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Red, blue or mix: choice of optimal light qualities for enhanced plant growth and development through *in silico* analysis

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Abstract. In smart greenhouse farming, the impact of light qualities on plant growth and development is crucial but lacks systematic identification of optimal combinations. This study addresses this gap by analysing various light properties' effects (photoperiod, intensity, ratio, light–dark order) on *Arabidopsis thaliana* growth using days-to-flower (DTF) and hypocotyl length as proxies to measure plant growth and development. After establishing suitable ranges through a comprehensive literature review, these properties varied within those ranges. Compared to white light, a 16-h cycle of blue light reduces DTF and hypocotyl length by 12 % and 3 %, respectively. Interestingly, similar results can be achieved using a shorter photoperiod of 14-h light (composed of 8 h of a mixture of 66.7 μmol $m^{-2}s^{-1}$ red and 800 μmol $m^{-2}s^{-1}$ blue lights (i.e. blue:red ratio of 12:1) followed by 6 h of monochromatic red light and 10-h dark. These findings offer potential for efficient growth light recipes in smart greenhouse farming, optimizing productivity while minimizing energy consumption.

KEYWORDS: Flowering time; hypocotyl elongation; light order; light quality; photomorphogenesis; plant growth and development; smart greenhouse farming.

1. INTRODUCTION

In 2017, The Food and Agriculture Organization of the United Nations published a report stating that by the year 2100, global population is expected to grow to around 11 billion, of which most population growth is expected to be in Asia and Africa (United Nation, 2017). This rapid growth inevitably brings forward rapid urbanization, leading to a reduction in agricultural farmland if no further deforestation is considered. The same report also stated that the population demographic is also likely to get much older, and this would hit farming in rural areas especially hard as the younger workforce migrates to cities, thereby reducing the farming workforce. The reduction in the workforce coupled with the ongoing climate changes that bring in more floods and drought would make it even more challenging to meet the growing food demand.

Controlled environment agriculture–a technology-oriented approach that provides crop with consistent optimal growing conditions and shields them from external elements–such as smart greenhouse farming has been identified as one of the viable solutions to achieve food security (Walter et al., 2017; Mohamed et al., 2021; O'Shaughnessy et al., 2021; Karanisa et al., 2022). By artificially controlling plant exposure to important growth variables, such as light and water, smart greenhouse farming has the

potential to be more sustainable than conventional farming practices with the 'more food with less' concept through better efficiency in managing the use of those variables (Aune et al., 2017; Kumar et al., 2019).

One of the important variables that notably influence plant development in smart greenhouse farming is light (Kami et al., 2010; Neo et al., 2022). Thus, it is not surprising to see many studies are dedicated in finding the most efficient lighting strategy for smart greenhouse farming usage, either through experimentation (Olvera-Gonzalez et al., 2013) or optimization theory (Mosharafian et al., 2021).

The speed breeding protocol pioneered in Watson et al. (2018) represents the pinnacle of the role of manipulating light in enhancing crop yield. Through experimentation, this approach has demonstrated that the growth of crops such as wheat and barley can be accelerated by at least two times when exposed to extended periods of light up to 22 h. More importantly, this protocol can be easily adapted for use in growth chambers and greenhouses (Ghosh et al., 2018), making it an appealing option for incorporating effective lighting management into intelligent greenhouse agriculture to boost crop productivity.

To establish a framework of artificial light management capable of speed breeding protocol in smart greenhouse farming, six different light properties of white light were analysed in a systematic manner to determine which property is the most influential on plant growth (Pereira et al., 2021). The study confirmed the conclusions of the literature review articles by Bian et al. (2015) and Ahmed et al. (2020). They concluded that photoperiod and intensity are the most influential properties and suggested that similar days-to-flower (DTF) and hypocotyl length can be achieved with light exposure of up to 18 h as opposed to using photoperiod of 22 h following the speed breeding protocol. Interestingly, the review by Bian et al. (2015) and Ahmed et al. (2020) indicated that light quality (colour) is a key property for plant development, which is also highlighted by Pereira et al. (2021) as a future research work.

In this study, following a similar approach to Pereira et al. (2021), we extend the use of a systematic approach to investigate the effect of light qualities and their associated properties on plant development as a possible extension to the speed breeding protocol. As detailed in the next section, there are numerous experimental studies with different suggestions on the preferred light qualities for plant growth and development. To reconcile this discordance, we explore the use of *in silico* analysis to provide a more representative quantitative range of the light qualities. Another advantage of *in silico* experiments is the provision of benchmarking using one or multiple plant species that presents a viable alternative to the conventional experimental approaches in determining the best conditions for plant growth and development.

The main contributions of this study are as follows: a comprehensive literature search compiling the range of light quality relevant for plant growth and development across various types of plants, followed by performing a systematic analysis on the effect of different blue and red light properties, that is, intensity, ratio, photoperiod and wavelength of light order on plant growth and development. For the light order, a total of 28 combinations of light–dark order are considered, which, to our best knowledge, is the first time being analysed in an *in silico* setting. Such exhaustive light combinations are considered to allow us to find the suitable light recipe that optimizes plant growth and development and eventually leads to enhanced yield and energy consumption, thereby further improving the sustainability of smart greenhouse farming.

2. METHODS

2.1. Identifying experimental lighting conditions through literature review

There are many experimental studies available in the literature that investigate the effect of different light qualities on different plants. To enable us to obtain a practical range of these different light properties for our analysis, a comprehensive literature search is carried out to identify all the possible ranges that have been considered. Specifically, in our literature search, we focused on studies that use either blue or red lights to investigate plant growth or developmental characteristics, and we narrowed this down to 34 publications that are relevant to our study. Supporting Information–Table 1 summarizes our findings from the 34 publications covering 14 different genera of plants used in experimental studies encompassing agriculturally important plants, as well as the model plant *Arabidopsis thaliana*. All these plants respond differently to the effect of light qualities and any agricultural benefits that can be acquired from these light qualities depend on whether the crop favours vegetative growth (development of roots and shoots) or reproductive growth (flowering and fruit or seed formation). For instance, fruit- and seed-based crops may benefit if the flowering were accelerated; vegetative crops benefit from light regimes that delay flowering.

Considering the varieties of plant genera, this naturally leads to the question of the relevance of the light experiments from other plant genera to *in silico* light analysis using a well-established *A. thaliana* mathematical model that relates input light to plant growth and development-related pathways (Seaton et al., 2015; De Caluwé et al., 2016; Chew et al., 2022). In Song et al. (2010), the authors found that the circadian gene expression of *A. thaliana* is shared in other eudicots in the plant kingdom, such as legumes, rice, duckweed, moss, alga and many more long-day plants within and even outside of the angiosperms (flowering producing and fruit seed bearing plants) clade. Moreover, the study in McClung (2013) concludes that in angiosperms, many of the circadian clock characteristics and functions of *A. thaliana* are retained. These two studies provide evidence that the circadian clock components that regulate growth and other characteristics of *A. thaliana* are shared by a plethora of other plants. Given this rich knowledge, we have on *A. thaliana*, we aim to understand plant growth behaviour in relation to various light qualities through mathematical modelling and to use these findings to provide inferences on the effect of light qualities on the growth behaviour of other plants.

It has been demonstrated in *A. thaliana* that the spectral quality of light is more important in regulating flowering time (Eskins, 1992; Guo et al., 1998) and hypocotyl length (Spaninks et al., 2020) under different photoperiods, that is, 14 h (Eskins, 1992), 16 h (Spaninks et al., 2020) and 18 h Guo et al.

(1998) and light intensities, that is, 25–164 μmol $m^{-2}s^{-1}$ (Eskins, 1992), 120 ± 10 μmol $m^{-2}s^{-1}$ (Spaninks et al., 2020) and 75–85 μmol $m^{-2}s^{-1}$ (Guo et al., 1998), with blue light being most effective at promoting flowering. Conversely, red light, with the red:blue ratio ranging from 2:1 to 10:1, has been demonstrated to promote vegetative growth, important in leafy plants such as lettuce, cabbage, spinach and basil (Hoenecke et al., 1992; Matsuda et al., 2007; Stutte et al., 2009; Lee et al., 2010; Vaštakaitė et al., 2015; Zhang et al., 2018; Zou et al., 2020). However, studies that have considered a mixture of red and blue in a 1:1 ratio or a pure blue instead have demonstrated greater biomass accumulation than with red light alone (Muneer et al., 2014; Kwack et al., 2015; Piovene et al., 2015). It is thus key to optimize spectral quality to balance vegetative and reproductive growth dependent on the requirements of the crop plant while, at the same time, promoting carbon fixation and plant growth.

Literature on fruit-, root- and shoot-based plants also has similar arguments, suggesting that the large variation from drawn conclusions is not unique to literature investigating leafy plants alone, with some studies concluding that red alone or with relatively small blue light as the supplement is optimal for plant growth (Brown et al., 1995; Hogewoning et al., 2007; Folta and Childers, 2008; Gangadhar et al., 2012; Hernández and Kubota, 2014; Paradiso et al., 2019) while others conclude that blue light alone if not blue light with red light as the supplement is better (Wang et al., 2009; Yoshida et al., 2012; Cope and Bugbee, 2013; Kwack et al., 2015; Piovene et al., 2015). All these mentioned studies do not use the same intensity or share a similar intensity range in their respective studies. The photosynthetic photon flux density (PPFD) values utilized in those studies range from around 50 to 300 μmol $m^{-2}s^{-1}$.

On the effect of PPFD on plants, a study in Hidaka et al. (2013) concludes that lighting with a PPFD of 400–1200 μmol $m^{-2}s^{-1}$ is far more effective than with PPFD ranging from 0 to 200 μmol $m^{-2}s^{-1}$ for strawberry. In another study in Fu et al. (2012), the authors discover that a range of PPFD 400–600 μmol $m^{-2}s^{-1}$ is the optimal intensity for lettuce depending on the altitude where the lettuce is from and grown. Both studies also discovered a plateau in the photosynthetic rate and suggest the reason for a lack of increase in crop yield even when light intensity is increased limitlessly.

One key takeaway point from this literature review is that a cohesive conclusion on the effect of light qualities is difficult to be established even when examining the plant from the same family with the same mutation and the same measuring indices. We thus wish to investigate the effect of all the ranges of light properties, such as spectrum, photoperiod and intensity, to establish a more cohesive conclusion on their effects on plant growth and development in a systematic manner using *A. thaliana* as a model. More importantly, it provides us the opportunity to fill any gaps on different combination of light properties that have not been previously considered.

2.2. *A. thaliana* simulation model

To investigate the optimal lighting strategy, the simulation model used in this study is from our previous works (Pay et al., 2022b,a). It comprises 27 ordinary differential equations (ODEs), where the input is the light, and the outputs are the growth-related circadian genes that are used to compute DTF and hypocotyl length as shown in Fig. 1.

These 27 ODEs describe the expressions of genes and proteins that form the plant circadian system and two downstream

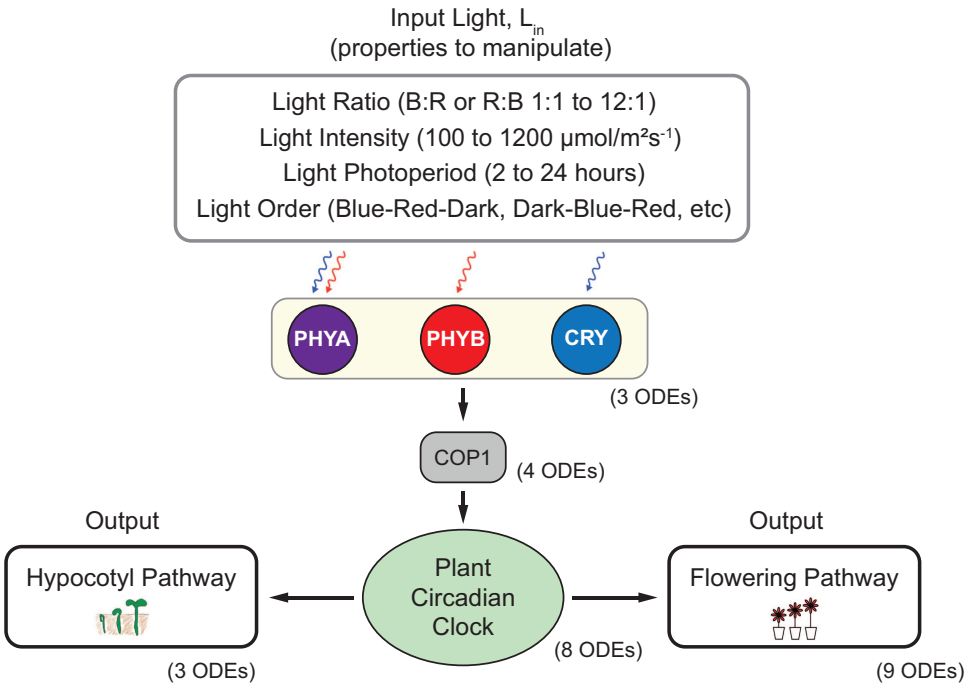

Figure 1. Overview of the interactions in *A. thaliana* mathematical model relating input light to output hypocotyl and flowering pathways.

pathways related to flowering and hypocotyl elongation. These ODEs are solved using MATLAB function `ode15s`. As a note, the notations used for all the ODEs follow (Pay et al., 2022b,a), and their respective parameter values are found in Supporting Information–Table 2.

2.2.1. Core plant circadian system

Eight ODEs form the core plant circadian system, which describes the dynamics of the CIRCADIAN CLOCK ASSOCIATED 1/LATE ELONGATED HYPOCOTYL, (CL) gene and protein, the PSEUDO RESPONSE REGULATOR 9/7, (P97) gene and protein, EARLY FLOWERING 4/LUX ARRHYTHMO, (EL) gene and protein and PSEUDO RESPONSE REGULATOR 5/TIMING OF CAB EXPRES-SION 1 and (P51) gene and protein.

$$
\begin{aligned}
\frac{d[CL]_m}{dt} &= (v_1 + L_a)\left(\frac{1}{1 + \left([P97]_p/K_1\right)^2 + \left([P51]_p/K_2\right)^2} + \right) \\
&= (k_{1L}\Theta_{PhyA} + k_{1D}(1 - \Theta_{PhyA}))[CL]_m \\
\frac{d[CL]_p}{dt} &= (p_1 + p_{1L}\Theta_{PhyA})[CL]_m - d_1[CL]_p \\
\frac{d[P97]_m}{dt} &= (v_2 + L_b) \\
&\quad \times \left(\frac{1}{1 + \left([CL]_p/K_3\right)^2 + \left([P51]_p/K_4\right)^2 + \left([EL]_p/K_5\right)^2}\right) \\
&\quad - k_2[P97]_m \\
\frac{d[P97]_p}{dt} &= p_2[P97]_m - (d_{2D}(1 - \Theta_{PhyA}) + d_{2L}\Theta_{PhyA})[P97]_p
\end{aligned}
$$

$$
\begin{aligned}
\frac{d[P51]_m}{dt} &= \frac{v_3}{1 + \left([CL]_p/K_6\right)^2 + \left([P51]_p/K_7\right)^2} - k_3[P51]_m \\
\frac{d[P51]_p}{dt} &= p_3[P51]_m - (d_{3D}(1 - \Theta_{PhyA}) + d_{3L}\Theta_{Phya})[P51]_p \\
\frac{d[EL]_m}{dt} &= \frac{\Theta_{PhyA} v_4}{1 + \left([CL]_p/K_6\right)^2 + \left([P51]_p/K_9\right)^2 + \left([EL]_p/K_5\right)^2} \\
&\quad - k_4[EL]_m \\
\frac{d[EL]_p}{dt} &= p_4 - d_{e1}[EL]_p \\
&\quad - \left(\frac{d_{e2}[COP1] + d_{e3}[COP1 : PhyA]}{[C_{tot}]}\right) \\
&\quad - \left(\frac{d_{e4}[COP1 : PhyB] + d_{e5}[COP1 : Cry1]}{C_{tot}}\right)[EL]_p,
\end{aligned}
\tag{1}
$$

where $C_{tot} = [COP1] + [COP1 : PhyA] + [COP1 : PhyB] + [COP1 : Cry1]$ is the total concentration of COP1.

2.2.2. Photoreceptors

Three ODEs are used to describe the three photoreceptors namely PHYTOCHROME A (PhyA), PHYTOCHROME B (PhyB) and CRYPTOCHROME (Cry1), which respond to red and blue lights.

$$
\begin{aligned}
\frac{d[PhyA]}{dt} &= (1 - \Theta_{PhyA})A_{p3} - \frac{A_{m7}[PhyA]}{A_{k7} + [PhyA]} \\
&\quad - q_2\Theta_{PhyA}[PhyA] + k_d[COP1 : PhyA] \\
&\quad - k_{mpac}\Theta_{PhyA}[PhyA][COP1], \\
\frac{d[PhyB]}{dt} &= B_{p4} - \frac{B_{m8}[PhyB]}{B_{k8} + [PhyB]} \\
&\quad - k_{mpbc}\Theta_{PhyB}[PhyB][COP1] \\
&\quad + k_d[COP1 : PhyB], \\
\frac{d[Cry1]}{dt} &= C_{p5} - \frac{C_{m9}[Cry1]}{C_{k9} + [Cry1]} \\
&\quad - k_{mpcc}\Theta_{Cry1}[Cry1][COP1] \\
&\quad + k_d[COP1 : Cry1].
\end{aligned}
\tag{2}
$$

2.2.3. COP1 interactions

The interaction of these photoreceptors with CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) protein, which acts as a key regulator of photomorphogenesis (biological response to light), is described using four ODEs.

$$
\begin{aligned}
\frac{d[COP1]}{dt} &= k_d[COP1 : PhyA] + k_d[COP1 : PhyB] \\
&\quad + k_d[COP1 : Cry1] + \frac{A_{m7}[COP1 : PhyA]}{A_{k7} + [COP1 : PhyA]} \\
&\quad + \frac{B_{m8}[COP1 : PhyB]}{B_{k8} + [COP1 : PhyB]} + \frac{C_{m9}[COP1 : Cry1]}{C_{k9} + [COP1 : Cry1]} \\
&\quad + q_2\Theta_{PhyA}[COP1 : PhyA] \\
&\quad - k_{mpac}\Theta_{PhyA}[PhyA][COP1] \\
&\quad - k_{mpbc}\Theta_{PhyB}[PhyB][COP1] \\
&\quad - k_{mpcc}\Theta_{Cry1}[Cry1][COP1]
\end{aligned}
$$

$$
\begin{aligned}
\frac{d[COP1 : PhyA]}{dt} &= k_{mpac}\Theta_{PhyA}[PhyA][COP1] \\
&\quad - k_d[COP1 : PhyA] \\
&\quad - \frac{A_{m7}[COP1 : PhyA]}{A_{k7} + [COP1 : PhyA]} \\
&\quad - q_2\Theta_{PhyA}[COP1 : PhyA], \\
\frac{d[COP1 : PhyB]}{dt} &= k_{mpbc}\Theta_{PhyB}[PhyB][COP1] \\
&\quad - k_d[COP1 : PhyB] \\
&\quad - \frac{B_{m8}[COP1 : PhyB]}{B_{k8} + [COP1 : PhyB]},
\end{aligned}
$$

$$\begin{aligned}\frac{d[COP1:Cry1]}{dt} &= k_{mpcc}\Theta_{Cry1}[Cry1][COP1] \\ &\quad - k_d[COP:Cry1] \\ &\quad - \frac{C_{m9}[COP1:Cry1]}{C_{k9}+[COP1:Cry1]}. \end{aligned} \tag{3}$$

2.2.4. *Hypocotyl pathway*

Three ODEs are used to describe the pathway related to hypocotyl elongation. They are PHYTOCHROME INTERACTING FACTOR (PIF), genes and proteins and HYPOP COTYL (HYP), which is used to calculate the hypocotyl length.

$$\begin{aligned}\frac{d[PIF]_m}{dt} &= \frac{v_5}{1+\left([EL]_p/K_{11}\right)^2} - k_5[PIF]_m, \\ \frac{d[PIF]_p}{dt} &= p_5[PIF]_m - d_{5D}(1-\Theta_{PhyA})[PIF]_p, \\ &\quad + d_{5L}\Theta_{PhyA}[PIF]_p \\ \frac{d[HYP]_p}{dt} &= g_1 + \frac{g_2[PIF]_p^2}{K_{12}^2+[PIF]_p^2}. \end{aligned} \tag{4}$$

2.2.5. *Flowering pathway*

The remaining nine ODEs are used to describe the genes and proteins in the flowering related pathway. They are GIGANTEA (GI) gene and protein, CYCLING DOF FACTOR 1 (CDF1) gene and protein, FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1) gene and protein, CONSTANS (CO) gene and protein and FLOWERING LOCUS T (FT) gene.

$$\begin{aligned}\frac{d[GI]_m}{dt} &= \frac{N_{v1}}{(NK_1+[CL]_p^2)(NK_2^2+[P51]_p^2)(NK_3^2+[EL]_p^2)} \\ &\quad + L_a - Nk_1[GI]_m, \\ \frac{d[GI]_p}{dt} &= Np_1[GI]_m - Nd_1[C_{tot}][EL]_p[GI]_p - Nd_2[GI]_p, \\ \frac{d[CDF1]_m}{dt} &= \left(Nv_2 + Nv_3\frac{[CL]_p^2}{NK_4^2+[CL]_p^2}\right) \\ &\quad \times\left(\frac{NK_5^2}{NK_5^2+([P97]_p+[P51]_p)^2}\right) - Nk_2[CDF1]_m, \\ \frac{d[CDF1]_p}{dt} &= Np_2[CDF1]_m - Nd_3N_{p3}[GI]_p[FKF1]_p[CDF1]_p \\ &\quad - Nd_3Np_4[GI]_p[CDF1]_p - Nd_3[CDF1]_p, \\ \frac{d[FKF1]_m}{dt} &= Nv_4\left(\frac{NK_6^2}{NK_6^2+[CL]_p^2}\right)\left(\frac{NK_7}{NK_7+[EL]_p}\right) \\ &\quad + L_b - NK_3[FKF1]_m, \\ \frac{d[FKF1]_p}{dt} &= Np_5[FKF1]_m, \\ &\quad - Np_6\left(Nd_4 - \Theta_{PhyA}\left(\frac{[GI]_p}{Ng_1+[GI]_p}\right)\right)[FKF1]_p, \end{aligned}$$

$$\begin{aligned}\frac{d[CO]_m}{dt} &= B_{CO} + \left(\frac{NK_8^2}{NK_8^2+[CDF1]_p^2}\right) \\ &\quad \times\left(Nv_5 + Nv_6(1-\Theta_{PhyA})\frac{[COP1]}{NK_9^2+[COP1]}\right) \\ &\quad - Nk_4[CO]_m, \\ \frac{d[CO]_p}{dt} &= Np_7[CO]_m \\ &\quad - Np_8(Nd_5 + Nd_6(1-\Theta_{PhyA})[COP1])[CO]_p \\ &\quad + Np_8\left(\Theta_{PhyA}\frac{[FKF1]_p}{Ng_2+[FKF1]_p}\right)[CO]_p, \\ \frac{d[FT]_m}{dt} &= \left(Nv_7 + Nv_8\frac{[PIF]_p}{NK_{10}+[PIF]_p}\right) \\ &\quad \times\left(Nv_9 + Nv_{10}\frac{NK_{11}}{NK_{11}+[CDF1]_p}\right) \\ &\quad \times\left(\frac{[CO]_p^2}{NK_{12}^2+[CO]_p^2}\right) - Nk_5[FT]_m. \end{aligned} \tag{5}$$

The equation of light input is given by

$$\begin{aligned}L_u &= q_{1u}[T_{PhyA}]\Theta_{PhyA} \\ &\quad + q_{3u}[T_{PhyB}]\log(\eta_1 I_{red}+1)\Theta_{PhyB} \\ &\quad + q_{4u}[T_{Cry1}]\log(\eta_2 I_{blue}+1)\Theta_{Cry1}, \end{aligned} \tag{6}$$

where $u \in a$ or b is the effect of light through PhyA or PhyB, q_{1u}, q_{3u} and q_{4u} are the light-induced synthesis rate through photoreceptors PhyA, PhyB and Cry1, respectively; $[T_{PhyA}]$, $[T_{PhyB}]$ and $[T_{Cry1}]$ are the total concentration of the three photoreceptors [see Supporting Information—Table 2]; I_{red} and I_{blue} are the light intensities for red and blue light, respectively; η_1 and η_2 are the normalization parameters of light intensity and Θ_{PhyA}, Θ_{PhyB} and Θ_{Cry1} are the light modes that take either 0 or 1, where 0 indicates dark while 1 indicates light. We used the initial condition of 1 for all the ODEs except [HYP], [COP1:PhyA], [COP1:PhyB] and [COP1:Cry], where zero initial conditions are used.

In Pay et al. (2022b,a) only one light colour (either blue, red or a mix of red and blue) is considered within the duration of the photoperiod. For example, if the photoperiod is 10 h, only monochromatic red or blue lights or a mixture of red and blue can be present for the entire duration of the 10 h. In this study, modifications have been made to the model to enable the insertion of multiple light colours within the duration of the photoperiod. For example, within this 10 h, we can now have monochromatic red light for 4 h followed by monochromatic blue light for 6 h or vice versa. This modification allows us to investigate the effect of multiple light colours and their order within the photoperiod on plant growth.

2.3. Plant growth indices

The output of the *A. thaliana* mathematical model is the hypocotyl and flowering pathways (see Fig. 1). The two indices

that are used as proxy for plant growth are DTF and hypocotyl length, which can be calculated from the two circadian genes namely FLOWERING TIME (FT) and PHYTOCHROME INTERACTING FACTOR (PIF) as follows:

2.3.1. Days-to-flower calculation

The calculation of DTF is given by,

$$\text{DTF (days)} = d_0 + \frac{a_0}{1 - (FT_{area}/a_1)}. \quad (7)$$

Equation (7) is an empirical equation where FT_{area} is the area under the curve for gene FT with unit (a.u.).day. a_0 is the function multiplier, a_1 is the lower limit of the area under the curve for gene FT and d_0 is the minimum flowering time. These three parameters are the tuneable parameters used to fit the experimental data (Corbesier et al., 1996; Salazar et al., 2009; Seaton et al., 2015). In this study, $d_0 = 16.55$ days, $a_0 = 1355.22$ days and $a_1 = 0.02$ (a.u.).days are considered, which have been estimated and calibrated in our previous work (Pay et al., 2022a).

2.3.2. Hypocotyl length calculation

The calculation of the hypocotyl length is given by,

$$\text{Hypocotyl length (mm)} = \int_0^D g_1 + \frac{g_2[PIF]_p^2}{K_{12}^2 + [PIF]_p^2} dt. \quad (8)$$

Equation (8) is taken from De Caluwé et al. (2016), where a Hill function parameterized by g_2 and K_{12} with a basal level g_1 are used to relate the hypocotyl length to the accumulation of protein PIF across the number of days, D. In this study, we consider $D = 10$ days, while $g_1 = 0.01$ mmh^{-1}, $g_2 = 0.1$ mmh^{-1} and $K_{12} = 0.56$ nM, which have been obtained from our previous work (Pay et al., 2022b). The calculation of DTF is rounded to the closest integer, while the hypocotyl length is rounded to two decimal places.

The simulation is carried out over 10 days, where the DTF and hypocotyl length calculated in this study are compared against the nominal values taken from Pereira et al. (2021) when simulated under white light condition. Simulation length of 10 days is chosen following the same number of days used in Pereira et al. (2021). Moreover, the model obtained in Pay et al. (2022b,a) is calibrated against experiment data when *A. thaliana* is 10 days old.

The nominal DTF and hypocotyl length of *A. thaliana* taken from (Pereira et al., 2021) are 21.62 days and 1.18 mm, respectively, and a shorter DTF and a hypocotyl length that is at least 1.00 mm are considered as improvement to its corresponding nominal values. The minimum acceptable hypocotyl length is set to 1.00 mm as further reduction of hypocotyl length can be a sign or cause of stunted growth (Derbyshire et al., 2007). Recall that these two nominal values were obtained using purely white light and, in this study, it is of interest to investigate whether the use of different light qualities at their associated properties could further improve plant growth compared to using white light.

2.4. Model fidelity

The simulation model used in this study has been previously calibrated and validated against experimental data from *A. thaliana* in our previous studies (Pay et al., 2022b,a). Specifically, the hypocotyl elongation and flowering time predicted from the simulation model under different light conditions are in agreement with experimental findings, which have been summarized in Table 3 of Pay et al. (2022b) and Figure 2 of Pay et al. (2022a), respectively.

To further evaluate the predictive capability of our simulation model, we compare our simulated outputs with experimental findings using other plants from published literature. The comparison is summarized in Table 1 and shows a good agreement with *A. thaliana*. For other plant types, the simulated outputs show good agreement qualitatively, where similar trends are observed across different plant types and phenotypes, considering that our model is calibrated using *A. thaliana*. Taken altogether, the comparison shown in Table 1 indicates the good predictive capability of our model, thereby warranting its use for our analysis in this study.

2.5. Light properties for simulation

Four light properties namely light ratio, light intensity, photoperiod and light order are analysed using the *A. thaliana* mathematical model as these light properties are often being considered whenever plants are grown in smart greenhouse farming as obtaining the optimal combination of those light properties can improve growth and lighting efficiency (Ahmed et al., 2020). The input light has a period of 24 h, where the pattern of light is repeated across 10 days. A brief description on how we set up each of the light properties for simulation is provided.

2.6. Light ratio

For our simulation, the red:blue and blue:red ratios are varied from 1:1 to 12:1 to cover all the possible light ratios listed in Supporting Information–Table 1. This is to allow us to identify possible different red and blue light ratios that are able to produce better results in terms of DTF and hypocotyl length than using either monochromatic blue or red light. The variation of the light ratios is reflected through light intensity for red or blue lights, that is, I_{red} and I_{blue} in Equation (6). For example, to realize a light ratio of blue:red of 3:1, we set $I_{blue} = 600\ \mu$mol m^{-2}s^{-1} and $I_{red} = 200\ \mu$mol m^{-2}s^{-1}.

2.7. Light intensity

While the daily light integral (DLI) is often used as a more representative measure of the rate of photosynthetically active radiation over a 24-h period in plant (Faust et al., 2005; Faust and Logan, 2018), in this study, we consider the light intensity (in terms of PPFD) instead. This is to ensure our simulation analysis is comparable with the experimental studies from the literature given in Supplementary Table 1, which mostly consider light intensity rather than DLI.

The light intensity for red and blue lights, that is, I_{red} and I_{blue} in Equation (6) used in the simulation is ranged from 100 to 1200 μmol m^{-2}s^{-1}, with a 100 μmol m^{-2}s^{-1} increment, totalling up

Table 1. Comparison between simulated hypocotyl length and flowering time with experimental results.

Plant type	Light conditions	Phenotypes	Experimental	Simulated	Reference
Brassica rapa	16L8D, Red 275 μmol m^{-2}s^{-1}, Blue 25 μmol m^{-2}s^{-1}	HL (8 days)	3.37–3.91 mm	0.408 mm	(Vaštakaitė et al., 2015)
	16L8D, Red 250 μmol m^{-2}s^{-1}, Blue 50 μmol m^{-2}s^{-1}	HL (8 days)	3.54–4.08 mm	0.400 mm	
	16L8D, Red 225 μmol m^{-2}s^{-1}, Blue 75 μmol m^{-2}s^{-1}	HL (8 days)	2.88–3.32 mm	0.398 mm	
	16L8D, Red 200 μmol m^{-2}s^{-1}, Blue 100 μmol m^{-2}s^{-1}	HL (8 days)	2.74–3.14 mm	0.395 mm	
Anethum graveolens	16L8D, Red 107.8 μmol m^{-2}s^{-1}, Blue 9.82 μmol m^{-2}s^{-1}	HL (14 days)	3.0–3.7 mm	0.726 mm	(Fraszczk, 2016)
	16L8D, Red 107.8 μmol m^{-2}s^{-1}, Blue 23.2 μmol m^{-2}s^{-1}	HL (14 days)	3.1–3.4 mm	0.710 mm	
	16L8D, Red 107.8 μmol m^{-2}s^{-1}, Blue 33.6 μmol m^{-2}s^{-1}	HL (14 days)	3.2–3.4 mm	0.700 mm	
	16L8D, Red 107.8 μmol m^{-2}s^{-1}, Blue 39.7 μmol $^{-2}$s^{-1}	HL (14 days)	2.9–3.1 mm	0.696 mm	
Petunia × *hybrida*	14L10D, Red 150 μmol m^{-2}s^{-1}	FT (35 days)	27.3–27.8 days	49.0 days	(Gautam et al., 2015)
	14L10D, Blue 150 μmol m^{-2}s^{-1}	FT (35 days)	25.8–26.5 days	23.7 days	
	18L6D, Red 150 μmol m^{-2}s^{-1}	FT (35 days)	29.8–30.3 days	43.9 days	
	18L6D, Blue 150 μmol m^{-2}s^{-1}	FT (35 days)	29.6–29.8 days	22.8 days	
A. thaliana	14L10D Blue 164 μmol m^{-2}s^{-1}	FT (10 days)	20–22 days	23.3 days	(Eskins, 1992)
	14L10D Red 87 μmol m^{-2}s^{-1}	FT (10 days)	50–55 days	56.2 days	

Note: 'HL' and 'FT' denote hypocotyl length and flowering time, respectively.

to a total of 12 different intensities, which is similar to the light intensity range considered in Hidaka et al. (2013).

The light intensity of 100–400 μmol m^{-2}s^{-1} is categorized as a lower range due to its relatively significant change of photosynthetic rate, as identified in Hidaka et al. (2013). This range allows improvements to be easily observed due to the relatively larger change to DTF and hypocotyl length due to the increase in photosynthetic rate and still retains the possibility of producing a light combination that provides improvement over the nominal values. The light combination that can provide improvement to the nominal value within the lower range of light intensity is more likely to be selected as the optimal one, as lower intensities can reduce the amount of energy needed per plant grown.

The light intensity of 500–800 μmol m^{-2}s^{-1} is categorized as medium range, as this range is the limit between the intensities used in Fu et al. (2012) and the light saturation point observed for strawberries in Hidaka et al. (2013). Any improvements to the plant growth from the nominal values in the medium range are likely to be attributed to the plant yet to experience stronger light stress, as the photosynthetic rate is still increasing, albeit at a slower rate compared to the photosynthetic range in the lower range.

The light intensity of 900–1200 μmol m^{-2}s^{-1} is categorized as high range as this range is beyond the limit set by Fu et al. (2012). The photosynthetic rate is still increasing (Hidaka et al., 2013), although it is not known whether the plant growth indices are going to increase or decrease around this range. Therefore, it cannot be exempted from the simulation study. Light intensity higher than 1200 μmol m^{-2}s^{-1} is unlikely to further improve plant growth and may potentially be detrimental to *A. thaliana*. Although there is no data on the photosynthetic rate from Hidaka et al. (2013) beyond this intensity, judging from the results provided in their study, it is likely that the photosynthetic rate has reached its plateau region and has stopped increasing further at this range. Moreover, further increases in the light intensity could reduce crop productivity and photochemical efficiency (Fu et al., 2012); thus, justifying the exclusion of using light intensity beyond 1200 μmol m^{-2}s^{-1}.

2.8. Photoperiod

In Pereira et al. (2021), the optimal photoperiod for achieving the smallest DTF hypocotyl length for *A. thaliana* is found to be 18 h when using white light. Here, the effect of photoperiod using different light colours will be investigated and the photoperiod is varied from 2 h to 24 h with an increment of 2 h. The photoperiods of less than 2 h are not considered in our simulation as the DTF calculation using Equation (7) returns a negative value. This is because at photoperiods less than 2 h, the second term in the denominator of Equation (7) is larger than the first term due to the low expression levels of gene FT. Recall that Equation (7) is an empirical equation where the parameters are estimated from experimental data for photoperiods larger than 2 h (Salazar et al., 2009). The omission of photoperiods shorter than 2 h should not affect our analysis as the DTF and hypocotyl length at photoperiod of 2 h are significantly larger than the nominal values, indicating improvement at these photoperiods is very unlikely.

2.9. Light order

The order of light is considered in simulation in the following manner: within a specified photoperiod across a 24-h period, a

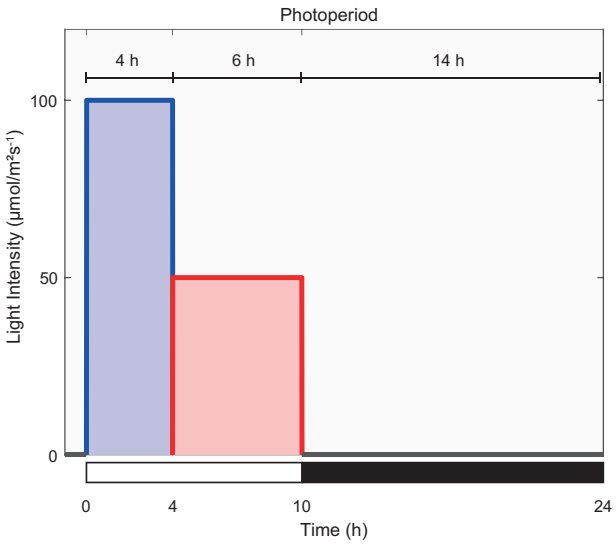

Figure 2. An illustration of a light with 10-h photoperiod followed by 14 h of dark. Within the 10-h photoperiod, the duration of blue light is 4 h followed by 6 h duration of red with the blue:red ratio of 2:1. The white and black bars below the figure denote how long the light is turned on and off, respectively.

specific light colour is provided first, for a determined duration within the photoperiod, followed by the next light colour, for the remaining duration of the photoperiod. At the end of the photoperiod, the duration of dark is inserted to account for a total of 24 h. This light order can also be reversed where dark will be provided first, followed by the light colours. Moreover, within the photoperiod, the durations for each light colour as well as the light ratios are varied. As an illustration, Fig. 2 shows a light input of 10-h photoperiod across a 24-h period with blue light first, followed by the red light with the light ratio of blue:red of 2:1 and ends with 14 h of dark.

In our simulation, we consider several combinations of light orders involving blue, red and mixture of blue and red lights plus dark. This results in a total number of 28 different combinations of light order. A summary of the light order used in this study is given in Fig. 3, where, for illustration, the light ratio of blue:red 10:1 with photoperiod of 14 h is shown. Note that in Fig. 3, only 14 combinations are shown, as the other 14 combinations have the order of the dark and the light reversed.

The purpose of considering the light order is to identify its impact on the two plant growth indices, and which combination order would provide the most improvement compared to the nominal values. While the effect of light order has been considered in several experimental studies (Ohtake et al., 2018; Lanoue et al., 2019; Viršilė et al., 2020; Huang et al., 2021), the key difference is that most of these studies consider alternating between red and blue lights without any duration for dark (i.e. photoperiod of 24 h). Moreover, not all the light order combinations have been considered due to different scopes of study. Thus, our analysis here could be useful in two aspects: providing a better guide for future experimental design and reducing the energy usage through the insertion of duration of dark.

2.10. Combined light properties

To cover all combinations of light properties described above, the following light properties variations are considered in our simulation. As there are four different light properties that need to be considered, we fix three light properties at a time while varying the fourth property across the range of interest. Specifically, we fix the light ratio, starting with blue:red ratio of 1:1, fix the light intensity, start with blue and red lights both with the intensity of 100 μmol m^{-2}s^{-1} to ensure the blue:red ratio of 1:1 and fix the photoperiod, starting with 2 h. We vary the light order following the 14 combinations plus their reversed order shown in Fig. 3. As a remark, in the case where the mix blue and red lights are considered their intensities abide by the utilized light ratio. We repeat this for photoperiod ranging from 2 h to 24 h, light ratio ranging from red:blue 1:1 to 12:1 and blue:red 1:1 to 12:1 and light intensity with the larger ratio ranging from 100 μmol m^{-2}s^{-1} to 1200 μmol m^{-2}s^{-1} while the smaller ratio ranging from 8.33 μmol m^{-2}s^{-1} (when the ratio of 12:11 is used) to 1200 μmol m^{-2}s^{-1} (when the ratio of 1:1 ratio used). This results in a total number of 1730 simulation sets. Readers who are interested in overall simulation sets are referred to the Data Availability section.

3. RESULTS AND DISCUSSION

3.1. Effect of only monochromatic blue and red lights

We begin our analysis by considering only the effect of monochromatic light (i.e. light conditions B1, Reverse-B1, R1 and Reverse-R1) on DTF and hypocotyl length. These light conditions are first considered given their wide usage in experiments as shown in Supporting Information–Table 1. Due to the monochromatic nature, only the variation in photoperiods and light intensities are considered and the results are shown in Fig. 4 while Table 2 presents the best improvement in DTF and hypocotyl length that can be achieved under these light conditions.

From Fig. 4, we observe improvements in DTF and hypocotyl length when light conditions B1 and Reverse-B1 are used. Across different light intensities, the DTF portrays a decreasing trend as photoperiods increase. The smallest DTF of 19 days, which is a 12 % reduction compared to the nominal DTF value of 21.62 days, can be observed with a light intensity of at least 900 μmol m^{-2}s^{-1}, at a photoperiod of 16 h. The hypocotyl length is also showing a decreasing trend as photoperiods increase but it is not significantly affected by light intensity given the plots at different intensities almost overlap each other. In the B1 light condition, the hypocotyl length has reduced to the threshold of 1.00 mm at a photoperiod of 14 h but the DTF is still not at its minimum value. On the other hand, in Reverse-B1 light condition, the hypocotyl length reaches the 1.00 mm threshold at photoperiod of 16 h and at the same time, the DTF is at its minimum.

For R1 and Reverse-R1 light conditions, we observe neither light intensity nor photoperiod can improve the DTF below the nominal value, despite the hypocotyl length displaying similar behaviour as the B1 and Reverse-B1 light conditions. The minimum DTF that both these light conditions are approximately

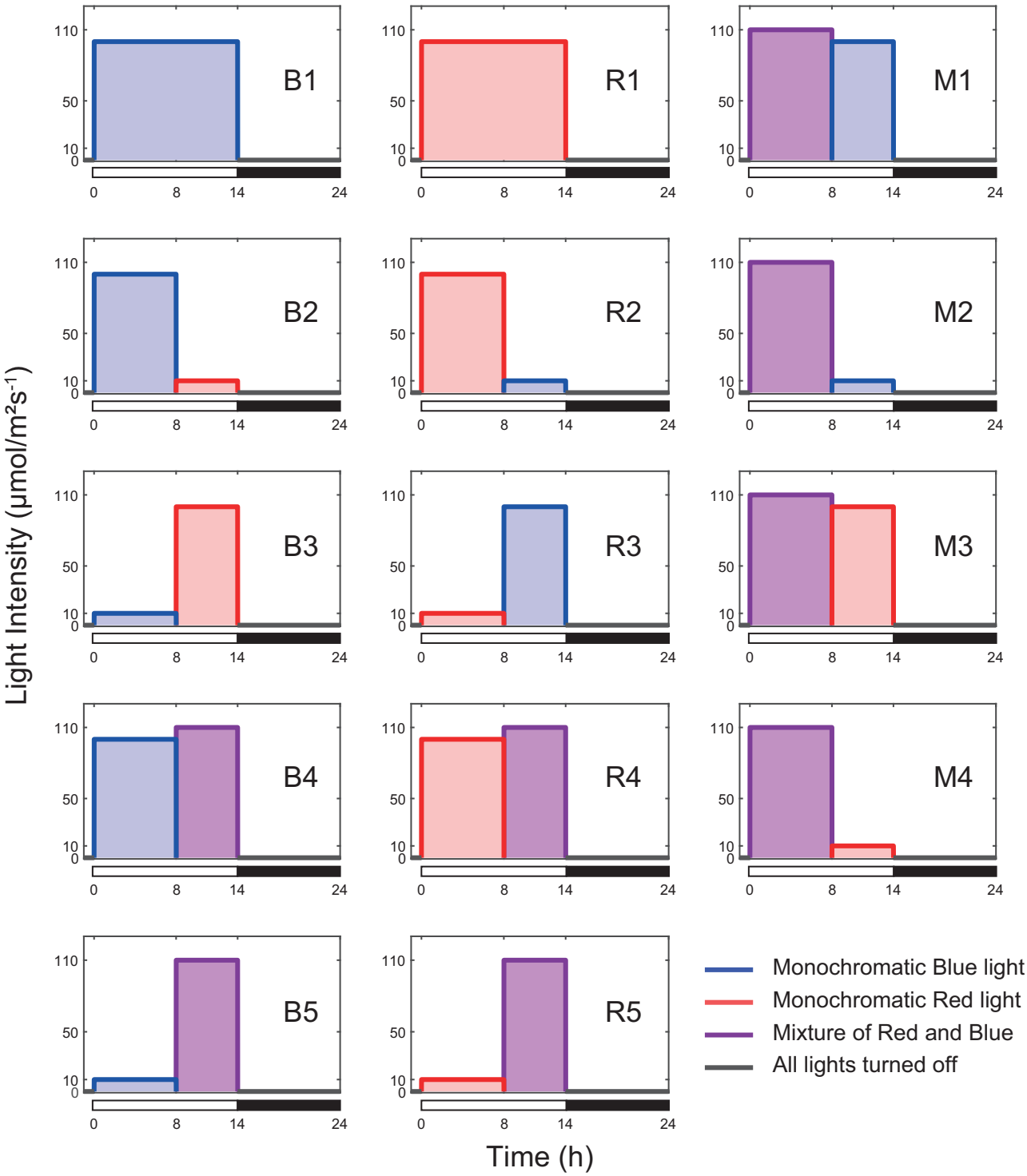

Figure 3. A summary of different light orders used in this study. Here, 14 combinations of light order are shown, whereas the other 14 have the order of the dark and the light reversed. The first, second and third columns correspond to monochromatic blue, red and mix of red and blue lights being first in the order, respectively. In this particular illustration, the photoperiod of 14 h with the blue:red ratio of 10:1 for (B2, B4, R3, R5, M1, M4) and red:blue ratio of 10:1 for (B3, B5, R2, R4, M2, M3) are shown. For the reversed order, we append the word 'Reverse' to the abbreviation (e.g. Reverse-B1 for dark first then monochromatic blue).

30 days at a light intensity of 1200 μmol m^{-2}s^{-1} and photoperiod of 16 h, which is an increase of 39 % from the nominal value. We also note the oscillatory trend in DTF for R1 and Reverse-R1 light conditions as photoperiod changes, which can be attributed to the following reasons: flowering is accelerated under very short-day (photoperiod $\leq$ 3 h) conditions before decelerating

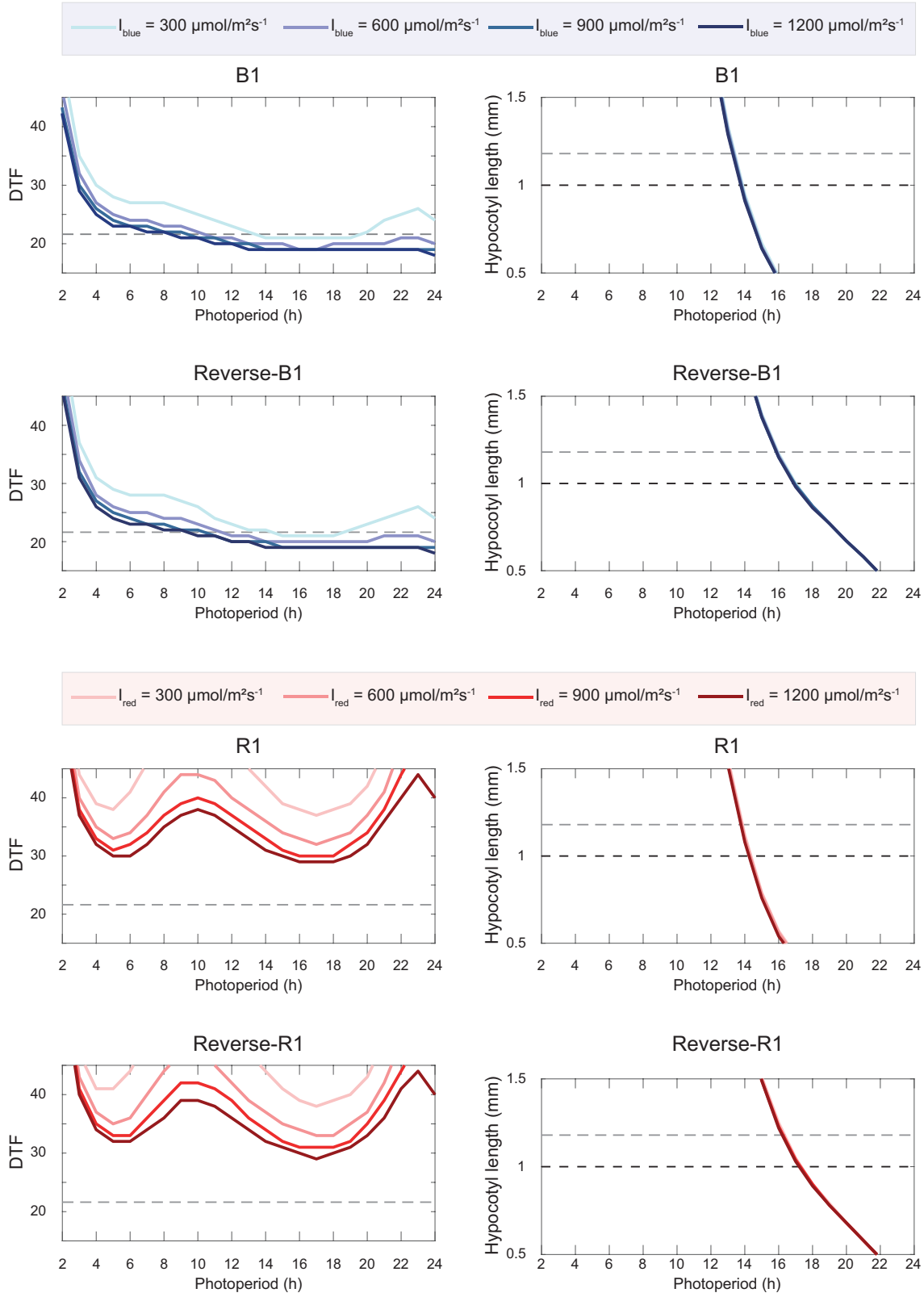

Figure 4. DTF and hypocotyl length under light conditions B1, Reverse-B1, R1 and Reverse-R1 across different photoperiod and light intensities. The gray dashed-lines in both DTF and hypocotyl length plots represent the nominal values and the black dashed-line in hypocotyl length plots represent the 1.00 mm threshold.

Table 2. Compilation of the best improvement of DTF and hypocotyl length from nominal values for each of the monochromatic light conditions (i.e. B1 and R1 and their reverse).

Light condition	Photoperiod	Light intensity (μmol m^{-2}s^{-1})	DTF (days)	Hypocotyl length (mm)
B1	12B12D	B: 900	20	1.81
Reverse-B1	8D16B	B: 900	19	1.15
R1	14R10D	R: 1200	31	1.08
Reverse-R1	8D16R	R: 1200	30	1.22

under short-day conditions (Luccioni et al., 2019) leading to a decrease and increase in DTF from photoperiod 2–10 h. Furthermore, Mockler et al. (2003) found that the difference in DTF between very short day and short day with long day conditions is small, leading to the decrease in DTF as photoperiod increases, resulting in the observed oscillatory trend. This oscillatory trend is also occurring in B1 and Reverse-B1 light conditions, albeit not as apparent as in R1 and Reverse-R1 light conditions, as the difference in DTF between a very short day to short day with long days is large (Mockler et al., 2003).

Taken altogether, these results suggest that monochromatic blue light plays a vital role in improving flowering compared to monochromatic red light. Furthermore, the Reverse-B1 light with photoperiod of 16 h is more preferred, as this light condition can improve both plant growth indices. More encouragingly, our results align with previous experimental studies (Eskins, 1992; Guo et al., 1998; Spaninks et al., 2020), where long-day monochromatic blue light has been shown to decrease the days required for flowering and produce hypocotyl length within a desirable limit.

3.2. Effect of light order

Previously, our analysis on monochromatic light indicates that Reverse-B1 light condition with a photoperiod of 16 h produces the best improvement for plant growth and development. Here, we extend our analysis by considering the effect of different light orders on DTF and hypocotyl length. Specifically, we are interested to know whether any further improvement can be achieved when light ratios and light orders are now considered. We introduce light conditions B2 to R5 with their reverse (i.e. the order of dark and light reversed) and repeat the simulation to obtain the DTF and hypocotyl length. These light conditions have either the blue or red lights first in the order. Note that our light order analysis is an extended version of the commonly used alternating light considered in experimental studies (Ohtake et al., 2018; Lanoue et al., 2019; Viršilė et al., 2020; Huang et al., 2021), where in those studies, the equivalent of our B2, B3, R2 and R3 with photoperiods of 24 are used. In addition, we would like to remark that the improvement observed through simulation in the two plant growth indices under different light orders is consistent with the findings of Ohtake et al. (2018). The best results from these light conditions are given in Tables 3 and 5. For the details of all the simulation results, see the Data Availability section.

From Tables 3 and 5, we observe that the largest improvement to the two plant growth indices is obtained with photoperiod of 16 h with an 8-h dark precedes them, that is, Reverse-B2, Reverse-B3, Reverse-B4, Reverse-B5, Reverse-R4 and Reverse-R5, which is similar to the monochromatic blue light Reverse-B1 light condition. Within this 16-h photoperiod, the duration of blue or mix blue and red lights is at least 12 h suggesting prolonged blue light exposure is essential. All these lighting conditions produce DTF of 19 days and hypocotyl length between 1.14 mm and 1.17 mm. For the remaining light conditions, we observe DTF between 20 and 30 days and hypocotyl length between 1.00 and 1.75 mm. An exception to this trend is observed for light condition B2, where a photoperiod of 14 h (8-h blue and 6-h red) followed by 10 h of dark can produce the same DTF of 19 days and hypocotyl length of 1.00 mm.

Next, we introduce additional four light conditions where the mix of blue and red light is the first in order, that is, M1–M4 with their reverse counterparts (third column of Fig. 3). With the introduction of these light conditions, we obtain DTF ranges between 18 and 24 days, while the hypocotyl length ranges between 1.00 and 1.17 mm. While it is compelling to conclude that the light condition that achieves DTF of 18 days is of interest, all these light conditions produce minimal improvement to the hypocotyl length from the nominal value. If a balance of improvement to both DTF and hypocotyl length is required, then M3 and M4 light conditions with photoperiod of 14 h followed by 10 h dark fit this requirement. Again, if we consider from the perspective of energy savings, M3, M4 and B2 light conditions are the top lighting candidates as similar DTF and hypocotyl length can be achieved with another 2 h reduction of photoperiod compared to using monochromatic light.

One probable explanation for the difference in the hypocotyl length when the light order is reversed is as follows. Given that the initial conditions of the ODEs are the same, in the reverse light condition, the circadian clock may perceive it as day even though it is night and begin employing the 10-day adaptation resulting in a longer hypocotyl length. Conversely, when the light condition is not reversed, the circadian clock may have achieved synchrony with light conditions from the onset of light thereby resulting in a shorter hypocotyl length.

We note an interesting observation related to hypocotyl length in the presence of red regardless of its duration and intensity. As long as red light is available, the hypocotyl length is sufficiently long to avert stunted growth and is not affected by photoperiod compared to the presence of blue light, which is influenced by photoperiod and order of dark to attain minimum hypocotyl length. In addition, the presence of the dominant intensity of blue light being first in the light order (e.g. M4 or B2

Table 3. Compilation of the best improvement of DTF and hypocotyl length from nominal values from the B2 to B5 light conditions and their reverse.

Light condition	Photoperiod	Light ratio and intensity (μmol m^{-2}s^{-1})	DTF (days)	Hypocotyl length (mm)
B2	14L10D (8B6R10D)	B:R 12:1 R: 83.33 B: 1000	19	1.00
Reverse-B2	8D16L (8D12B4R)	R:B 1:1 R: 1200 B: 1200	19	1.17
B3	14L10D (8D12B4R)	R:B 1:1 R: 900 B: 900	20	1.00
Reverse-B3	8D16L (8D14B2R)	R:B 1:1 R: 1200 B: 1200	19	1.17
B4	12L12D (2B10M12D)	R:B 1:1 R: 1100 B: 1100	20	1.75
Reverse-B4	8D16L (8D2B14M)	B:R 12:1 R: 75 B: 900	19	1.14
B5	12L12D (2B10M12D)	R:B 1:1 R: 1100 B: 1100	20	1.75
Reverse-B5	8D16L (8D2B14M)	R:B 1:1 R: 700 B: 700	19	1.14

Table 4. Compilation of the best improvement of DTF and hypocotyl length from nominal values from R2 to R5 and their reverse.

Light condition	Photoperiod	Light ratio and intensity (μmol m^{-2}s^{-1})	DTF (days)	Hypocotyl length (mm)
R2	14L10D (2R12B10D)	R:B 7:1 R: 1100 B: 157.14	25	1.00
Reverse-R2	8D16L (8D2R14B)	R:B 1:1 R: 900 B: 900	20	1.15
R3	14L10D (10R4B10D)	B:R 1:1 R: 1100 B: 1100	26	1.00
Reverse-R3	8D16L (8D2R14B)	B:R 2:1 R: 450 B: 900	20	1.15
R4	14L10D (8R6M10D)	R:B 7:1 R: 900 B: 128.57	28	1.00
Reverse-R4	8D16L (8D2R14M)	B:R 1:1 R: 1100 B: 1100	19	1.14
R5	14L10D (12R2M10D)	B:R 1:1 R: 800 B: 800	30	1.00
Reverse-R5	8D16L (8D2R14M)	B:R 1:1 R: 1100 B: 1100	19	1.14

light conditions) provides the most improvement, particularly to DTF. These two observations, which are also consistent with previous studies, suggest that the presence of red light ensures the hypocotyl grow sufficiently (Takase et al., 2003; Sellaro et al., 2009) while the blue light helps with the promotion of flowering (Costine et al., 2022).

Table 5. Compilation of the best improvement of DTF and hypocotyl length from nominal values from the M1 to M4 light conditions and their reverse.

Light condition	Photoperiod	Light ratio and intensity (μmol m^{-2}s^{-1})	DTF (days)	Hypocotyl length (mm)
M1	14L10D (4M10B10D)	B:R 1:1 R: 100 B: 100	24	1.00
Reverse-M1	8D16L (8D12M4B)	B:R 1:1 R: 1100 B: 1100	18	1.14
M2	14L10D (4M10B10D)	R:B 8:1 R: 800 B: 100	22	1.00
Reverse-M2	8D16L (8D12M4B)	B:R 1:1 R: 1100 B: 1100	18	1.14
M3	14L10D (6M8R10D)	B:R 1:1 R: 900 B: 900	19	1.00
Reverse-M3	8D16L (8D12M4R)	B:R 1:1 R: 1200 B: 1200	18	1.17
M4	14L10D (8M6R10D)	B:R 12:1 R: 66.67 B: 800	19	1.00
Reverse-M4	8D16L (8D12M4R)	B:R 1:1 R: 1200 B: 1200	18	1.17

3.3. Effect of light ratio and light intensity

After establishing that the light conditions M3, M4 and B2 with photoperiod of 14 h being the desired light condition for plant growth, where no further improvement in DTF or hypocotyl can be made, we turn our attention to investigating what light ratio and light intensity entail, focussing on energy efficiency. While these three light conditions yield identical DTF and hypocotyl length, their light ratio and light intensity are different. For M3, the light ratio B:R of 1:1 with intensity of 900 μmol m^{-2}s^{-1} is used. For M4, the light ratio B:R of 12:1 with blue intensity of 800 μmol m^{-2}s^{-1} and red intensity of 66.67 μmol m^{-2}s^{-1} are used. Finally, for B2, the light ratio B:R of 12:1 but with blue intensity of 1000 μmol m^{-2}s^{-1} and red intensity of 83.33 μmol m^{-2}s^{-1} are used. Consider that energy efficiency is inversely proportional to light intensity (Yan et al., 2019), and light conditions with smaller light intensity would be preferred. If we consider aggregated use of these lights, we have total intensities of 1800 μmol m^{-2}s^{-1}, 866.67 μmol m^{-2}s^{-1} and 1083.33 μmol m^{-2}s^{-1} for M3, M4 and B2 light conditions, respectively. This indicates that among the three light conditions, M3 uses the most energy, whereas M4 uses the least energy, thereby making M4 the preferred light conditions among the three.

3.4. Effect of the order of dark

In general, when implemented in a smart greenhouse environment, the light–dark cycle that the plant is exposed to is repeated over a 24 h period. Here, we are interested in investigating whether the order of dark (i.e. dark precedes or succeeds light) matters. In other words, when the plant is transferred to the smart greenhouse environment, should it be exposed to dark that precedes or succeeds light?

In Tables 2 and 5, we have provided the best DTF and hypocotyl length measurements from each of the light conditions. We also collate the DTF and hypocotyl length where the order of dark is reversed for each of the light conditions shown in Tables 2 and 5. Note that the best improvement in plant growth indices in each light condition shown in Tables 2 and 5 may not necessarily mean its reverse light conditions would provide the best improvement in plant growth indices as well. For example, in Table 2, the best improvement of plant growth indices for light condition B1 occurs at 12B12D with a DTF of 20 days and hypocotyl length of 1.81 mm. Under the same photoperiod but with its order of dark reverse, that is, Reverse-B1 with 12D12B, the DTF is 20 days and the hypocotyl length is 2.65 mm. For convenience of analysis, we call this scenario, 'Best Light First'. Similarly, in Table 2, the best improvement of plant growth indices for Reverse-B1 occurs at 8D16B with DTF of 19 days and hypocotyl of 1.15 mm. Under the same photoperiod, but with now dark succeeds light, that is, B1 with 16B8D, we have DTF of 19 days and hypocotyl length of 0.46 mm and we call this scenario 'Best Dark First'. With this, we end up collating DTF and hypocotyl length for 56 different light conditions.

Our analysis (Suppporting Information—Fig. S1) suggests the order of dark has no strong influence on DTF but has a significant influence on hypocotyl length. The substantial variation of hypocotyl length between order of dark is not surprising given that short or long hypocotyl have been observed when plants are either grown in darkness (skotomorphogenesis) or in the

presence of light (photomorphogenesis) (Vandenbussche et al., 2005). Our results indicate that the order of dark can be potentially exploited to provide a competitive advantage to plants depending on the germination type of the plant, that is, between hypogeal (germination below ground) and epigeal (germination above ground) germination.

3.5. Power consumption calculation

In this section, we provide simple calculation of power consumption of the suggested light conditions for comparison of their energy usage given that lighting power consumption has often been seen as the impediment to realize sustainability in smart farming (Ahamed et al., 2023), The power consumption model, which is based on Ahn et al. (2017) and Lan and Tan (2015), is given by,

$$\text{Power, P[kW]} = \frac{I_{PPFD} \times C \times A}{\eta \times 1000}, \tag{9}$$

where I_{PPFD} is the light intensity in μmol m^{-2}s^{-1} and C is the illuminance to PPFD conversion factor, A is the grow area in m^2, 1000 is the conversion to kW and η is the luminous efficacy in lm/W.

The light emitting diode (LED) lights are typically powered by an LED driver, which is an AC/DC converter that converts AC grid power into DC power suitable for the LED lights. As such, we can rewrite the combined luminous efficacy as $\eta_{comb} = \eta \times \eta_{PCE}$, where η_{PCE} is the AC/DC power conversion efficiency that takes a value between 0 and 1. We can then rewrite Equation (9) as

$$\text{Power, P[kW]} = \frac{I_{PPFD} \times C \times A}{\underbrace{\eta \times \eta_{PCE}}_{\eta_{comb}} \times 1000}. \tag{10}$$

As the typical electricity billing unit is kWh, to convert kW from Equation (10) to kWh, we multiply Equation (10) with the photoperiod and the DTF, that is,

$$\text{Power, P[kW]} = \frac{I_{PPFD} \times C \times A}{\eta \times \eta_{PCE} \times 1000} \times \text{Photoperiod} \times \text{DTF}. \tag{11}$$

In our calculation, we assume that a 1.2 m by 1.2 m grow area is used resulting in $A = 1.44$ m^2. Conventionally, an LED driver is considered efficient if $\eta_{PCE} = 0.9$, that is, the LED driver is able to convert 90% of the input power into useful electricity (Esteki et al., 2023). The typical values of C and η for red and blue lights are adopted from Ahn et al. (2017), while for white light, they are adopted from Lee and Kim (2012); Masoud and Murnick (2013) and Ahn et al. (2017). The parameters associated with white light are included for comparison with the power consumption based on the light condition suggested in Pereira et al. (2021). All these parameters are summarized in Table 6.

Using Equation (11) and the parameters given in Table 6, we computed the power consumption for three light conditions that produce the best growth indices under monochromatic light (Reverse-B1), mixed light (M4) and the white light conditions of 18L6D from Pereira et al. (2021) and they are given in Table 7. For the details of the calculation, see Supporting Information—Table 3.

Table 6. Parameter value used for power consumption calculation.

Parameters	Values
C (Blue)	11.9
C (Red)	9.9
C (White)	68.2
η (Blue)	26 lm/W
η (Red)	50 lm/W
η (White)	70 lm/W

Table 7. Comparison of power consumption for three different light conditions.

Light conditions	Power consumption
Reverse-B1 (8D16B) $I_{blue} = 900\ \mu$mol m^{-2}s^{-1}	200.36
M4 (8M6R10D) $I_{blue} = 800\ \mu$mol m^{-2}s^{-1} $I_{red} = 66.7\ \mu$mol m^{-2}s^{-1}	94.67
White (18L6D) $I_{blue} = 900\ \mu$mol m^{-2}s^{-1}	109.20

From Table 7, we observe that among the three light conditions, the power consumption is the least for M4 light condition. Interestingly, despite Reverse-B1 uses 2 h less in photoperiod compared to white light, the power consumption is almost double, primarily due to the larger I_{PPFD} in blue light compared to white light. Nevertheless, it is encouraging to note that by using different light colour combinations, such as M4, instead of only monochromatic light, the power consumption can be reduced while attaining good growth indices.

4. CONCLUSIONS

There have been extensive studies on the effect of light qualities on plant development as evidenced by the numerous studies summarized in Supporting Information—Table 1. Despite extensiveness, most of these studies often consider only a small portion of the light properties, primarily due to the arduous experimental task and different scope of study. The community would benefit tremendously if there were a methodical approach in narrowing down the range of light properties to be investigated. In this study, we have carried out a systematic analysis identifying the combination of the most suitable blue and red light properties for enhanced plant growth that can be used in smart greenhouse farming. The *in silico* analyses are carried out using the *A. thaliana* mathematical model that relates light input to flowering and hypocotyl length output pathways, where the comparison is made against a nominal value obtained from a previous study using only white light (Pereira et al., 2021). To ensure all the blue and red light properties are considered, we conducted a comprehensive literature search on experimental studies that investigate the relationship between light quality and plant growth (Supporting Information—Table 1). From that search, we are able to narrow down to four key blue and red light properties namely light ratio, light intensity, light photoperiod and light order (see also Fig. 1), which have significant effect

on plant development and are also highlighted in a review paper in Ahmed et al. (2020).

For monochromatic light, our analyses show that a photoperiod of 8-h darkness followed by 16-h blue light with an intensity of 900 μmol $m^{-2}s^{-1}$ (Reverse-B1) can reduce the DTF from the nominal value of 21.62 days to 19 days and hypocotyl length from the nominal value of 1.18 mm to 1.15 mm, which is an improvement of 12 % and 3 %, respectively.

We further our investigation by considering the combination involving different light colours, as depicted in Fig. 3. Interestingly, when combinations of different light colours are considered, we observed similar improvement in DTF and hypocotyl length that can be achieved with another further 2 h reduction in photoperiod. The M4 light condition, which has a 14-h light that is made up of 8-h mix blue and red with intensity of 800 μmol $m^{-2}s^{-1}$ and 66.67 μmol $m^{-2}s^{-1}$, respectively, 6-h red light, followed by 10-h dark yields DTF of 19 days and hypocotyl length of 1.00 mm. This further reduction of 2 h from using monochromatic light is a welcoming finding as this could further reduce energy usage while achieving similar outcome.

In terms of light ratio and light intensity, the ratio of blue:red ranging from 10:1 to 12:1 with intensity of red ranging from 66.67 μmol $m^{-2}s^{-1}$ to 100 μmol $m^{-2}s^{-1}$ and blue ranging from 800 μmol $m^{-2}s^{-1}$ to 1000 μmol $m^{-2}s^{-1}$ could yield comparable improvements in DTF and hypocotyl length compared to the nominal values. These light ranges concur with the finding from Piovene et al. (2015) where strawberries and basil seem to grow well under these light ranges. If energy efficiency is to be taken into account, lower light intensity is preferred, and our analysis tips the balance to M4 light condition being the most energy efficient as shown through the power consumption calculation given in Table 7.

Finally, we found that the order of dark has marginal effect on flowering but has a significant effect on hypocotyl length. Our analysis, however, can help practitioners strategize ways to take advantage of the order of darkness and give plants that germinate through either epigeal or hypogeal processes their particular competitive advantage.

The findings from our study have a great prospect in aiding smart greenhouse farming practitioners particularly those employing speed breeding protocol in setting the appropriate lighting system in their farming practices. Our model can be used to provide an optimal combination of the use of different light qualities to promote the desired plant growth and development pathways. Moreover, the resulting optimal combination of the light qualities has the potential to reduce energy consumption. Energy consumption has always been an issue in speed breeding-based farming practice (Jahne et al., 2020), where energy consumption from light alone accounts for more than 30 % of the total production cost (Eaves and Eaves, 2018). As illustrated in Table 7, the use of optimal light combinations such as M4 light condition can reduce energy consumption by 13.3 % compared to white light, which is often used in speed breeding-based farming practices.

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SUPPORTING INFORMATION

The following additional information is available in the online version of this article –

CONTRIBUTIONS BY THE AUTHORS

A.M.H.C.: Data curation, Formal analysis, Investigation, Methodology, Writing–original draft, Writing–review and editing, M.L.P.: Methodology, Resources, Software, Validation, Writing–original draft, Writing–review and editing, J.C.: Supervision, Validation, Writing–review and editing, F.H.: Funding acquisition, Supervision, Validation, Writing–review and editing, L.C.R.: Supervision, Resources, Writing–original draft, Writing–review and editing, H.A.: Funding acquisition, Supervision, Validation, Methodology, Writing–review and editing, M.F.: Conceptualization, Formal analysis, Supervision, Project administration, Funding acquisition, Writing–original draft, Writing–review and editing.

CONFLICT OF INTERESTS

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY

All the MATLAB simulation codes and simulated data are available at https://github.com/mathiasfoo/lightquality.

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