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An Extended Plant Circadian Clock Model for Characterising Flowering Time under Different Light Quality Conditions

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Abstract: Speed breeding has recently emerged as an innovative agricultural technology solution to meet the ever-increasing global food demand. In speed breeding, typically various light qualities (e.g., colour, duration, intensity) are modified to manipulate the circadian clock of the plants, which in turn alter the plant growth and enhance the productivity such as by reducing the flowering time. In order to develop a comprehensive framework describing plant growth, a model incorporating the effect of various light qualities on plant growth needs to be established. Recently a mathematical model of the plant circadian clock for *Arabidopsis thaliana* has been developed to characterise the hypocotyl growth subject to multiple light quality properties. This is a first step towards developing a more comprehensive model that links light quality, plant circadian clock and plant growth. In this work, we extend the model by adding the effect of various light qualities on the flowering time. The proposed model can capture the flowering time behaviours of plant when subject to red, blue, and mixed lights and can be used to guide experiment of light properties manipulation for optimised plant growth via hypocotyl growth and flowering time.

Keywords: Plant Circadian Clock; Flowering Time; Light Quality; Speed Breeding; *Arabidopsis thaliana*

1. INTRODUCTION

According to the United Nations (UN), the global population is predicted to reach 9.7 billion by 2050 [1, 2]. Feeding almost 10 billion people in an environmentally sustainable manner, i.e., by lowering the greenhouse gas emission and without expanding the cultivatable land area is a great challenge. It is predicted that food production needs to increase 56% compared to the level of production in 2010 to feed the global population by 2050. In this context, cutting-age technological solutions such as speed breeding [3, 4] is going to play a major role as it can increase food production in a sustainable and efficient manner without expanding the land use.

Conventionally, the development of new cultivar (i.e., production of plant variety that is cultivated through selective breeding) is very time consuming and may take a decade for new varieties to mature [4]. Speed breeding can help to reduce this time drastically by manipulating environmental conditions. In [3], it was shown that by manipulating the photoperiod, crop productivity can be enhanced up to two times compared to the conventional counterpart. This clearly highlights the advantage of speed breeding method over conventional breeding. Following the line of work presented in [3], many other experimental studies are conducted for different plants, where different environmental conditions are modified. For more details, interested readers may consult the reviews [4, 5], and the references therein.

In previous studies, light qualities are often used for the purposes of speed breeding. However, most of the existing experimental studies use heuristic approach to modify the light properties and evaluate the breeding performance according to the obtained results. This method is very time consuming and requires lots of resources and man power as multiple experiments need to be run in parallel. Moreover, only a limited number of light properties can be modified due to practical limitations. As such, one cannot determine with certainty whether the obtained results are truly optimal. In this context, the "digital twin" of the plants can be very useful to represent the behaviour of the plants subject to external conditions, which is predominantly light quality in the case of speed breeding.

In order to develop the plant digital twin, an accurate mathematical representation of the plant behaviour subject to various light qualities is essential. In this context, mathematical modelling of the plant circadian system (PCS) plays an important role. The PCS is responsible for plant physiological response to light and contributes to plant growth. Due to growth in research literature on speed breeding, a large number of experimental results detailing the effect of various light qualities on the plant growth are already available. However, very few supporting theoretical results are proposed to explain the experimental findings, which are essential, for building a digital twin for plant growth studies. One of the pioneering model in this area was proposed in [6], where a single feedback loop involving activator and repressor genes is considered to model the behaviour of PCS. Later on, various other models were proposed to incorporate

the effect of complex genetic regulatory networks on the physiological response of plants [7, 8]. A comprehensive model evolution of the PCS in *Arabidopsis thaliana* with increasing complexity can be found in [9, Fig. 1].

In our previous work [10], we modelled the effect of various light qualities on the hypocotyl length, which is the first stage of plant growth. In the second stage, flowering will happen and in the final step, ripening will happen, which will ultimately determine the yield. As such, extending the model developed in [10] by considering flowering time as one of the outputs would be the next logical step. In [11], the authors have developed a mathematical model relating PCS to flowering time that solely considers white light. In this work, we modify that model by taking into account the effect of blue, red, and mixed lights and incorporate it into our previously developed model [10], which distinguishes this current work from that of [11]. The inclusion of flowering time to the existing hypocotyl length would thereby provide more flexibility in manipulating lighting conditions for speed breeding purpose.

The rest of the article is organised as follows. Sec. 2.describes the formulation of the extended mathematical model of PCS with photoperiodic flowering pathway, which is capable to show the effect of light qualities on flowering time. Sec. 3. presents the simulation results and relevant discussions, and finally, conclusions are presented in Sec. 4.

2. MATHEMATICAL MODELLING

To incorporate the photoperiodic flowering pathways, we have extended our previous model, which is able to explain the effect of different light qualities on hypocotyl growth through competitive binding mechanism between photoreceptors and CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1) by adding the complex gene regulatory network for flowering pathway mechanism. For this purpose, we have considered the flowering time module proposed in [11]. It is to be noted here that one of the main gene in controlling flowering is CONSTANS (CO). It has been demonstrated in [12] that CO plays a fundamental role in reducing the flowering time. The complex interaction between FLAVIN-BINDING, KELCH REPEAT, F-BOX 1 (FKF1) and GIGANTEA (GI) protein complex activates the CO gene and thus regulates the gene expression of CO, which in turn induces flowering. In our previous work, the *GI* gene was not considered. Here, instead of modifying the GI equation used in [11], which is taken from [7], we considered the GI equation used in [13, 14], which follows a similar genetic interaction as considered in [10]. An overview of the gene regulatory network considered in this work is given in Fig. 1 and the modified ordinary differential equations (ODEs) are given below:

$$\frac{d\,[GI]_m}{dt} = L_a + \frac{Nv_1}{(NK + [CL]_p^2)(NK_2^2 + [P51]_p^2)(NK_3^2 + [EL]_p^2)} - Nk[GI]_m \tag{1}$$

$$\frac{d\,[GI]_p}{dt} = Np_1\,[GI]_m - Nd_1\,[Ctot]\,[EL]_p\,[GI]_p - Nd_2\,[GI]_p \tag{2}$$

$$\frac{d\,[CDF1]_m}{dt} = \left(Nv_2 + Nv_3\frac{[CL]_p^2}{NK_4^2 + [CL]_p^2}\right)\left(\frac{NK_5^2}{NK_5^2 + ([P97]_p + [P51]_p)^2}\right) - Nk_2[CDF1]_m \tag{3}$$

$$\frac{d\,[CDF1]_p}{dt} = Np_2[CDF1]_m - Nd_3(Np_3[GI]_p[FKF1]_p + Np_4[GI]_p + 1)[CDF1]_p \tag{4}$$

$$\frac{d\,[FKF1]_m}{dt} = L_b + Nv_4\left(\frac{NK_6^2}{NK_6^2 + [CL]_p^2}\right)\left(\frac{NK_7}{NK_7 + [EL]_p}\right) - Nk_3[FKF1]_m \tag{5}$$

$$\frac{d\,[FKF1]_p}{dt} = Np_5[FKF1]_m - N_{p6}\left(Nd_4 - \Theta_{PHYA}\left(\frac{[GI]_p}{Ng_1 + [GI]_p}\right)\right)[FKF1]_p \tag{6}$$

$$\frac{d\,[CO]_m}{dt} = B_{CO} + \left(\frac{NK_8^2}{NK_8^2 + [CDF1]_p^2}\right)\left(Nv_5 + Nv_6(1 - \Theta_{PhyA})\frac{[COP1]}{NK_9^2 + [COP1]}\right) - Nk_4[CO]_m \tag{7}$$

$$\frac{d\,[CO]_p}{dt} = Np_7[CO]_m - Np_8\left(Nd_5 + Nd_6(1 - \Theta_{PhyA})[COP1] - \Theta_{PhyA}\frac{[FKF1]_p}{Ng_2 + [FKF1]_p}\right)[CO]_p \tag{8}$$

$$\frac{d\,[FT]_m}{dt} = \left(Nv_7 + Nv_8\frac{[PIF]_p}{NK_{10} + [PIF]_p}\right)\left(Nv_9 + Nv_{10}\frac{NK_{11}}{NK_{11} + [CDF1]_p}\right)\left(\frac{[CO]_p^2}{NK_{12}^2 + [CO]_p^2}\right) - Nk_5[FT]_m \tag{9}$$

$$L_i = Nq_{1i}([T_{PhyA}])\Theta_{PhyA} + Nq_{3i}([T_{PhyB}])log(\eta_1 I_{red} + 1)\Theta_{PhyB} + Nq_{4i}([T_{Cry}])log(\eta_2 I_{blue} + 1)\Theta_{Cry} \tag{10}$$

where the subscripts in $[c]_m$ and $[c]_p$ represent the mRNA and protein concentrations of the plant genes, respectively, while the index c denotes genes *GI, CDF1, FKF1, CO* and *FT*. The effect of light input is denoted as L_i, where $i \in \{a \text{ or } b\}$. I_{red} and I_{blue} represent the red and blue light intensity respectively, η is the normalisation parameter of light intensity and the parameters $\Theta_{PhyA}, \Theta_{PhyB}$ and Θ_{Cry1} represent the light and darkness for photoreceptors phyA, phyB and cry1, respectively. The activation of Θ depends on whether sole blue or red or mix of blue and red lights is used. For more details, see [10].

To characterise the effect of various light qualities on flowering, we compute the days-to-flowering under different light qualities and durations following [15], where the equation to calculate the days-to-flowering (DTF) is given by:

$$DTF = d_0 + \frac{a_0}{1 - \left(\frac{FT_{area}}{a_1}\right)} \tag{11}$$

where FT_{area} is the area under the curve for *FT* mRNA for one circadian cycle. The parameters d_0 is taken from [15], whereas parameter a_0 and a_1 is tuned by comparing the flowering time data with different light qualities and duration. Here, FT mRNA is used for DTF calculation as it is the downstream gene regulated by CO as can be seen in Eqs. 7, 8 and 9.

2.1 Model Parameter Estimation

The extended flowering pathways consists of 9 ODEs with 50 parameters. In order to estimate those parameters, we use the temporal reference profiles of relevant genes in the flowering pathway under different light qualities taken from [16]. All the ODEs were numerically solved using the `ode15s` solver in MATLAB. The parameters are estimated by minimising the following cost function using the MATLAB function "`fminsearch`":

$$e = \sum_{i=1}^{N} \frac{\left([CO]_m^*(i) - [CO]_m(i)\right)^2}{N \times \max\left([CO]_m^*\right)} + \sum_{i=1}^{N} \frac{\left([FT]_m^*(i) - [FT]_m(i)\right)^2}{N \times \max\left([FT]_m^*\right)}$$

where the superscript * represents the temporal reference profile taken from [16], the notation 'max' is the maximum value of the reference profiles and N is the total simulation time points. The value of the parameters are given in Table 1. It is to be noted here that these parameter values are not unique and depending on the choice of objective function, these parameter values may change. Nonetheless, the parameter values given in Table 1 qualitatively match the experimental data well and are suited for our purpose. In calculating the area under the curve for *FT* mRNA for obtaining the DTF, the trapezoidal integration method has been used.

Table 1. Estimated model parameters

Parameter description	Name	Value	Units
GI synthesis	Nv1	0.0003	$nM.h^{-1}$
CDF1 synthesis	Nv2	0.211	$nM.h^{-1}$
CDF1 CL-induced synthesis	Nv3	2.5138	$nM.h^{-1}$
FKF1 synthesis	Nv4	1.8777	$nM.h^{-1}$
CO synthesis	Nv5	0.505	$nM.h^{-1}$
CO COP1-induced synthesis	Nv6	1.2439	$nM.h^{-1}$
FT synthesis	Nv7	0.4391	$nM.h^{-1}$
FT PIF-induced synthesis	Nv8	0.5555	$nM.h^{-1}$
FT synthesis	Nv9	0.0148	$nM.h^{-1}$
FT CDF1-induced synthesis	Nv10	1.0602	$nM.h^{-1}$
GI mRNA degradation	Nk1	0.4267	h^{-1}
CDF1 mRNA degradation	Nk2	0.6638	h^{-1}
FKF1 mRNA degradation	Nk3	0.7895	h^{-1}
CO mRNA degradation	Nk4	0.8493	h^{-1}
FT mRNA degradation	Nk5	0.1651	h^{-1}
GI translation	Np1	0.299	h^{-1}
CDF1 translation	Np2	0.1006	h^{-1}
CDF1 FKF1-GI-induced translation	Np3	2.3479	nM^{-2}
CDF1 GI-induced translation	Np4	0.6093	nM^{-1}
FKF1 translation	Np5	1.0137	h^{-1}
FKF1 GI-induced translation	Np6	0.0005	h^{-1}
CO translation	Np7	1.4739	h^{-1}
CO COP1 and FKF1-induced translation	Np8	4.1832	h^{-1}
GI degradation (Ctot and GI)	Nd1	38.9463	$nM^{-2}h^{-1}$
GI degradation	Nd2	0.0191	h^{-1}
CDF1 degradation (FKF1-GI and GI)	Nd3	0.1957	h^{-1}
FKF1 degradation	Nd4	380.0541	–
CO degradation	Nd5	1.0573	–
CO degradation (COP1)	Nd6	59.2134	nM^{-1}
Inhibition: GI by CL	NK1	0.1041	nM.h
Inhibition: GI by P51	NK2	0.1222	nM.h
Inhibition: GI by EL	NK3	0.2812	nM.h
Activation: CDF1 by CL	NK4	0.1126	nM.h
Inhibition: CDF1 by P97 and P51	NK5	0.9227	nM.h
Inhibition: FKF1 by CL	NK6	0.3369	nM.h
Inhibition: FKF1 by EC	NK7	0.0063	nM.h
Inhibition: CO by CDF1	NK8	0.055	nM.h
Activation: CO by COP1	NK9	1.4102	nM.h
Activation: FT by PIF	NK10	16.9214	nM.h
Inhibition: FT by CDF1	NK11	0.0436	nM.h
Activation: FT by CO	NK12	0.999	nM.h
FKF1 light-induced synthesis through PhyA	Nq1b	0.019	$nM.h^{-1}$
FKF1 light-induced synthesis through PhyB	Nq3b	0.0028	$nM.h^{-1}$
FKF1 light-induced synthesis through Cry	Nq4b	1.7141	$nM.h^{-1}$
GI light-induced synthesis through PhyA	Nq1a	8.8732	$nM.h^{-1}$
GI light-induced synthesis through PhyB	Nq3a	0.0504	$nM.h^{-1}$
GI light-induced synthesis through Cry	Nq4a	0.9601	$nM.h^{-1}$
Stabilisation: FKF1 by GI	Ng1	30.274	$nM.h^{-1}$
Stabilisation: CO by FKF1	Ng2	0.0012	$nM.h^{-1}$
Basal transcription rate of CO mRNA	Bco	0.0144	$nM.h^{-1}$
	d_0	16.55	Days
	a_0	1355.22	–
	a_1	0.02	–

3. RESULTS AND DISCUSSIONS

Our previous PCS model can successfully regenerate free-running time under different mutant genotypes, experimental phase response curve (PRCs) under different light qualities stimulus conditions. It is also able to capture the hypocotyl growth qualitatively. This is a good initial step towards model-based crop productivity enhancement design as hypocotyl is the first indicator of plant growth and consequently the productivity. The newly incorporated flowering pathway is then crucial for crop reproduction. To illustrate the effectiveness of our model, we compared the DTF generated from our model with the experimental data from [17]. The result is graphically plotted in Fig. 2. In the result, Long Day (LD) is characterised by 18 hours of light and 6 hours of dark, whereas Short Day (SD) is characterised by 9 hours of

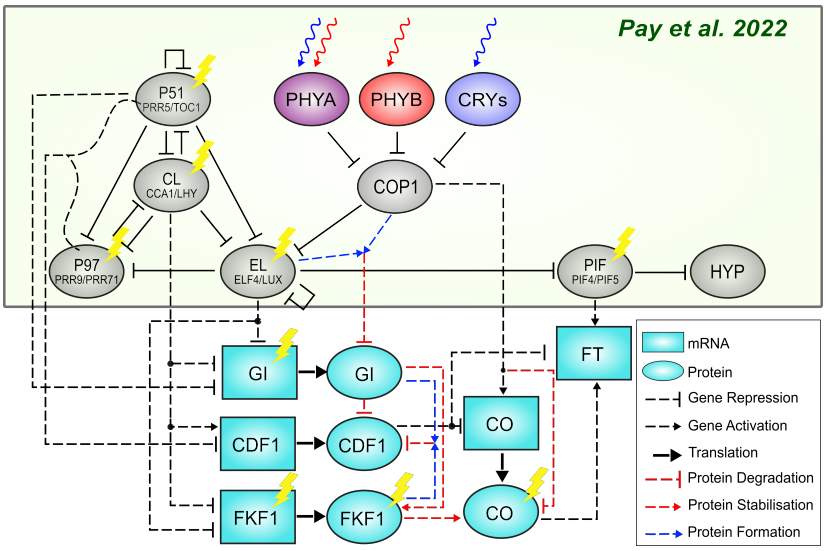

Fig. 1. Overview of gene regulatory interactions in plant circadian clock for hypocotyl growth and flowering time. The newly added gene regulation are represented by dashed lines. Previous plant circadian model with hypocotyl growth [10] is given in the green box.

light and 15 hours of dark. Specifically, our model shows that the flowering time under LD conditions is shorter than that in SD, which is similar to the experimental results. In addition, the model captures the trend of flowering time under different light qualities for both LD and SD conditions. These results are encouraging as they show that our model qualitatively match the experimental data well bearing in mind that the model parameters are estimated using another set of experimental data (i.e., from [16]).

From the result, we can see that LD condition promotes early flowering compared with SD condition. This is because the strong bonding of GI-FKF1 complex due to the peak expression of GI coincides with FKF1, deactivates the transcription repressors of CO and CDF and induces the daytime expression of CO. This leads to the physical interaction between FKF1 and CO protein. This interaction stabilises the CO protein and induces FT expression, which triggers early flowering. In the SD condition, the peak expression of GI is more advanced than the FKF1 expression. This weakens the bonding between GI-FKF1 complex and causes fast degradation of the CO protein [18–20]. In both LD and SD conditions, blue light results in early flowering, followed by mixed and red light. This result is inline with the existing literature. In [21], it was found that blue light promotes the expression of CO, which in turn activates FT and results in early flowering [22]. While red light degrades the CO protein, which results in late flowering [23].

To demonstrate the applicability of our model, we simulate and compute the area under the curve of the PIF protein and *FT* mRNA to obtain the hypocotyl length and DTF, respectively across different photoperiods, light intensities and light qualities. The values of the light intensities used in this study are taken from [17]. The results are shown in Figs. 3 to 5. The results are consistent with the trend observed in [11], where both the DTF and hypocotyl length decrease exponentially for photoperiod greater than 8h before reaching quasi steady-state value as photoperiod lengthens. Interestingly, for the hypocotyl length, the model suggests that different light intensities do not alter the hypocotyl length and this finding is consistent with literature [24, 25]. On the other hand, our model shows that light intensities have substantial effect in changing the flowering time with shorter flowering time under higher light intensity, which is again consistent with literature [26]. Both flowering time and hypocotyl length converge to quasi steady-state value for photoperiod greater than 14 hours across different light qualities and intensities. This quasi steady-state region will be useful in our analysis in determining the optimal light condition for speed breeding, which is part of our future studies.

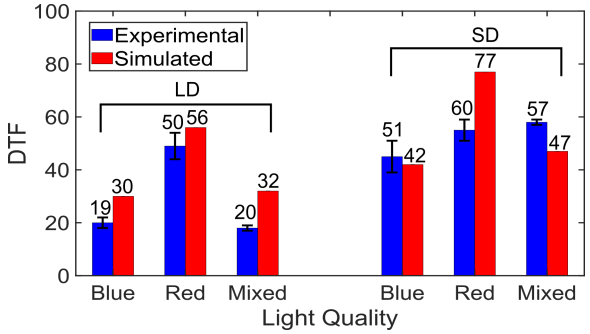

Fig. 2. Effect of light quality on the flowering time measured as days-to-flowering (DTF). The light intensity profiles are taken from [17].

4. CONCLUSIONS AND FUTURE WORKS

This study has presented an extended mathematical model of PCS that is able to characterise the hypocotyl length and flowering time for various light qualities. The simulation and experimental results shows the successful incorporation of the flowering pathways to our pre-

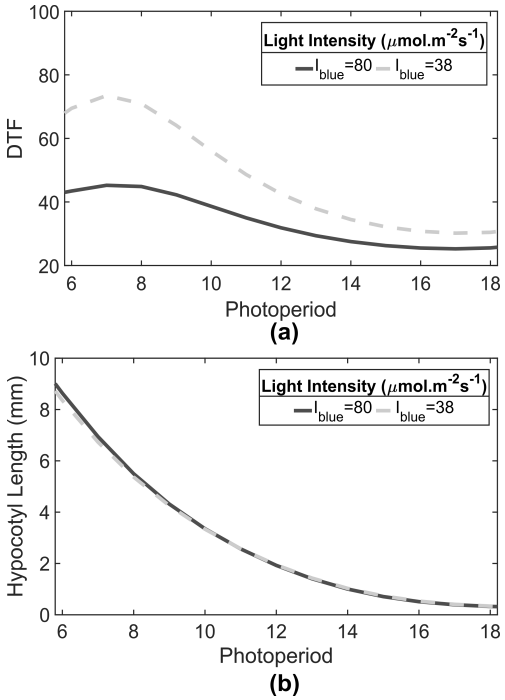

Fig. 3. Effect of photoperiod on DTF (a) and hypocotyl length (b) under different blue light intensities. The light grey dashed line represents lower light intensity whereas dark grey solid line represents higher light intensity.

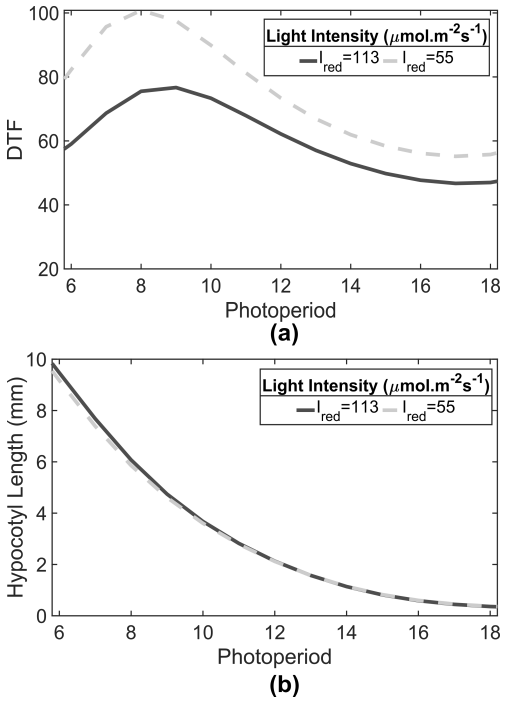

Fig. 4. Effect of photoperiod on DTF (a) and hypocotyl length (b) under different red light intensities. The light grey dashed line represents lower light intensity whereas dark grey solid line represents higher light intensity.

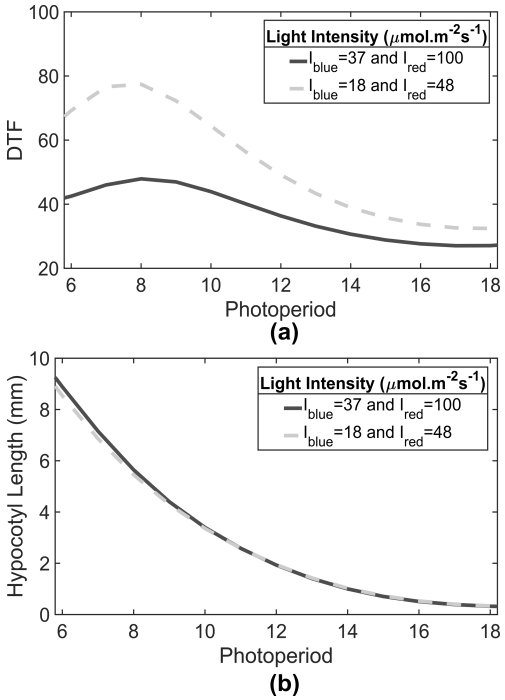

Fig. 5. Effect of photoperiod on DTF (a) and hypocotyl length (b) under different mixed light intensities. The light grey dashed line represents lower light intensity whereas dark grey solid line represents higher light intensity.

viously developed model, where the proposed model has qualitatively capture the trend for flowering time for both LD and SD conditions under three different light qualities. Furthermore, by varying the photoperiod, we observe consistent trend in hypocotyl length and flowering time with literature. But more importantly, the results from the model provide insightful analysis that can be used for determining the optimal light quality combinations for enhanced crop productivity e.g. through speed breeding. The model provides a good starting point for further development of mathematical model related to crop-productivity enhancement research. Further improvement of the model is needed to ensure not only qualitative but also quantitative matching. In the current model, it is assumed that the incident light is received fully by the plant. However, in practice, this may not be the case as we did not consider the effect of angle and distance of the plant from the light source. So, integrating the absorption level of light by the plant through photoreceptors can be considered to enhance the developed model.

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