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Phytochrome B1/B2 and auxin transport are involved in the regulation of shoot: root ratio by far-red radiation in tomato

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ABSTRACT

Plants possess a set of photoreceptors to perceive changes in the light spectrum. Phytochromes (PHY) B1/B2 sense changes in red: far red ratios and are involved in mediating the shade-avoidance responses (SAR) in tomato. Far red (FR) increases the fraction of dry mass partitioning to the shoot at the expense of the root in tomato, but the control of this response has not yet been explained. We studied the role of phytochromes and auxin transport in the regulation of shoot: root ratio. We hypothesized that a loss-of-function mutation in *phyB1/B2* leads to a strong increase in shoot: root ratio, similar to the effect of reduced R: FR ratio in wildtype plants. We also hypothesized that the *phyB1/B2* double mutation suppresses shoot: root ratio responses when exposed to a reduced R: FR ratio. Furthermore, we hypothesized that the increased shoot: root ratio is linked to the changes in auxin transport between shoot and root. To test these hypotheses, we conducted an experiment in a climate chamber where both wildtype and *phyB1/B2* double mutant tomato plants (*Solanum lycopersicum* cv. Moneymaker) were grown for 21 days with 0, 55 or 85 μmol m^{-2} s^{-1} FR in a background of white + red LED light at 150 μmol m^{-2} s^{-1}. On the 14th day, auxin polar transport inhibitor 1-N-naphthylphthalamic acid (NPA) was applied at the shoot-root junction. *PhyB1/B2* mutants showed a higher shoot: root ratio than the wildtype plants. Both wildtype and *phyB1/B2* mutants responded to FR with an increase in shoot: root ratio. Blocking auxin transport from shoot to root led to an increase in shoot: root ratio for both genotypes under all light conditions. These results suggest that, similar to other SAR responses like stem elongation, the response of shoot: root ratio to additional FR also involves the regulation by phytochromes, possibly via affecting auxin transport between shoot and root.

1. Introduction

Light is one of the most important environmental factors influencing the growth and development of plants by not only serving as the driving force for photosynthesis but also as a signal alerting plants to changes in the growth environment. Shading by neighboring plants, which means a decrease in light intensity and a decrease in the red: far red (R:FR) ratio, is one of the most intensively studied environmental signals. Upon the detection of shading, which suggests competition for light, plants impose a set of morphological and physiological responses to maximize their light capture and to ensure reproductive success (Franklin, 2008; Yang et al., 2016). These responses, collectively termed shade avoidance responses, typically involve stem elongation (Huber and Wiggerman, 1997; Botterweg-Paredes et al., 2020), changes in leaf angles (Michaud et al., 2017), increased apical dominance (Finlayson, 2007), and accelerated flowering (Devlin et al., 1998). In addition to the well-documented elongation responses to low R: FR ratio (Ma and Li, 2019), many authors also reported responses in dry mass production and partitioning. Cao et al. (2018) and Kalaitzoglou et al. (2019) reported that a low R: FR ratio increased the total plant dry mass in young tomato (*Solanum lycopersicum*) plants. Similarly, higher biomass was reported for ornamental crops such as geranium (*Pelargonium* × *hortorum*) and petunia (*Petunia* × *hybrida*) (Park and Runkle, 2017), leafy vegetables such as lettuce (Jin et al., 2021), as well as fruiting tomato (Kalaitzoglou et al., 2019).

A low R: FR ratio led to changes in the partitioning of dry mass between organs, often favoring the growth of shoots over roots (Keiller and Smith, 1989; Page et al., 2009). In the vegetative phase of plant growth, the dry mass partitioning between the above- and below-ground parts has been related to the activities of the organs, as suggested by the

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"functional equilibrium" theory (Brouwer, 1963). Based on this, it is reasonable to speculate that changes in the light spectrum sensed by the shoot organs may cause shifts in the functional equilibrium between shoot and root, thus influencing the dry mass partitioning between the two parts. The detection of changes in R: FR ratio is mediated by the phytochrome photoreceptor family, which exists as two photo-interconvertible isoforms: the red-light absorbing form P_r (biologically inactive) and the far-red absorbing form P_{fr} (biologically active) (Chen et al., 2005). The biologically active P_{fr} translocates to the nucleus to mediate the downstream shade avoidance responses (Ruberti et al., 2012). Auxin signaling is heavily involved in regulating shade avoidance responses in *Arabidopsis thaliana* (Iglesias et al., 2018). Shading or a low R: FR ratio affects not only the biosynthesis of auxin in *A. thaliana* (Li et al., 2012), but also its transport and perception (Keuskamp et al., 2010; Kohnen et al., 2016). Other phytochromes, such as PHYE, may be required to mediate tomato's elongation responses to FR in the absence of PHYB1 and PHYB2 (Schrager-Lavelle et al., 2016). These results also suggest that FR's impact on dry mass partitioning between shoot and root may be mediated by multiple phytochromes, possibly via affecting auxin biosynthesis and transport.

Despite the intensive studies on *A. thaliana,* little is known about the regulation of dry mass partitioning between shoot and root in tomato, an important crop that has substantial and genotypically-conserved responses of shoot: root ratio to increasing FR (Ji et al., 2021). In this paper, we aim to understand the role of phytochrome B, which is mainly responsible for sensing the R: FR ratio (Weller et al., 2000), in controlling the shoot: root ratio of young tomato plants. Further, we investigate the possible involvement of auxin transport in the control of shoot: root ratio as a response to changes in R: FR ratio. We hypothesize that a loss-of-function mutation in *phyB1/B2* leads to a strong increase in shoot: root ratio similar to the effect of reduced R: FR ratio on wildtype plants. We also hypothesize that the *phyB1/B2* double mutation will eliminate or repress the plant's response in shoot: root ratio when exposed to additional FR. Furthermore, we hypothesize that the FR-induced increase in shoot: root ratio requires the existence of auxin transport between the shoots and roots.

2. Materials and methods

2.1. Plant materials and growth conditions

An experiment was conducted in a fully-controlled climate chamber of Wageningen University. Wildtype tomato (accession LA2706, *Solanum lycopersicum* L. cv Moneymaker) and a *phyB1/phyB2* double mutant (accession LA4364 in the background of cv. Moneymaker) were used in this experiment. The seeds of these genotypes were obtained from the UC Davis/C.M. Rick Tomato Genetics Resource Center (Davis, CA, USA) and maintained by Wageningen University (Wageningen, the Netherlands). The seeds were treated with 70% ethanol for 1 min, followed by 28 min in 3% sodium hypochlorite before sowing in trays containing vermiculite. The trays were kept in darkness for three days, after which they were placed under fluorescent tubes (TL-D 58 W/840, Philips, Eindhoven, The Netherlands) with a photosynthetic photon flux density (PPFD) of 120 μmol m^{-2} s^{-1} and a photoperiod of 16 h. Two weeks after sowing, uniform seedlings were transplanted individually into plastic pots (11×11×12 cm) containing expanded clay grids (Ø=6 mm) and grown for three weeks. A day temperature of 20 °C, night temperature of 18 °C, relative humidity of 70% and photoperiod of 16 h was maintained during the whole experimental period. Plants were irrigated with nutrient solution (electrical conductivity 2.1 dS m^{-1}, pH 5.5) containing 1.2 mM NH_4^+, 7.2 mM K^+, 4.0 mM Ca^{2+}, 1.8 mM Mg^{2+}, 12.4 mM NO_3^-, 3.3 mM SO_4^{2-}, 1.0 mM PO_4^{2-}, 35 μM Fe^{3+}, 8.0 μM Mn^{2+}, 5.0 μM Zn^{2+}, 20 μM B, 0.5 μM Cu^{2+}, 0.5 μM MoO_4^{2-}.

2.2. Light treatments

Three light treatments were applied: white + red (WR) without additional far red (FR), WR with 55 μmol m^{-2} s^{-1} FR and WR with 85 μmol m^{-2} s^{-1} FR (Fig. S1, Table 1). All lighting was provided by overhead LED modules (WR: Greenpower PM-DR/W-120, FR: Greenpower PM-FR-120, Philips, Eindhoven, the Netherlands). The PPFD of WR was maintained at around 150 μmol m^{-2} s^{-1} at plant height for all light treatments by adjusting the height of the LED fixtures. The spectral distribution and photon flux density (PFD) was measured using a spectroradiometer (USB 2000 + UV-VIS; Ocean Optics, Duiven, the Netherlands). Phytochrome photostationary state (PSS) in each treatment was calculated based on the measured spectra as the ratio of P_{fr} to the total of P_{fr} and P_r according to Sager et al. (1988).

2.3. 1-N-naphthylphthalamic acid treatments

Auxin polar transport inhibitor 1-N-naphthylphthalamic acid (NPA, Sigma-Aldrich, Zwijndrecht, the Netherlands) was applied 14 days after transplanting. NPA 1% (w/w) was prepared by dissolving NPA in warm lanolin (Dražeta et al., 2004). Then, it was applied in a 3–5 mm thick ring around the stem at the root-shoot junction using a syringe. Control plants were treated in the same way with lanolin but without NPA.

2.4. Data collection

Plants were destructively measured 21 days after transplanting. Each plant was cleaned off any remaining growth medium and was separated into leaves, stem, and root. Leaf area of each plant was measured with a leaf area meter (LI-3100 area meter, Li-Cor Biosciences, Lincoln, USA). Each plant part was dried in a ventilated oven for 48 h at 105 °C and weighed for dry mass.

2.5. Growth component analysis

Effect of different treatments on the shoot: root ratio was analyzed by separating shoot: root ratio into its underlying components (Fig. S2). Shoot: root ratio is determined as shoot dry mass divided by root dry mass. Shoot dry mass was determined as the sum of leaf dry mass and stem dry mass.

2.6. Experimental set-up and statistical analysis

The experiment was a split-plot design with light and genotype as the main factors and NPA application as the sub-factor. Each combination of light condition and genotype was repeated four times, and each

Table 1
Photosynthetic photon flux density (PPFD), photon flux density of far red, red: far red ratio (R: FR) and phytochrome photostationary state (PSS) value of the light measured at the top of canopy in treatments with low, medium or high far red.

Parameter[a]	Unit	Light Treatment		
		0 FR	55 FR	85 FR
PPFD	μmol m^{-2} s^{-1}	151 ± 3[b]	151 ± 4	148 ± 4
Blue	μmol m^{-2} s^{-1}	18 ± 1	17 ± 2	17 ± 1
Green	μmol m^{-2} s^{-1}	26 ± 2	26 ± 2	25 ± 1
Red	μmol m^{-2} s^{-1}	105 ± 4	108 ± 5	101 ± 4
Far red	μmol m^{-2} s^{-1}	1 ± 0.1	55 ± 1	85 ± 2
Red: blue		6 ± 0.1	6 ± 0.1	6 ± 0.2
Red: far red		100 ± 2.1	2 ± 0.1	1 ± 0.1
PSS		0.88	0.77	0.73

[a] For the calculations of ratios, PFD was integrated over 100 nm intervals for blue (400–500 nm), green (500–600 nm), red (600–700 nm) and far red (700–800 nm).

[b] All values are means ± s.e.m. s.e.m of PSS was very small (0.001–0.002) and is therefore not shown.

repetition was conducted in an isolated climate chamber compartment. Within each light-genotype plot, three randomly selected plants were applied with only lanolin, and three other plants were applied with lanolin containing NPA. Treatment effect on root: shoot ratio was analyzed using analysis of variance (ANOVA). Assumptions of homogeneity and normality of residuals were satisfied as tested by Bartlett's test and Shapiro-Wilk test at $\alpha = 0.05$, respectively. Fisher's unprotected least significant difference (LSD) test was used for mean separation. The unprotected method was used because we also applied it for separating interaction means when the F-test for the interaction was not significant at $\alpha = 0.05$. For the growth component analysis, each component was compared between treatments using Student's t-test (n = 4, with three plants per repetition). All statistical analyses were performed in Genstat (18th Edition, VSN International Ltd., Hemel Hempstead, UK) at $\alpha = 0.05$.

3. Results

3.1. Effect of far red and auxin transport inhibitor on the shoot: root ratio

Shoot: root ratio was higher in the loss-of-function *phyB1/B2* mutant than in the wildtype (Fig. 1). In both wildtype and mutant, despite a positive tendency, adding 55 μmol m^{-2} s^{-1} of FR did not significantly affect the shoot: root ratio. Adding 85 μmol m^{-2} s^{-1} of FR, however, increased the shoot: root ratio significantly. Also, the application of NPA at the root-shoot junction significantly increased the shoot: root ratio for both the wildtype and mutant in each light treatment.

3.2. Growth component analysis

The *phyB1/B2* mutant plants showed a lower root as well as a lower shoot dry mass compared to wildtype plants. However, reduction in root mass was stronger than the reduction in shoot mass, resulting in an increased shoot: root ratio of the *phyB1/B2* mutant plants compared to wildtype (Fig. 2). Decreased shoot dry mass resulted from decreased leaf dry mass and stem dry mass, although stem dry mass was not significantly affected by the mutation when no FR was present (Fig. 2A).

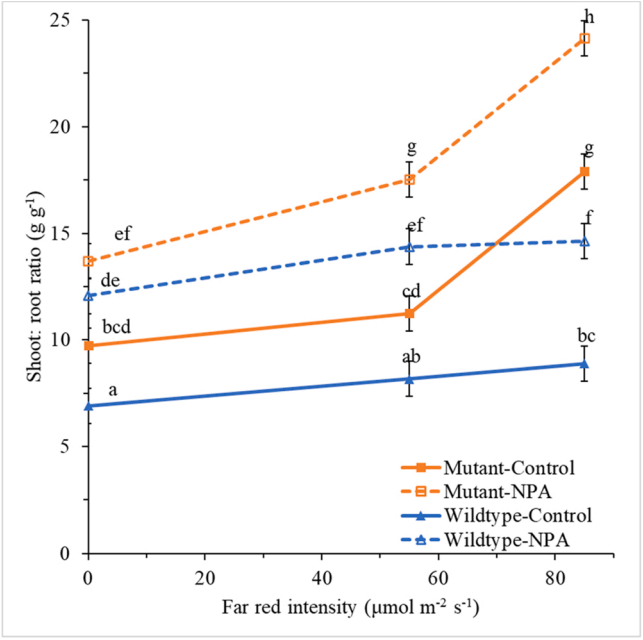

Fig. 1. Effects adding 0, 55, or 85 μmol m^{-2} s^{-1} of far red on the shoot: root ratio in a white + red background light (150 umol m^{-2} s^{-1}). Dashed and solid lines, respectively, represent plants with or without the application of N-1-naphthylphthalamic acid (NPA) at the root-shoot junction in wildtype (blue lines) and phyB1/B2 mutant (orange lines). Error bar represents standard error of means (n = 4,with three plants per repetition) and different letters denote significant differences according to Fisher's unprotected LSD test ($\alpha = 0.05$).

The addition of FR increased shoot: root ratio in both wildtype and *phyB1/B2* mutant (Fig. 3). In the wildtype, FR increased shoot: root ratio by increasing shoot dry mass, with no significant effect on root dry mass. Increased stem dry mass was the main reason for the increase in shoot dry mass, while the increase in leaf dry mass was only statistically significant at 85 μmol m^{-2} s^{-1} FR. In the *phyB1/B2* mutant, FR decreased both root and shoot dry mass, but root dry mass reduction was stronger, resulting in an increased shoot: root ratio (Fig. 3C, D). Further, the reduction of shoot dry mass due to FR in *phyB1/B2* mutant resulted from a reduced leaf dry mass, while stem dry mass was hardly affected. Responses were all dosage-dependent: stronger response at higher PFD of FR.

In both wildtype and *phyB1/B2* mutant, NPA application increased shoot: root ratio due to a stronger decrease in root dry mass than in shoot dry mass (Fig. 4). In the wildtype, both leaf dry mass and stem dry mass were decreased by NPA application while only leaf dry mass was affected by NPA application in the *phyB1/B2* mutant. The wildtype was more responsive to NPA treatment than the *phyB1/B2* mutant. Absolute values of all parameters used in the growth component analysis are shown in Table S1.

4. Discussion

4.1. Phytochrome regulation of shoot: root ratio

Wildtype tomato plants showed a significant increase in shoot: root ratio with increasing FR (Fig. 1). This increase is not only in accordance with the conserved FR-induced increase in shoot: root ratio observed among various tomato genotypes (Ji et al., 2021), but also with previous studies of Kasperbauer (1987), Lee et al. (2016), and Cao et al. (2018). This increase was mainly a result of higher shoot dry mass caused by FR-induced stem growth. Phytochromes are the main photoreceptors responsible in sensing R: FR ratio, and a loss-of-function phytochrome mutant grown without FR is similar to the wildtype grown with FR (Devlin et al., 1999). The addition of FR is often reported to improve tomato biomass production improvement can be attributed to improved photosynthesis (Zhen and van Iersel, 2017; Zhen and Bugbee, 2020) and improved plant architecture and light distribution (Zhang et al., 2019).

Interestingly, both the mutant and wildtype showed an increased shoot: root ratio with different responses in shoot and root biomass. Both root and shoot biomass of wildtype increased with increasing FR in a dosage-dependent manner (Fig. 3). For *phyB1/B2* double mutant, however, plant biomass was decreased. This reduction in plant mass as a result of mutation in *phyB1/B2* was also reported by Weller et al. (2000). An increased shoot: root ratio compared to the wildtype was observed for the mutant plant (Fig. 1) as a result of a stronger reduction in root dry mass than in shoot dry mass (Fig. 2). This may result from a strong stem and petiole elongation in the double mutant and reduction in the leaf area extension (Fig. S3, Devlin et al., 1999).

Increasing FR leads to an increase in both leaf and stem dry mass. Increased leaf growth favors biomass production which, to some extent, may benefit from an extended internode length and, consequently, an improved light interception. Indeed, Sarlikioti et al. (2011) observed in a simulation study a higher light interception and canopy photosynthesis for plants with longer internodes. However, such a response may be a saturation or optimal response. Further increase of FR (or decrease of R: FR ratio), which strongly favors stem elongation, leads to limitation of biomass partitioning to leaves and leaf area extension. This limitation, combined with the reduction in photosynthetic capacity (Ji et al., 2019) and chlorophyll content (Kalaitzoglou et al., 2019), may lead to a reduction in biomass production that mitigates the positive effect of FR. This may explain the reduced biomass observed in the *phyB1/B2* mutants grown with FR.

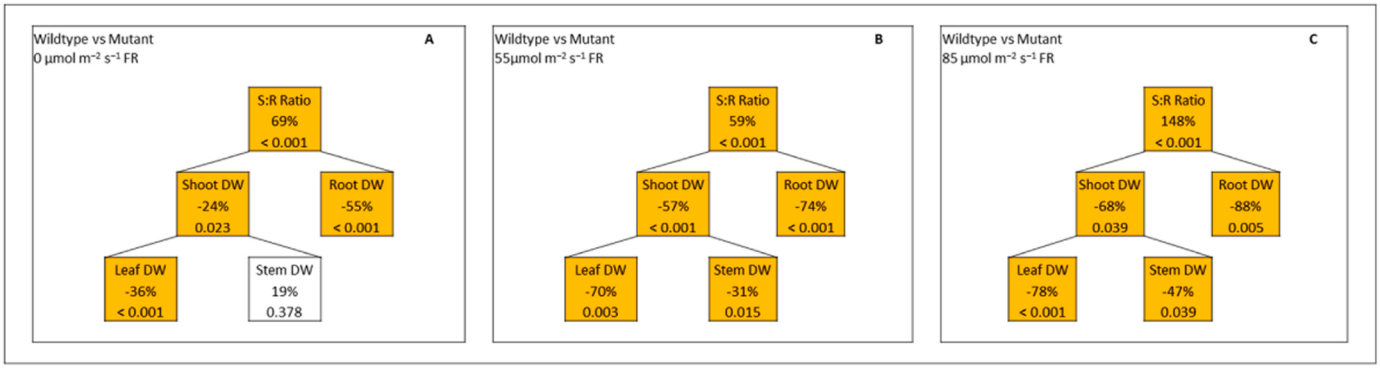

Fig. 2. Effect of loss-of-function mutation of phyB1/B2 on the components determining shoot: root ratio when 0(A), 55(B) or 85 µmol m^{-2} s^{-1} of far red (C) was added in a white + red background LED light (150 umol m^{-2} s^{-1}). The percentages represent the relative changes in the components when comparing mutant with wildtype. P-value of the t-test (n = 4,with three plants per repetition) is indicated in each component with a significant difference ($P < 0.05$) being highlighted in yellow.

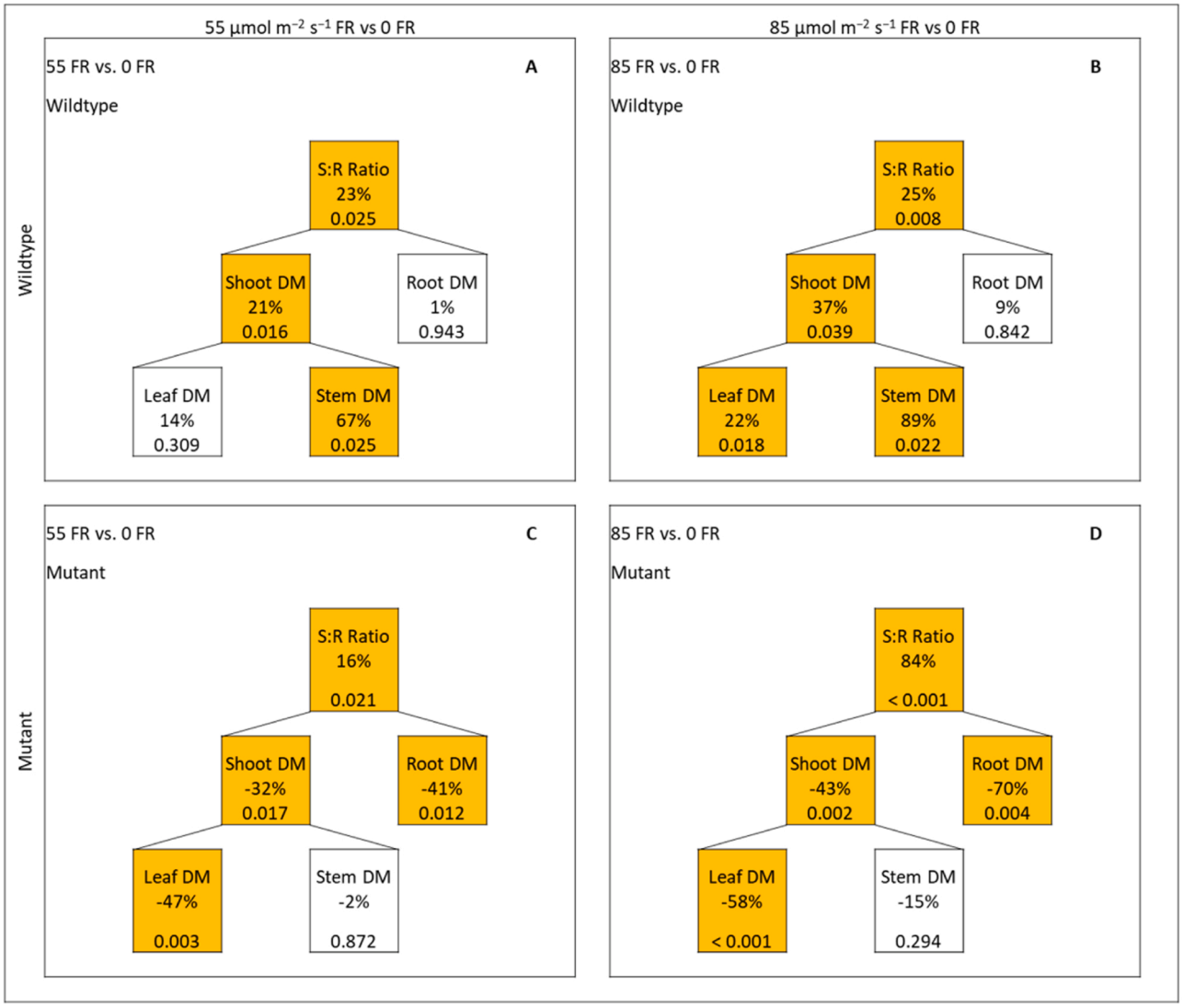

Fig. 3. Effect of adding 55, or 85 µmol m^{-2} s^{-1} of far red in a white + red background LED light (150 umol m^{-2} s^{-1}) on the components determining shoot: root ratio in wildtype (A, B) and phyB1/B2 mutant (C, D). The percentage represents the relative change in the components when compared with no FR. P-value of the t-test (n = 4,with three plants per repetition) is indicated in each component with a significant difference ($P < 0.05$) being highlighted.

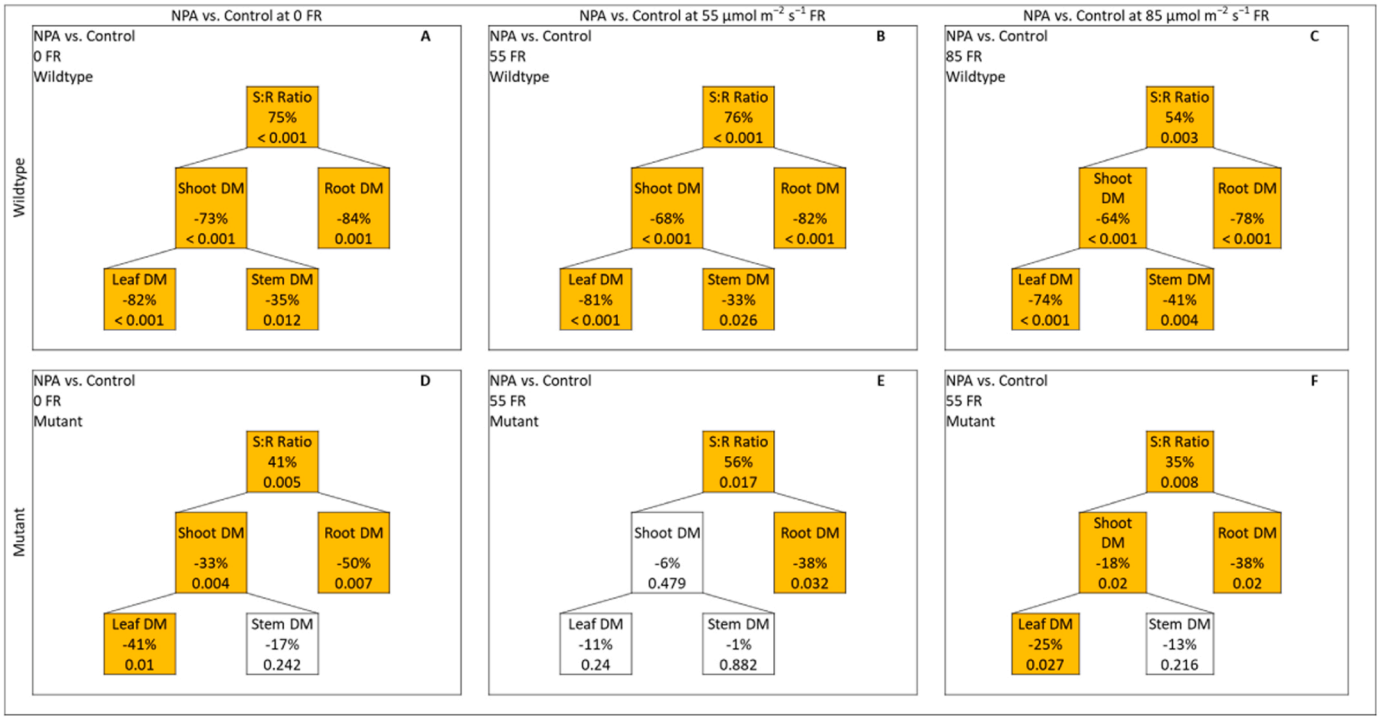

Fig. 4. Effect of 1% (w/w) N-1-naphthylphthalamic acid (NPA) applied in a ring of lanolin at the root-shoot junction on components determining shoot: root ratio in wildtype (A, B, C) and phyB1/B2 mutant (D, E, F) under different light conditions. A mock ring of lanolin without NPA was applied for the control treatment at the root-shoot junction. The percentage represents the relative change in the components when compared between the genotypes. P-value of the t-test (n = 4,with three plants per repetition) is indicated in each component with a significant difference ($P < 0.05$) being highlighted.

When looking at biomass in absolute terms, it is difficult to determine whether a change in stem dry mass is the cause or the consequence of changes in processes such as stem elongation. Dry mass partitioning between organs is determined by the relative sink strength of the organs (Marcelis, 1996). A higher fraction of dry mass partitioning to the stem suggests a higher relative sink strength in the stem. No previous study touched on the FR effect on the sink strength of vegetative organs. However, the expression of genes related to source-to-sink sugar transport, and sugar metabolism in the sink, are subject to phytochrome regulation (Fridman and Zamir, 2003; Kocal et al., 2008; Ernesto Bianchetti et al., 2018). Considering the direct relationship between sink strength and sugar metabolism as well as transportation (Osorio et al., 2014), and the increase of sugar metabolism under additional FR (Ji et al., 2020), we reason that FR may increase the shoot: root ratio by increasing shoot relative sink strength. Whether this increase results from higher shoot sink strength, lower root strength, or more complicated changes in the sink strength of each organ requires dedicated studies.

Arabidopsis phytochrome genes *PHYB* and *PHYD* are closely linked with tomato *PHYB1, PHYB2* while *Arabidopsis PHYA* is similar to tomato *PHYA* (Hauser et al., 1995). In *Arabidopsis*, the *phyB/phyD* double mutant showed little response to R:FR ratio (Aukerman et al., 1997; Devlin et al., 1999). This was not the case in tomato, as earlier studies showed that *phyA/B1/B2* triple mutant still retains phytochrome responses (Weller et al., 2000). The *phyB1/B2* double mutant was still capable in responding with elongation to additional FR (Fig. 3), showing that other members of the phytochrome family, such as *PHYE*, are able to mediate the elongation responses to FR in the absence of *PHYB* (Schrager-Lavelle et al., 2016). Tomato *phyB1/B2* double mutant also responded to additional FR with increased shoot: root ratio (Fig. 1), which suggest that the change in shoot: root ratio is also a phytochrome-regulated response to FR that can be regulated by other phytochromes in absence of *PHYB1* and *PHYB2* in tomato.

4.2. Interaction between phytochrome and auxin in regulating shoot: root ratio under FR

Auxin concentration negatively correlates with R:FR ratio (Holalu and Finlayson, 2017), suggesting the involvement of auxin in FR-induced changes in plant growth. The perception of FR by PHYB leads to the accumulation of phytochrome interaction factors (PIFs) and induces growth responses via upregulated auxin synthesis (Li et al., 2012; Pantazopoulou et al., 2017; Courbier et al., 2020). Similar to wildtype plants grown under additional FR, *phyB1/B2* mutant plants grown without FR also showed significantly higher shoot: root ratio than wildtype plants grown without FR (Fig. 1). An earlier study (Tucker, 1977) reported a significantly elevated auxin level in stems and mature leaves of six-week-old tomato plants when grown with additional FR. Furthermore, at a transcriptional level, Reddy et al. (2013) reported a reduced average expression of auxin-responsive genes under a higher R: FR. This suggests that the *phyB1/B2* mutant may have a constitutively elevated auxin level in the shoots, which stimulates an increase in shoot: root ratio and stem elongation. Auxin is transported from the shoot apex towards the base and from the shoot to the root. NPA was demonstrated to be a rapid, long-lasting, and systemic inhibitor of auxin transport, and it was validated to be a useful tool in evaluating the roles of auxin transport in plant growth (Brewer et al., 2015). The application NPA at the shoot-root junction effectively blocks the transport from shoot to root and substantially reduced the auxin level in the root (Reed et al., 1998). Hence, blocking shoot-to-root auxin transport should increase shoot: root ratio just as wildtype grown under FR, or as *phyB1/B2* mutant grown without FR. Indeed, when NPA was applied at the shoot-root junction, we observed a significant increase in stem elongation (Fig. S4) and shoot: root ratio (Fig. 1, Fig. 4). Especially, the NPA application strongly reduced root growth relative to that of shoot growth. This is in agreement with reports demonstrating that blocking auxin transport with NPA suppressed the development and growth of roots (Reed et al., 1998; Casimiro et al., 2001). More interestingly, the

effect of NPA application was less substantial in the mutant (Fig. 4D-4 F) than that in the wildtype (Fig. 4A-4 C), and it was also less substantial in treatments with high FR (Figs. 4C, 4F) than that with no FR (Figs. 4A, 4D). This may suggest that, under high FR conditions and/or the absence of active phytochrome B, the auxin level in the shoot is already elevated to trigger a strong increase in shoot: root ratio. Under this circumstance, blocking shoot-root auxin transport may not further influence shoot: root ratio anymore. Collectively, these results demonstrated the interacting roles between phytochrome and auxin in controlling shoot: root ratio in tomato. Further evidence on the distribution of auxin in plant organs and the corresponding expression of genes for auxin biosynthesis, transport, and auxin responses is needed in future research to fully explain the mode-of-action of auxin in controlling shoot: root ratio in plants as affected by FR.

5. Conclusion

FR increases shoot: root ratio in tomato. This increase involves the regulation by *PHYB1/B2*, as shown by the strong increase of shoot: root ratio in the *phyB1/B2* double mutant. The *phyB1/B2* double mutant still showed an increase in shoot: root ratio when FR increased, hence providing evidence for the involvement of also other phytochromes in the regulation of shoot: root ratio in tomato. Phytochrome regulation of shoot: root ratio in response to FR is likely mediated by affecting auxin transport.

CRediT authorship contribution statement

Yongran Ji: Conceptualization, Investigation, Formal analysis, Data curation, Writing – original draft. **Jarno Mooren:** Investigation, Data curation. **Leo F. M. Marcelis:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing. **Ep Heuvelink:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

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

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.envexpbot.2023.105471.

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