

1 Letters

2 **HY5 suppresses, rather than promotes, ABA-mediated inhibition of post-germination**
3 **seedling development**

4 Dear Editor,

5 Seed germination and post-germination seedling establishment are crucial early developmental
6 events in angiosperms. Although the demarcations between these two successive events appear
7 to be elusive, they have been defined as distinct developmental processes and identified to
8 involve separate regulatory mechanisms at the molecular level. Seed germination is marked by
9 the protrusion of embryonic root out of the seed coat. Post-germination seedling establishment
10 denotes the developmental window after germination that involves the opening, greening and
11 expansion of cotyledons or foliar leaves, marking the switch to autotrophic development (Lopez-
12 Molina et al., 2001; Weitbrecht et al., 2011).

13 Light is one of the most prominent environmental signals that influence early developmental
14 events in plants. A well-coordinated regulation of light and abscisic acid (ABA) signaling
15 pathways is crucial to optimize the timing and pace of germination and post-germination
16 seedling establishment, especially under stress conditions (de Wit et al., 2016; Vaishak et al.,
17 2019). The bZIP transcription factor ELONGATED HYPOCOTYL5 (HY5) is a key positive
18 regulator of photomorphogenesis (Oyama et al., 1997; Gangappa and Botto, 2016). HY5 also
19 acts as a major integrating factor for light and ABA pathways. A previous study identified that
20 HY5 promotes ABA signaling by directly binding to the promoter of *ABSCISIC ACID*
21 *INSENSITIVE5* (*ABI5*) and inducing its expression (Chen et al., 2008).

22 During seedling development, the protein level of HY5 is tightly controlled by the E3 ubiquitin
23 ligase CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), which ubiquitinates HY5 and
24 targets it for proteasome-mediated degradation (Ang et al., 1998; Osterlund et al., 2000).
25 Recently, we have reported that COP1 promotes ABA-mediated inhibition of post-germination
26 seedling establishment (Yadukrishnan et al., 2020). We observed that *cop1* mutants show ABA
27 hyposensitivity during post-germination seedling development (Yadukrishnan et al., 2020).
28 Previous evidence suggests that *hy5* is less sensitive to ABA-inhibition of seedling growth (Chen
29 et al., 2008). While the germinated Col-0 remains in a prolonged arrested state with ABA

treatment, *hy5* rapidly grows and establishes into seedlings (Chen et al., 2008). Together, these reports suggest that despite COP1 being a negative regulator of HY5, *cop1* and *hy5* mutants do not show opposite ABA sensitivities during seedling development. This prompted us to revisit the ABA-hyposensitive phenotype of *hy5* mutants during post-germination seedling growth in light.

The *hy5* allele used by Chen et al. (2008) was a T-DNA insertion mutant (SALK_096651) in Columbia background. To validate the ABA hyposensitive post-germination phenotype of *hy5*, we monitored its seedling establishment percentage under cycling light in absence and presence of ABA. By the 6th day, both Col-0 and *hy5* attained 100% seedling establishment in the absence of ABA (Fig. 1A,B). However, in the presence of ABA, seedling establishment was considerably slower in *hy5* as compared to the wild type. While ~30% of the Col-0 seedlings attained establishment by 6 days, *hy5* mutants had not started establishment (Fig. 1A,B). Our observation indicated that *hy5* mutant might be hypersensitive to ABA during post-germination seedling development, which is contradictory to the previous report.

To validate this further, we studied the post-germination ABA sensitivity of other widely used *hy5* mutant alleles – *hy5-215* and *hy5-ks50* (Fig. 1A,B). Although some of the previous studies have shown the ABA-hyposensitive germination phenotype of *hy5-215* mutant, its post-germination ABA sensitivity has not been quantitatively reported (Xu et al., 2014; Fernando and Schroeder, 2015; Srivastava et al., 2015; Yang et al., 2018). Thus, we monitored the seedling establishment of *hy5-215* in the presence and absence of ABA. While the wild type and *hy5-215* showed 100% seedling establishment in the absence of ABA, *hy5-215* showed significantly slower seedling establishment in 1 μ M ABA as compared to Col-0 (Fig. 1A,B). In the presence of ABA, ~ 25% of Col-0 seedlings established by the 6th day, whereas only ~5% of *hy5-215* seedlings established (Fig. 1A,B).

Since both *hy5* (SALK_096651) and *hy5-215* are in the genetic background of Columbia ecotype, we further verified the phenotype in the *hy5-ks50* allele in the Wassilewskija (Ws) background. When grown in the presence of 1 μ M ABA, the seedling establishment rate of the wild-type Ws ecotype was higher than in the Col-0 ecotype (Fig. 1A,B). However, the *hy5-ks50* mutant showed significantly less seedling establishment in the presence of ABA as compared to the Ws wild type (Fig. 1A,B). The seedling establishment of *hy5-ks50* in ABA was greater than

hy5 (SALK_096651) and *hy5-215*, indicating that the post-germination ABA sensitivity is generally weaker in Ws genetic background (Fig. 1A,B). All the *hy5* mutant alleles tested showed varying extents of ABA hypersensitive seedling establishment, underlining that HY5 might be a negative regulator of ABA-mediated post-germination seedling growth arrest, contrary to what has been known.

Seed age can affect dormancy thereby modulating germination and post-germination phenotypes of seedlings both in the presence and absence of ABA (Weitbrecht et al., 2011; Shu et al., 2016). All the seeds used in the experiment mentioned above (Fig. 1A,B) were freshly harvested. To verify if seedling establishment in Col-0 and *hy5* mutants varies between different seed batches, we compared three seeds batches, Batch A (freshly harvested), Batch B (harvested 6 months ago) and Batch C (harvested one year ago) (Fig. 1C). Sensitivity to ABA decreased in both Col-0 and *hy5* mutants with seed age (Fig. 1C). However, in all the batches, *hy5* and *hy5-215* showed enhanced sensitivity to ABA compared to Col-0 (Fig. 1C). In our experiments, seeds were stratified for a period of 3 days, whereas the protocol followed by Chen et al. (2008) is slightly ambiguous as the Figure 2 legend mentions stratification, while the methods section refers to a previous paper that does not include stratification (Xiong et al., 2001). To investigate if stratification modulates seedling establishment, we compared the establishment of stratified and non-stratified Batch C seeds (Fig. 1D). *hy5* mutants showed ABA-hypersensitive seedling establishment phenotypes irrespective of the stratification treatment, although bypassing the stratification caused a stronger inhibition (Fig. 1D). Taking these data into consideration, we suspect that a difference in seed age and dormancy levels between Col-0 and *hy5* seeds used by Chen et al. (2008) could possibly have contributed towards the reduced ABA sensitivity of *hy5* during seedling establishment seen before.

We further asked whether the ABA hypersensitivity of *hy5* mutants is confined to the post-germination development of seedlings or it starts from the germination process itself. To test this, we monitored the germination rates of these mutants in the presence and absence of ABA (Fig. 1E-G). In the absence of ABA, freshly harvested Col-0, *hy5* (SALK_096651) and *hy5-215* seeds germinated at similar rates, whereas in the presence of ABA, the germination rates of *hy5* mutants were marginally faster than Col-0 (Fig. 1E), which is in agreement with previous reports (Chen et al., 2008; Xu et al., 2014; Fernando and Schroder, 2015; Yang et al., 2018). When we

performed the same experiment with the one-year-old seed batch, *hy5* mutants showed slower germination rates compared to wild-type, reiterating the role of dormancy or seed age in modulating sensitivity of *hy5* mutants to ABA (Fig. 1F). Next, we investigated the role of stratification in regulating germination of *hy5* mutants in the presence and absence of ABA. In one-year-old seeds in the absence of stratification, *hy5* mutants germinated faster than Col-0 (Fig. 1G), which is opposite to their hypersensitive response when stratified (Fig. 1F). This emphasizes the role of stratification in regulating germination under stress.

Since Chen et al. (2008) performed their germination assays on filter paper, we also verified the germination of one-year-old seeds on filter paper in the presence and absence of ABA and found that *hy5* mutants retain the ABA-hypersensitive germination phenotype in this condition as well (Fig. 1H). When the seeds germinated on water-soaked filter paper were transferred to ABA-containing plates for further growth, *hy5* mutants continued to show ABA-hypersensitive responses during seedling establishment, indicating that the post-germination ABA hypersensitivity of *hy5* mutants is not a consequence of its delayed germination in ABA (Fig. 1I). Together, these results indicate that ABA sensitivity of *hy5* mutants during early development is highly influenced by levels of dormancy in different seed batches and stratification of the seeds, which might have been overlooked in some of the previous studies.

According to our observations, while *hy5* mutants show ABA hypersensitivity during post-germination development, *cop1* mutants show ABA hyposensitivity (Yadukrishnan et al., 2020). Since HY5 acts downstream of COP1 in light signaling and during germination, we asked if COP1 and HY5 act in a similar module to regulate post-germination ABA sensitivity. To test this, we grew *cop1-4 hy5-215* double mutants (Rolauffs et al., 2012) in the presence and absence of ABA and studied their post-germination ABA sensitivity (Fig. 2A,B). In the absence of ABA, all lines achieved 100% seedling establishment by 4 days (Fig. 2A,B). In 1 μ M ABA, *cop1-4* and *hy5-215* exhibited ABA hyposensitive and hypersensitive seedling establishment respectively. The *cop1-4 hy5-215* double mutant showed ABA sensitivity similar to *hy5-215* (Fig. 2A,B). The epistatic phenotype of *hy5-215* over *cop1-4* suggests that HY5 is necessary for the ABA hyposensitive seedling establishment phenotype of *cop1-4*, and HY5 acts downstream of COP1 to regulate ABA-mediated inhibition of post-germination development (Fig. 2C).

To conclude, sensing light cues from the environment and integrating them with the ABA pathway might be crucial for making the decision to switch to autotrophic growth. Under stress conditions, ABA dictates the seedling to remain in a prolonged post-germination quiescent state, whereas light favours photomorphogenic growth and autotrophic establishment of the seedling. The interaction of HY5, COP1, and possibly other regulators of light signaling with the ABA pathway might be decisive in determining the right timing for seedling establishment.

ACCESSION NUMBERS

HY5 - AT5G11260; *COP1* - AT2G32950; *ABI5* - AT2G36270

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S.D and P.Y. designed the study and wrote the article. P.Y. and P.V.R performed the experiments. All authors revised the manuscript.

Figure Legends

Figure 1. HY5 negatively regulates ABA-mediated inhibition of post-germination seedling establishment (A) Representative images and (B) seedling establishment rates of Col-0, *hy5* (SALK_096651), *hy5-215*, Ws and *hy5-ks50* grown on 0.5x Murashige and Skoog (MS) plates complemented with and without 1μM ABA for 6 days. (C) Seedling establishment rates of three different batches of Col-0, *hy5* and *hy5-215* seeds grown on 0.5xMS plates without (white bars) and with (colored bars) 1μM ABA for 6 days. Batch A, B, and C represent freshly harvested, 6-month-old, and 1-year-old seed batches, respectively. (D) Seedling establishment rates of non-stratified and stratified Col-0, *hy5* and *hy5-215* seeds (Batch C) on 0.5xMS plates without (white bars) and with (colored bars) 1μM ABA for 6 days. (E & F) Germination rates of (E) Batch A and (F) Batch C Col-0, *hy5* and *hy5-215* seeds on 0.5xMS plates without and with 1μM ABA counted up to 5 days after stratification treatment. (G) Germination rates of non-stratified Batch C seeds of Col-0, *hy5* and *hy5-215* on 0.5xMS plates without and with 1μM ABA counted up to 5 days after imbibition. (H) Germination rates of Col-0, *hy5* and *hy5-215* seeds (Batch C) on filter paper soaked with sterile water without or with 1μM ABA counted up to 5 days after stratification treatment. (I) Seedling establishment rates of Batch C seeds of Col-0, *hy5* and *hy5-215* germinated on water-soaked filter paper after stratification and transferred on the second day to 0.5xMS plates without or with 5μM ABA and grown for 2 more days. Half-strength MS plates containing 1% (w/v) agar and no added sucrose were used in the experiments. Plates were kept in long days (16h light /8h dark) with 80 μmol m⁻² s⁻¹ white light. Seeds were scored as germinated upon the emergence of radicle out of the testa and endosperm. Seedling

establishment was marked by complete opening and greening of cotyledons. Values represent mean \pm SEM of three experiments with ≥ 50 seeds used in each experiment. Letters above the bars indicate statistical groups as determined by one-way ANOVA followed by Tukey's post-hoc test ($P \leq 0.05$). Asterisks represent statistically significant difference between the individual mutants and the wild type (*** $P < 0.001$, ** $P < 0.01$) as determined by one-way ANOVA followed by Dunnett's post-hoc test.

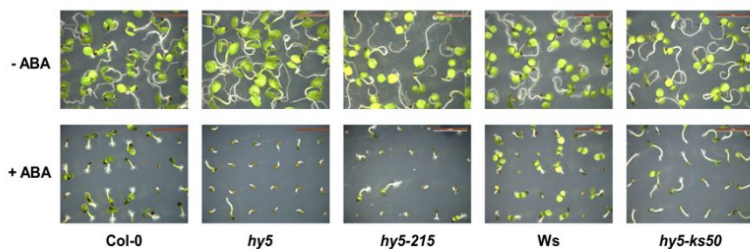
Figure 2. HY5 acts downstream of COP1 to regulate ABA-mediated inhibition of post-germination seedling establishment (A) Representative images and (B) seedling establishment rates of 4- days-old Col-0, *cop1-4*, *hy5-215* and *cop1-4 hy5-215* on 0.5x Murashige and Skoog (MS) plates complemented with and without 1 μ M ABA. Plates were kept in long days (16h light /8h dark) with 80 μ mol m⁻² s⁻¹ white light after stratification. Seedling establishment was marked by complete opening and greening of cotyledons. Values represent mean \pm SEM of three experiments with ≥ 50 seeds used in each experiment. Letters above the bars indicate statistical groups as determined by one-way ANOVA followed by Tukey's post-hoc test ($P \leq 0.05$). (C) Model showing the regulation of ABA-mediated inhibition of early seedling development by the COP1-HY5 regulatory module.

LITERATURE CITED

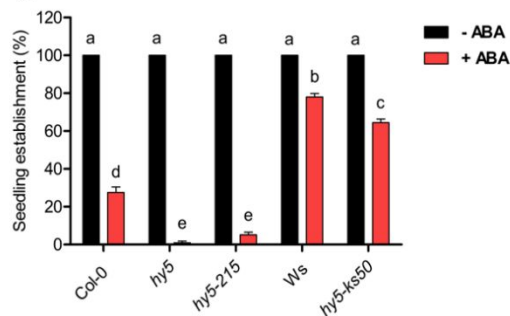
- Ang LH, Chattopadhyay S, Wei N, Oyama T, Okada K, Batschauer A, Deng XW** (1998) Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of Arabidopsis development. *Molecular Cell* **1**: 213-222
- Chen H, Zhang JY, Neff MM, Hong SW, Zhang HY, Deng XW, Xiong LM** (2008) Integration of light and abscisic acid signaling during seed germination and early seedling development. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 4495-4500
- de Wit M, Galvão VC, Fankhauser C** (2016) Light-Mediated Hormonal Regulation of Plant Growth and Development. *Annu Rev Plant Biol* **67**: 513-537
- Fernando VCD, Schroeder DF** (2015) Genetic interactions between DET1 and intermediate genes in Arabidopsis ABA signalling. *Plant Science* **239**: 166-179
- Gangappa SN, Botto JF** (2016) The Multifaceted Roles of HY5 in Plant Growth and Development. *Molecular Plant* **9**: 1353-1365
- Lopez-Molina L, Mongrand S, Chua NH** (2001) A postgermination developmental arrest checkpoint is mediated by abscisic acid and requires the AB15 transcription factor in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America* **98**: 4782-4787

- Osterlund MT, Hardtke CS, Wei N, Deng XW** (2000) Targeted destabilization of HY5 during light-regulated development of Arabidopsis. *Nature* **405**: 462-466
- Oyama T, Shimura Y, Okada K** (1997) The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus-induced development of root and hypocotyl. *Genes Dev* **11**: 2983-2995
- Rolauffs S, Fackendahl P, Sahm J, Fiene G, Hoecker U** (2012) Arabidopsis COP1 and SPA genes are essential for plant elongation but not for acceleration of flowering time in response to a low red light to far-red light ratio. *Plant Physiol* **160**: 2015-2027
- Shu K, Liu XD, Xie Q, He ZH** (2016) Two Faces of One Seed: Hormonal Regulation of Dormancy and Germination. *Mol Plant* **9**: 34-45
- Srivastava AK, Senapati D, Srivastava A, Chakraborty M, Gangappa SN, Chattopadhyay S** (2015) Short Hypocotyl in White Light1 Interacts with Elongated Hypocotyl5 (HY5) and Constitutive Photomorphogenic1 (COP1) and Promotes COP1-Mediated Degradation of HY5 during Arabidopsis Seedling Development. *Plant Physiol* **169**: 2922-2934
- Vaishak KP, Yadukrishnan P, Bakshi S, Kushwaha AK, Ramachandran H, Job N, Babu D, Datta S** (2019) The B-box bridge between light and hormones in plants. *J Photochem Photobiol B* **191**: 164-174
- Weitbrecht K, Muller K, Leubner-Metzger G** (2011) First off the mark: early seed germination. *Journal of Experimental Botany* **62**: 3289-3309
- Xiong L, Gong Z, Rock CD, Subramanian S, Guo Y, Xu W, Galbraith D, Zhu JK** (2001) Modulation of abscisic acid signal transduction and biosynthesis by an Sm-like protein in Arabidopsis. *Dev Cell* **1**: 771-781
- Xu DQ, Li JG, Gangappa SN, Hettiarachchi C, Lin F, Andersson MX, Jiang Y, Deng XW, Holm M** (2014) Convergence of Light and ABA Signaling on the ABI5 Promoter. *Plos Genetics* **10**
- Yadukrishnan P, Rahul PV, Ravindran N, Bursch K, Johansson H, Datta S** (2020) CONSTITUTIVELY PHOTOMORPHOGENIC1 promotes ABA-mediated inhibition of post germination seedling establishment. *Plant J* **103**: 481-496
- Yang B, Song Z, Li C, Jiang J, Zhou Y, Wang R, Wang Q, Ni C, Liang Q, Chen H, Fan LM** (2018) RSM1, an Arabidopsis MYB protein, interacts with HY5/HYH to modulate seed germination and seedling development in response to abscisic acid and salinity. *PLoS Genet* **14**: e1007839

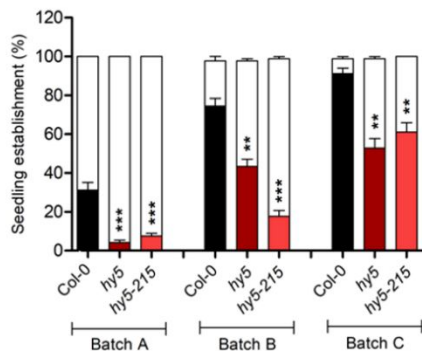
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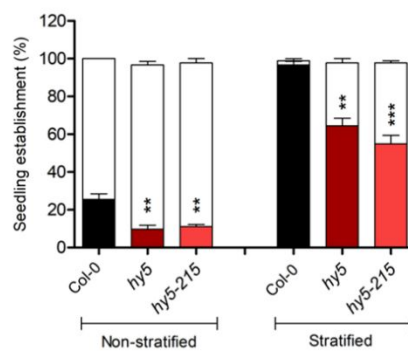
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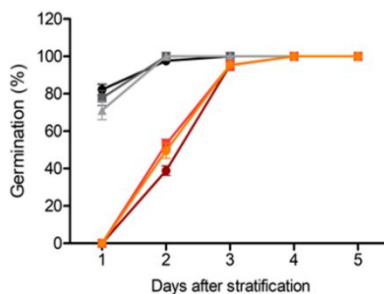
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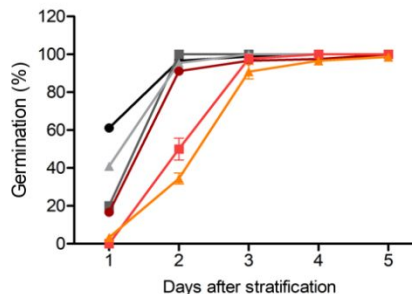
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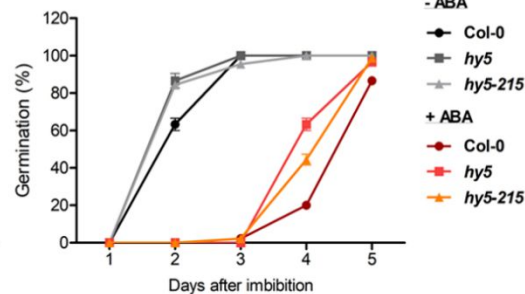
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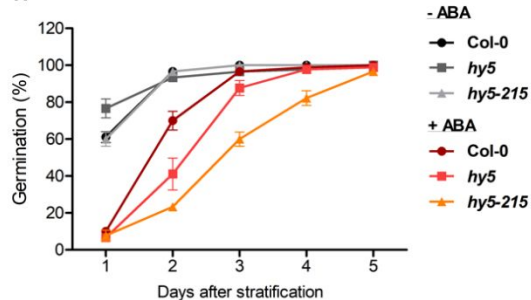
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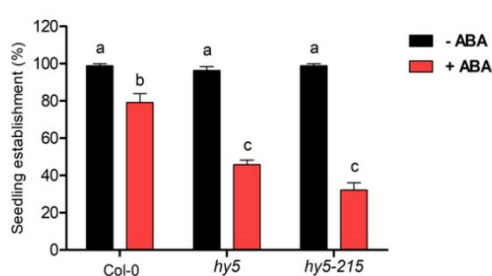
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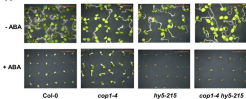
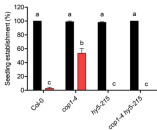
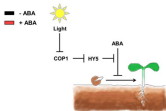


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Parsed Citations

Ang LH, Chattopadhyay S, Wei N, Oyama T, Okada K, Batschauer A, Deng XW (1998) Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of Arabidopsis development. *Molecular Cell* 1: 213-222

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Chen H, Zhang JY, Neff MM, Hong SW, Zhang HY, Deng XW, Xiong LM (2008) Integration of light and abscisic acid signaling during seed germination and early seedling development. *Proceedings of the National Academy of Sciences of the United States of America* 105: 4495-4500

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de Wit M, Galvão VC, Fankhauser C (2016) Light-Mediated Hormonal Regulation of Plant Growth and Development. *Annu Rev Plant Biol* 67: 513-537

Pubmed: [Author and Title](#)

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Fernando VCD, Schroeder DF (2015) Genetic interactions between DET1 and intermediate genes in Arabidopsis ABA signalling. *Plant Science* 239: 166-179

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Gangappa SN, Botto JF (2016) The Multifaceted Roles of HY5 in Plant Growth and Development. *Molecular Plant* 9: 1353-1365

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Lopez-Molina L, Mongrand S, Chua NH (2001) A postgermination developmental arrest checkpoint is mediated by abscisic acid and requires the AB15 transcription factor in Arabidopsis. *Proceedings of the National Academy of Sciences of the United States of America* 98: 4782-4787

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Osterlund MT, Hardtke CS, Wei N, Deng XW (2000) Targeted destabilization of HY5 during light-regulated development of Arabidopsis. *Nature* 405: 462-466

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Oyama T, Shimura Y, Okada K (1997) The Arabidopsis HY5 gene encodes a bZIP protein that regulates stimulus-induced development of root and hypocotyl. *Genes Dev* 11: 2983-2995

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Rolauffs S, Fackendahl P, Sahn J, Fiene G, Hoecker U (2012) Arabidopsis COP1 and SPA genes are essential for plant elongation but not for acceleration of flowering time in response to a low red light to far-red light ratio. *Plant Physiol* 160: 2015-2027

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Shu K, Liu XD, Xie Q, He ZH (2016) Two Faces of One Seed: Hormonal Regulation of Dormancy and Germination. *Mol Plant* 9: 34-45

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Srivastava AK, Senapati D, Srivastava A, Chakraborty M, Gangappa SN, Chattopadhyay S (2015) Short Hypocotyl in White Light1 Interacts with Elongated Hypocotyl5 (HY5) and Constitutive Photomorphogenic1 (COP1) and Promotes COP1-Mediated Degradation of HY5 during Arabidopsis Seedling Development. *Plant Physiol* 169: 2922-2934

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Vaishak KP, Yadukrishnan P, Bakshi S, Kushwaha AK, Ramachandran H, Job N, Babu D, Datta S (2019) The B-box bridge between light and hormones in plants. *J Photochem Photobiol B* 191: 164-174

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Weitbrecht K, Muller K, Leubner-Metzger G (2011) First off the mark: early seed germination. *Journal of Experimental Botany* 62: 3289-3309

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Xiong L, Gong Z, Rock CD, Subramanian S, Guo Y, Xu W, Galbraith D, Zhu JK (2001) Modulation of abscisic acid signal transduction and biosynthesis by an Sm-like protein in Arabidopsis. *Dev Cell* 1: 771-781

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Xu DQ, Li JG, Gangappa SN, Hettiarachchi G, Liu F, Andersson M, Jiang Y, Deng XW, Holm M (2014) Convergence of Light and ABA

Signaling on the ABI5 Promoter. Plos Genetics 10

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Yadukrishnan P, Rahul PV, Ravindran N, Bursch K, Johansson H, Datta S (2020) CONSTITUTIVELY PHOTOMORPHOGENIC1 promotes ABA-mediated inhibition of post germination seedling establishment. Plant J 103: 481–496

Pubmed: [Author and Title](#)

Google Scholar: [Author Only](#) [Title Only](#) [Author and Title](#)

Yang B, Song Z, Li C, Jiang J, Zhou Y, Wang R, Wang Q, Ni C, Liang Q, Chen H, Fan LM (2018) RSM1, an Arabidopsis MYB protein, interacts with HY5/HYH to modulate seed germination and seedling development in response to abscisic acid and salinity. PLoS Genet 14: e1007839

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