is influenced by photoperiod (Erwin and Warner, 2002; Mattson and Erwin, 2005; Runkle and Heins, 2003). Photoperiodic flowering responses are determined primarily by the length of the dark period, also known as the critical night length (Thomas and Vince-Prue, 1997). Plants have been categorized into photoperiodic classes, depending on how they respond to the critical night length, including long-day (LD) plants (LDPs), in which flowering is most rapid when uninterrupted dark periods are shorter than some genotype-specific critical night length (Vince, 1969). When the ambient photoperiod is short, commercial growers accelerate flowering of LDPs and inhibit flowering of short-day (SD) plants by using low-intensity (photoperiodic) lighting during the beginning or middle of the night.

Light quality, or the distribution of wavelengths, can cause a broad range of morphological and developmental changes in plants. It is detected by three identified families of photoreceptors in plants, including the phytochromes (Kami et al., 2010). The phytochromes exist in red- [R (600–700 nm); peak absorption at 660 nm] and far-red- [FR (700–800 nm); peak absorption at 730 nm] absorbing forms, P_R and P_{FR}, respectively (Hayward, 1984; Sager et al., 1988). Phytochromes have the potential to control a wide variety of plant responses, including seed germination, plant architecture, flowering, tuberization, bud dormancy, and shade-avoidance responses such as extension growth (Smith, 2000). The ratio of R to FR light (R:FR) incident on the plant influences the phytochrome photoequilibria (PPE) within the plant, although not in a linear manner (Fig. 1). Upon absorbing R light, P_R converts mainly to the P_{FR} form. The P_{FR} form largely converts back to the P_R form under FR light, or through a natural, gradual conversion during the dark period (Thomas and Vince-

Abbreviations: FR, far-red light; LD, long days; LDP, long-day plants; LEDs, light-emitting diodes; NI, night interruption; PAR, photosynthetic active radiation; P_{FR}, far red-absorbing phytochrome; PPE, phytochrome photoequilibrium; P_R, red-absorbing phytochrome; R, red light; SD, short days.

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Prue, 1997). The total pool of phytochrome in light-grown plants is constant, but the relative amounts in the P_{FR} and P_R forms fluctuate with changes to the light environment and during darkness.

During the night, P_{FR} promotes flowering in LDPs when present in sufficient concentrations and is associated with a high PPE. During long nights (SDs), P_{FR} slowly converts to P_R, leaving insufficient P_{FR} to promote flowering. However, if this dark period is interrupted with light for a sufficient period of time (e.g., >2 h), the conversion of P_{FR} to P_R is also interrupted, leaving enough P_{FR} to effectively promote flowering. Although the flower-promoting P_{FR} form of phytochrome depends on the R light conversion of P_R to P_{FR}, several studies have shown that a moderate R:FR during the photoperiod is more effective at promoting flowering in some LDPs than a high R:FR (Kim et al., 2002; Runkle and Heins, 2003; van Haeringen et al., 1998).

In nature, the light environment changes during the day, with the R:FR ranging from 1.15 under full sun to 0.70 at twilight (Lund et al., 2007). The R:FR can also vary significantly within layers of a plant canopy. These differences can occur between leaf layers of the same plant or between layers of a complex plant community (Smith and Holmes, 1977). Leaves at the top of a canopy receive unfiltered sunlight with a relatively high R:FR. As light passes through a plant canopy, the plant tissues absorb most of the photosynthetic light, whereas FR light is primarily transmitted through or reflected to the lower canopy (Smith, 1994). The R-depleted light under a plant canopy has a reduced R:FR, which can be as low as 0.05 under a dense canopy (Smith, 1982). Changes in the R:FR are a more dependable indicator of the proximity of potentially competing neighbors than associated reductions in light intensity (Smith, 2000). In commercial greenhouses, the R:FR of light is commonly altered by human-imposed factors such as plant spacing (plant density), canopy shading from plants in hanging baskets, use of electric lighting, and use of light-filtering films. Plants detect a low R:FR ratio and respond by increasing extension growth to compete for photosynthetic light (Morgan and Smith, 1978). This shade-avoidance response enables them to react to potential competition for light before it actually occurs. If elongation growth fails to bring a plant into an unshaded environment, other aspects of the shade-avoidance response can cause early flowering and seed production, thus increasing the chance of perpetuating the plant (Smith, 2000).

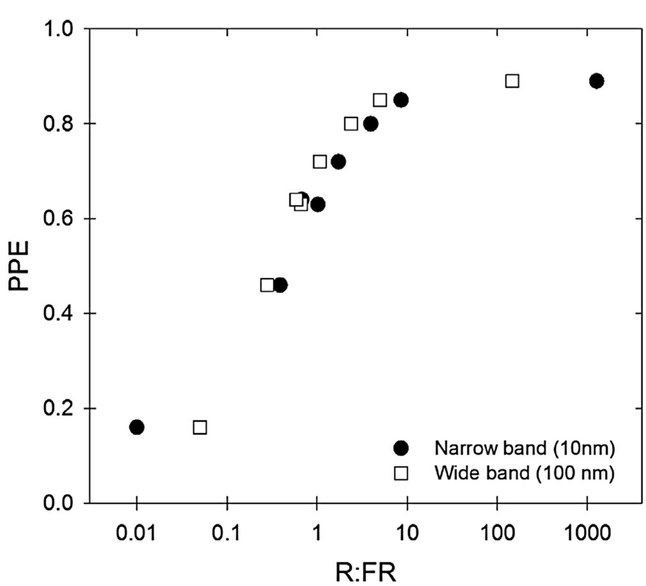

Fig. 1. The relationship between narrow- or wide-band ratios of red (R) to far-red (FR) light and phytochrome photoequilibrium (PPE). See Table 1 for additional information.

In greenhouses, horticultural crops are produced in controlled environments in which environmental factors such as temperature, light intensity, light quality, and photoperiod are manipulated beyond the realm of natural conditions. The characteristics of the light environment can have significant effects on plant growth, morphology, and flowering. The ability to elicit desirable plant responses to the R:FR and photoperiod in greenhouses allows commercial growers to produce ornamental plants that are in flower on predetermined market dates. In temperate regions, peak production of annual bedding plants and ornamental herbaceous perennials begins when the natural day lengths are short (<12 h). Many ornamental crops [e.g., *Petunia* (*Petunia* × *hybrida*) and snapdragon (*Antirrhinum majus*)] have an LD flowering response, and therefore lighting is commonly provided to accelerate flowering of LDPs. NI lighting is typically provided to LDP for 4 h because shorter durations can be less effective (Runkle et al., 1998).

Commercial growers traditionally used incandescent lamps to deliver photoperiodic lighting but only about 10% of their energy consumption is emitted as visible light and their longevity is relatively short (Kanter, 2009; Thimijan and Heins, 1983). With the phaseout of incandescent lamps, growers need more efficient sources of light to control flowering of photoperiodic crops. Compact fluorescent lamps are one alternative; they can promote flowering in some LDPs and are more energy efficient than incandescent lamps (Whitman et al., 1998). However, fluorescent lamps, which emit a relatively high R:FR and create a high PPE, were was less effective at promoting flowering in *Petunia* than incandescent lamps, which emit a moderate R:FR and create an intermediate PPE (Runkle et al., 2012).

Compared to conventional lamps, light-emitting diodes (LEDs) have many desirable characteristics, including a very long operating life, full instantaneous irradiance when powered, and improving electrical efficiencies (Bourget, 2008; Morrow, 2008; Nelson and Bugbee, 2014). Here, LEDs were used to quantify the effect of the PPE of night-interruption (NI) lighting on flowering of several LD ornamental crops, with comparisons to plants under incandescent lamps. We postulated that flowering in LDPs would be increasingly promoted as the R:FR decreased and thus the PPE decreased. Preliminary results showed that NI lighting that created an intermediate PPE was the most effective at promoting flowering of one *Petunia* and one snapdragon cultivar (Craig and Runkle, 2012). Here, we present a more comprehensive study that quantifies how the PPE controls flowering responses of a range of LDPs without the possibly confounding effects of other light wavebands or environmental parameters.

2. Materials and methods

2.1. Plant material and culture

Seven- to 10-d-old seedlings of the LDPs *Petunia* 'Shock Wave Ivory', 'Easy Wave White', and 'Wave Purple Improved'; *Rudbeckia* (*Rudbeckia hirta*) 'Denver Daisy'; and snapdragon 'Liberty Classic Cherry' grown in 288-cell (6-mL) plug trays were received from a commercial greenhouse (C. Raker and Sons, Inc., Litchfield, MI, USA). In addition, rooted cuttings of *Fuchsia* (*Fuchsia* × *hybrida*) 'Trailing Swingtime' grown in 36-cell (32-mL) liner trays were received from the same source. These varieties were selected according to their commercial popularity, as well as previous photoperiod research experience. The young plants were subsequently grown under noninductive SDs (natural day length truncated to a 9-h photoperiod with blackout cloth) in a research greenhouse at 20 °C until transfer to the NI treatments. On the day of transfer, the young plants were transplanted into 10-cm (430-mL) round plastic pots containing a commercial peat-perlite medium (Suremix; Michigan Grower Products, Inc., Galesburg, MI,