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# Shade avoidance syndrome in soybean and ideotype toward shade tolerance

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**Abstract** The shade avoidance syndrome (SAS) in soybean can have destructive effects on yield, as essential carbon resources reserved for yield are diverted to the petiole and stem for exaggerated elongation, resulting in lodging and susceptibility to disease. Despite numerous attempts to reduce the unfavorable impacts of SAS for the development of cultivars suitable for high-density planting or intercropping, the genetic bases and fundamental mechanisms of SAS remain largely unclear. The extensive research conducted in the model plant *Arabidopsis* provides a framework for understanding the SAS in soybean. Nevertheless, recent investigations suggest that the knowledge obtained from model *Arabidopsis* may not be applicable to all processes in soybean. Consequently, further efforts are required to identify the genetic regulators of SAS in soybean for molecular breeding of high-yield cultivars suitable for density farming. In this review, we present an overview of the recent developments in SAS studies in soybean and suggest an ideal planting architecture for shade-tolerant soybean intended for high-yield breeding.

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## Introduction

Soybean (*Glycine max* (L.) Merr.), an annual crop domesticated from the wild *Glycine soja* Sieb & Zucc in East Asia, is the world's most important source of vegetable protein and oil for both human consumption and animal feed. With a projected 17% increase in total soybean production from 2021 to 2029 to meet the demand of ever-growing world population (Vogel et al. 2021), it is vital to continue improving soybean yields to guarantee sustainable agricultural practices.

High-density planting is an essential management practice for maximizing soybean yields (Masino et al. 2018; Suhre et al. 2014; Xu et al. 2021). Particularly, Xu et al. demonstrated that increasing planting density from 135,000 to 315,000 plants per hectare resulted in a 46.7% increase in soybean yield (Xu et al. 2021). Moreover, narrow row spacing allows for earlier canopy closure, more light interception, faster growth rates, and consequently higher yields (De Bruin and Pedersen 2008; Liebert and Ryan 2017). Several studies have consistently demonstrated that narrow rows (15 inches) increased soybean yields by 10–15% when compared to wider rows (30 inches) in the US soybean-producing area (Khan et al. 2020; Walker et al. 2010; Thompson et al. 2015).

Intercropping is a sustainable agricultural practice that involves the simultaneous cultivation of two or more

crops over an extended period of time (Xu et al. 2020; Li et al. 2020; Brooker et al. 2015). It is widely implicated around the world and offers opportunities for sustainable agricultural intensification, with up to 16–29% less land and 19–36% less fertilizer use compared to monocropping systems (Li et al. 2020). Soybeans are often grown as shorter crops alongside taller ones, such as maize in intercropping systems (Iqbal et al. 2019). A previous study found that the land equivalent ratio (LER) ranges from 1.64 to 2.36 in the mechanized maize-soybean intercropping systems, which suggests that at least 64% more land is needed for monocropping to match the yield of intercropping (Iqbal et al. 2019).

Although high-density planting and intercropping have been proven to be highly advantageous for soybean production, there are a number of obstacles preventing their widespread adoption — one of which being the limited light resources. when canopy closes, the vertical fluxes of photosynthetically active radiation (PAR, 400–700 nm), decreases to 10% of sunlight (Sattin et al. 1994). Furthermore, most far-red light (FR, 700–800 nm) is reflected or transmitted by upper or neighboring leaves. The ratio of red to far-red light (R:FR) gradually decreases from 1.35 in the soybean monocropping system to 0.55 in the maize–soybean intercropping system (Yang et al. 2014; Li et al. 2021; Yao et al. 2017). In addition, close canopy results in a low blue light (LBL) condition. Both reduced R:FR and LBL cues evoke a variety of morphological and physiological changes in soybean (Green-Tracewicz et al. 2011; Wu et al. 2017; Dougher and Bugbee 2004), which limits the yield potential of soybean under high-density planting and intercropping conditions (Yang et al. 2014; Janczak-Pieniazek et al. 2021; Shafiq et al. 2020; Hitz et al. 2019; Dougher and Bugbee 2004; Lyu et al. 2021; Wheeler et al. 1991; Green-Tracewicz et al. 2012).

In this review, we provide a summary of the recent advancements in soybean shade avoidance syndrome (SAS) and propose an ideal plant architecture that is suitable for high-density planting or intercropping.

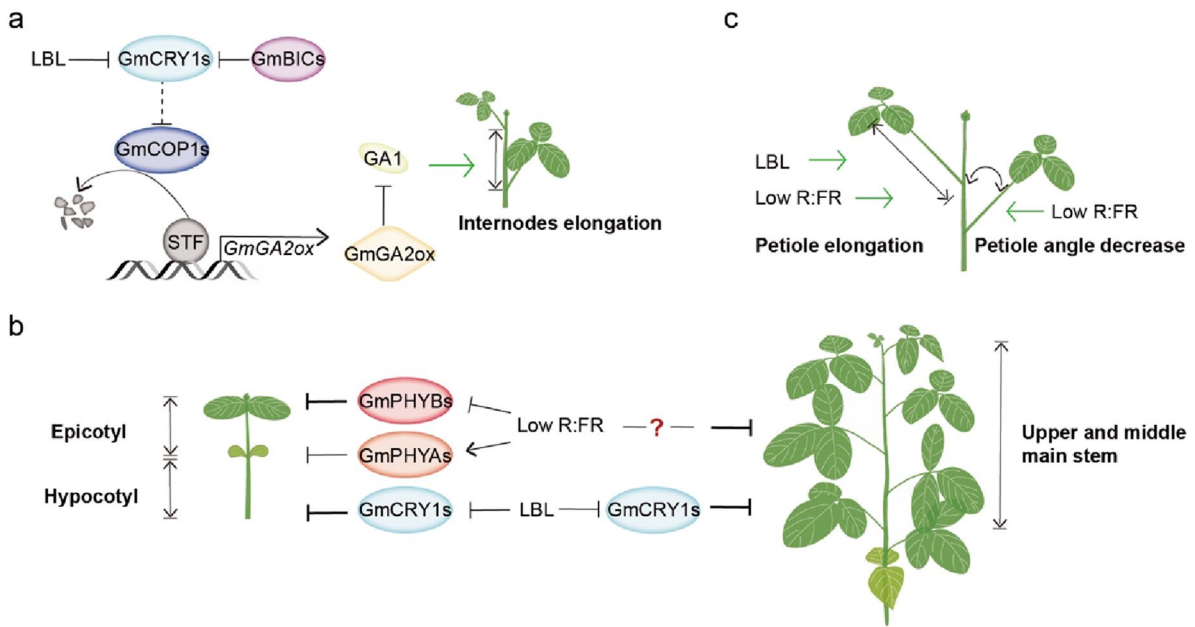## Soybean SAS and underlying mechanism

### Exaggerated stem elongation (ESE)

ESE as a typical SAS in soybean can be efficiently induced by the reduction of the total amount of visible light in the range of 400–700 nm, also known as

photosynthetically active radiation (PAR) (Hitz et al. 2019; Yang et al. 2018). Blue light (400–480 nm) is a primary component of PAR. Several studies have showed that LBL is the predominant cue inducing ESE in soybean (Hitz et al. 2020; Lyu et al. 2021; Dougher and Bugbee 2004, 2001; Britz and Sager 1990).

Plants possess several photoreceptors that are sensitive to changes in the spectral composition of light (Casal 2013; Paik and Huq 2019). Cryptochromes (CRYs), which evolved from DNA-repairing enzymes, can detect fluctuations in blue light and modulate SAS in plants (Pedmale et al. 2016; Keller et al. 2011). Overexpression of the four *GmCRY1s* genes (*GmCRY1a, b, c, d*) resulted in a shade-tolerant phenotype and suppressed ESE of soybean under LBL conditions (Lyu et al. 2021). Although single mutants of each *GmCRY1* paralog did not show a clear phenotype, the *Gmcry1s-qm* quadruple mutants (*Gmcry1a1b1c1d*) exhibited constitutive ESE reminiscent to that of wild-type soybean plants grown under LBL conditions, indicating that the *GmCRY1* genes have a redundant role in mediating LBL-induced SAS in soybean. The Blue-Light Inhibitor of Cryptochromes (BIC), which act as an on-off switch for CRYs, can inhibit the activity of CRYs by preventing blue light–dependent dimerization of CRYs (Wang et al. 2016). Mu et al. reported that the overexpression of *GmBIC* genes in soybean resulted in obvious ESE under normal light conditions (Mu et al. 2022). In contrast, the *Gmbic1a1b2a2b* quadruple mutant showed an attenuated ESE under LBL conditions, similar to that observed in the *GmCRY1b* overexpression lines (Mu et al. 2022; Lyu et al. 2021). These findings demonstrate that GmCRY1s have a critical role in mediating LBL-induced ESE in soybean (Fig. 1a).

The GA2-oxidases are GA-deactivating enzymes that reduce the levels of bioactive GAs in plants (Yamaguchi 2008). Transcriptome analysis revealed that the expression levels of *GA2-oxidase-7a/b* (*GA2OX7a/b*) genes were downregulated in the *Gmcry1s-qm* mutant, while overexpression of *GmCRY1b* led to their upregulation. Overexpression of *GmGA2ox7a* resulted in reduced stem length and abolished LBL-induced ESE in soybean. Therefore, the integration of GmCRY1-mediated signals with the gibberellins (GAs) metabolism highlights the key role of the GA pathway in regulating ESE in soybean (Fig. 1a). Interestingly, Wang et al. recently reported that the copy numbers of the *GA2ox8a/b* genes are higher in cultivated soybeans than in wild *G. soja*, which positively correlates with

**Fig. 1** Responses of stem and petiole under shade conditions and underlying mechanism regulated by photoreceptors in soybean. **a** GmCRY1s mediate internodes elongation induced by LBL. **b** LBL constitutively promotes stem elongation. Low R:FR promotes hypocotyl and epicotyl at the juvenile stage but inhibits internode elongation at the adult stage. **c** LBL and low R:FR cues increase petiole length and decrease petiole angle

*GA2ox8a/b* expression levels and negatively associated with trailing growth and shoot length (Wang et al. 2021). Moreover, they detected a strong selection signal between cultivated soybean and wild *G. soja* in the genomic region covering these two genes, implying that humans have manipulated the *GA2ox* genes to suppress ESE during soybean domestication.

Soybean TGACG-motif binding factors 1/2 (STF1/2) are a pair of basic leucine zipper motif (bZIP) transcription factors that share homology with the HY5 protein, which is known to promote photomorphogenesis in *Arabidopsis* (Cheong et al. 1998; Song et al. 2008). In soybean, STF1/2 can directly bind to the *GmGA2ox-7* promoter and enhance its expression. The expression pattern of *STF1/2*, with upregulation in the *GmCRY1b* overexpression line and downregulation in the *Gmcry1s-qm* mutant, is in agreement with the expression pattern of *GmGA2ox* genes (Lyu et al. 2021). Moreover, overexpression of *STF1/2* results in dwarf phenotype that is comparable to that observed in the *GmCRY1b* overexpression lines. These findings indicate the presence of a GmCRY1-STF-GA pathway that regulates LBL-induced ESE in soybean.

The *CONSTITUTIVE PHOTOMORPHOGENIC 1* (*COP1*) gene encodes an E3 ligase which acts as a key regulator repressing photomorphogenesis (Wang et al. 2001; Osterlund et al. 1999). Upon exposure to blue light, CRY1 interacts strongly with COP1 protein, resulting in the inhibition of COP1-dependent degradation of HY5 (Yang et al. 2001). In soybean, GmCRY1a is found to co-localize with GmCOP1b both in the nucleus and cytoplasmic photo-bodies, suggesting GmCRY1s can inhibit the activity of GmCOP1s when exposed to blue light (Xiong et al. 2019). Moreover, the *Gmcop1a1b* double mutant displayed a markedly dwarf phenotype, featuring shortened hypocotyls and epicotyls. Notably, this mutant completely suppressed LBL-induced hypocotyl and epicotyl elongation (Ji et al. 2022). It has been reported that GmCOP1s can interact with STF1/2 and decrease STF1/2 protein abundance (Shin et al. 2016; Ji et al. 2022), which supports that GmCOP1s act as negative regulators of GmCRY1-STF-GA module, and consequently promote LBL-induced ESE in soybean (Fig. 1a).

The low R:FR ratio, which serves as a signal for the competition of neighbor vegetations, has a complex role in regulating the internode elongation of

soybean at the different growth stages. Kasperbauer et al. and Thomas et al. independently reported that exposure to short irradiation with far-red light at the end of the daily photoperiod (EOD-FR) strongly promoted soybean internode elongation (Thomas and Raper Jr 1985; Kasperbauer et al. 1984). However, continuous supplemental irradiation with far-red light to white light (low R:FR) only promoted epicotyls and hypocotyls elongation, but retarded the growth of the middle and upper stems, thereby reducing the final plant height of soybean (Fig. 1b) (Hitz et al. 2019; Pausch et al. 1991; Green-Tracewicz et al. 2011; Lyu et al. 2021). These results provide evidence for the complex regulation of soybean internode elongation by low R:FR signals, which is influenced by the duration and timing of far-red light exposure.

Phytochrome (PHY) photoreceptors are responsible for detecting decrease in the R:FR ratio by converting the far-red light absorbing active form (Pfr) of PHY to the red light absorbing inactive form (Pr) (Pierik and de Wit 2014). GmPHYB1 is the predominant PHY involved in this process in soybean (Zhao et al. 2022a; Wu et al. 2013). When grown under white or red-light conditions, the *GmphyB1* mutant displays elongated hypocotyl and epicotyl phenotypes, similar to those of wild-type soybean grown under low R:FR conditions. Although the growth of the *GmphyB2* mutant is normal, the hypocotyl and epicotyl of the *GmphyB1phyB2* double mutant are significantly longer than those of the *GmphyB1* mutant under white or red-light conditions. This observation indicates that *GmPHYB2* exhibits functional additivity with *GmPHYB1* in suppressing hypocotyl and epicotyl elongation (Fig. 1b) (Zhao et al. 2022a). Additionally, the *E4* gene encoding the GmPHYA2 protein also inhibits hypocotyl elongation in soybean. Compared to plants homozygous for the *E4* allele, their near isogenic lines (NILs) with the *e4* genotype showed elongated hypocotyls under continuous far-red light (Liu et al. 2008). Consistent with this, the *GmphyA1A2* mutants displayed an elongated hypocotyl phenotype at the seedling stage (Zhao et al. 2022a). These results suggest that GmPHYA1/2 functions as a negative regulator of stem elongation under low R:FR conditions (Fig. 1b).

By conducting a quantitative trait locus (QTL) mapping analysis, Zhao et al. discovered *qSAR1*, a major QTL involved in shade-induced stem elongation, located in a 554-kb region on chromosome 10. Within this region, there are 44 genes, including four candidate genes (*Glyma10G209600 ELF6*, *Glyma.10g209700 SAUR46*, *Glyma.10g210200 NPH3*, and *Glyma.10g210600 ARF16*) that are known to be crucial regulators in SAS network in *Arabidopsis* (Zhao et al. 2022b). Additionally, Hou et al. investigated 185 soybean accessions using 639 SNP and 98 SSR markers and identified 75 makers related to plant height response to low light intensity (Hou et al. 2022). These findings on soybean SAS provide essential information for identifying the elite alleles associated with the regulation of shade-induced stem elongation in soybean.

Tender stem

In addition to triggering stem elongation, shade conditions can also induce a decrease in stem diameter and mechanical strength, which can contribute to the lodging of soybean. It has been reported that, in soybean–maize intercropping conditions, the stem diameter, breaking strength, and biomass of soybean decreased by 56.1%, 56.1%, and 38.2%, respectively, compared to those of soybean in monoculture systems (Liu et al. 2015). Low PAR was identified as the primary factor responsible for the reduction in stem diameter, rather than low R:FR (Hitz et al. 2019). The strength of the stem is positively correlated with the content and composition of lignin and cellulose, which are the major structural carbohydrates in plants (Hussain et al. 2019b; Li et al. 2022). Multiple genes that are involved in the biosynthesis of lignin and cellulose, including those encoding p-coumarate 3-hydroxylase (C3H), cinnamoyl-CoA reductase (CCR), caffeoyl-CoA O-methyltransferase (CCoAOMT), and peroxidase (POD), were downregulated under decreased PAR (Liu et al. 2018; Hussain et al. 2019b). This may partially explain the tender stem of soybean under shade conditions.

Excessive petiole elongation

In the context of shade conditions, petiole elongation is a crucial response in soybean, enables it to acquire adequate sunlight radiation for a single plant, while excessive petiole elongation can negatively impact the yield of planted communities (Ohashi et al. 2021).

It has been reported that soybean with short petioles tend to achieve higher yields per unit area by modifying the canopy profile under density farming conditions (Liu et al. 2020). Interestingly, LBL primarily induces stem elongation, while low R:FR enhances petiole elongation, suggesting distinct roles and mechanisms of LBL and low R:FR cues in regulating SAS in soybean (Fig. 1c) (Pausch et al. 1991; Thomas and Raper Jr 1985; Lyu et al. 2021). While the molecular mechanisms behind petiole elongation in soybean under shade conditions are unclear, several mutants with short petioles have been identified, including *M657*, *lps3*, *spwp*, *dsp1*, *dsp2*, and *rlsp1* (Jun and Kang 2012; Liu et al. 2019; Gao et al. 2022; Wang et al. 2022; Jun et al. 2009). These genetic variants provide valuable resources for future research into the intricate pathways and biological processes that regulate shade avoidance responses in soybean.

The regulation of shade-induced petiole elongation in soybean is believed to involve several plant hormones, including brassinosteroid and auxin. In a recent study, Chen et al. demonstrated that an MYB transcription factor, *GmMYB14*, serves as a transcriptional activator of *GmBEN1* to counteract the effect of brassinosteroid. The overexpression of *GmMYB14* was found to promote a short leaf petiole phenotype and improve yield under high-density planting conditions (Chen et al. 2021a). Additionally, Su et al. identified a dwarf mutant with shortened petioles, named *dmbn*, and utilized map-based cloning and genetic experiments to identify the *GmIAA27* gene as the cause of the *dmbn* locus (Su et al. 2022). These findings provide important insights into the complex genetic and molecular mechanisms underlying petiole elongation regulation in soybean, with potential implications for improving crop yield and productivity.

## Erected leaf petiole

The degree of inclination between the leaf petiole and stem, known as Leaf Petiole Angle (LPA), is a fundamental factor in determining plant architecture in soybean. Cultivars that can tolerate high-density planting conditions tend to have more upright leaves, which minimizes mutual shading (Liu et al. 2020). Studies have suggested that low R:FR signal is a key factor in regulating LPA (Fig. 1c) (Lyu et al. 2021). Recently, Zhang et al. reported that the auxin efflux transporter

*PINFORMED1* (*GmPIN1*) regulates soybean leaf petiole angle by determining polar auxin transport (Zhang et al. 2022). The expression levels of *GmPIN1* and the auxin content were found to be high on the lower side of the petiole, leading to asymmetric cell expansion. The *Gmpin1abc* and *Gmpin1bc* multiple mutants displayed a compact architecture and smaller petiole angle compared to the wild-type plants (Zhang et al. 2022). Auxin biosynthesis is a crucial step in shade-regulated hyponastic leaf movement in *Arabidopsis*. The amplitude of leaf movement was significantly reduced in the *taa1/sav3* mutants, which are defective in auxin biosynthesis, under high R:FR conditions (Tao et al. 2008; Michaud et al. 2017). These findings suggest a close relationship between auxin signals and leaf petiole angle in soybean, which provides a sound basis further investigations into the mechanisms regulating LPA.

## Accelerated leaf senescence

Leaf senescence is a life history trait that is controlled by both developmental programs and environmental conditions, such as light availability (Han et al. 2006). Under low R:FR conditions, soybean leaf senescence is accelerated as characterized by increased chlorophyll and protein loss, as well as increased exudation of amino acids from detached irradiated leaves (Guiamet et al. 1989). Moreover, blue light also plays a role in the regulation of leaf senescence. Overexpression of *CRY2a* delayed leaf senescence, while the *CRY2a-RNAi* and *CRYPTOCHROME-INTERACTING BASIC-HELIX-LOOP-HELIX 1* (*CIB1*) overexpression transgenic lines exhibited premature leaf senescence. This suggests that GmCRY2a acts antagonistically to GmCIB1 in the regulation of light-induced leaf senescence in soybean, where GmCRY2a interacts with GmCIB1 in a blue light dependent manner and represses its DNA binding activity for senescence-associated genes such as *WRKY DNA BINDING PROTEIN53b* (*WRKY53b*) (Meng et al. 2013).

## Reduced root biomass

Shade signals can significantly affect not only the aboveground plant architecture but also the growth and morphology of roots (Sun et al. 2003; Lee et al. 2016; Zhang et al. 2022). In soybean, low R:FR treatments induce a shift in carbon allocation from roots

to shoots, resulting in reduced total root length, surface area, and volume (Gal et al. 2015). In the maize-soybean intercropping system, the shade created by maize inhibits primary root growth and decreases root biomass and root-shoot ratio of soybean (Ephrath et al. 1993; Zhou et al. 2019). While the effect of low blue light on soybean roots remains unclear, some studies suggest that reduced blue light leads to decreased root growth (Britz, 1990). However, other research did not find any statistically significant change in root dry mass with varying blue light fractions (Dougher and Bugbee 2001).

Others

In addition to the aforementioned SAS, shading signals can also cause a variety of other phenotypic changes in soybean, such as alterations in the number of branches and flowering time. Studies have shown that low R:FR or LBL reduces the number of branches, and the total number of nodes of each branch is negatively correlated with the duration of shading during the VC to V6 stages (Green-Tracewicz et al. 2011; Dougher and Bugbee 2001; Acock and Acock 1987). Additionally, while low R:FR treatment is known to accelerate flowering in *Arabidopsis*, it delays the flowering transition in soybean (Cober and Voldeng 2001). Despite this knowledge, the underlying mechanisms of these SAS in soybean are still not well understood and warrant more research.

## SAS in *Arabidopsis* as a reference to soybean

Extensive research has been conducted to explore SAS in *Arabidopsis*, offering a useful reference for understanding SAS in soybean (Pierik and Ballare 2021; Galstyan et al. 2011; Fernandez-Milmanda and Ballare 2021). However, many studies have demonstrated that soybean exhibits distinct responses to shade signals in comparison to *Arabidopsis*, signifying that the knowledge of SAS in *Arabidopsis* may not be fully transferable to soybean.

In *Arabidopsis*, low R:FR treatments induce typical SAS, including promotion of hypocotyl and petiole elongation, upward reorientation of leaves (leaf hyponasty), a decrease of branching number and acceleration of flowering (Franklin 2008; Wang et al. 2016; Michaud et al. 2017; Gonzalez-Grandio et al.

2013; Devlin et al. 1999). Phytochrome photoreceptors detect the low R:FR ratio and convert from the far-red light–absorbing active form (Pfr) to the red light–absorbing inactive form (Pr) (Franklin and Whitelam 2007). The inactivation of Pfrs, particularly PfrB, releases the repression of PHYTOCHROME-INTERACTING FACTORs (PIFs) transcription factors and promotes stem elongation (Buti et al. 2020). Under low R:FR conditions, PIF7 undergoes dephosphorylation and is localized in the nucleus, where it plays a crucial role in the shade avoidance response (Burko et al. 2022; Huang et al. 2018). PIF3, PIF4, and PIF5 show increased protein stabilization under low R:FR (Leivar et al. 2008). Collectively , PIFs up-regulate the expression of *YUCCA* genes (*YUC2*, *YUC5*, *YUC8*, and *YUC9*) that encode auxin biosynthesis enzymes (Fernandez-Milmanda and Ballare 2021), thus increase auxin production in cotyledons. The PHYB-PIF-auxin signaling pathway is well established (Fig. 2a, b), highlighting the importance of auxin biosynthesis and transport in controlling stem elongation in response to low R:FR (Fernandez-Milmanda and Ballare 2021).

In addition to the auxin pathway, the regulation of shade avoidance response also involves the gibberellin (GA) pathway in *Arabidopsis*. Low R:FR ratios result in the upregulation of genes, such as *GA20ox*, which encode enzymes responsible for the biosynthesis of bioactive GAs (Hisamatsu et al. 2005). The bioactive GAs interact with their receptor, GA-INSENSITIVE DWARF1 (GID1), leading to ubiquitination and subsequent proteasomal degradation of DELLA proteins (Harberd et al. 2009). It has been observed that the abundance of DELLA proteins decreases in response to low R:FR ratios and increasing planting density (Djakovic-Petrovic et al. 2007). DELLAs have been shown to sequester PIFs, thereby preventing their activation of growth-promoting genes (Feng et al. 2008). Additionally, DELLAs also stimulate the degradation of certain PIF proteins through the ubiquitin-proteasome system (Li et al. 2016).

Under the canopy, the reduction in blue light irradiance (LBL) also acts as shade signal independently inducing many of the same shade responses as low R:FR ratio (Huber et al. 2021; Keuskamp et al. 2012). The blue light photoreceptors, cryptochrome (CRYs), are responsible for detecting LBL signals. CRY1 and CRY2 physically interact with PIF4 and PIF5 to regulate the expression of genes involved in cell wall remodeling and
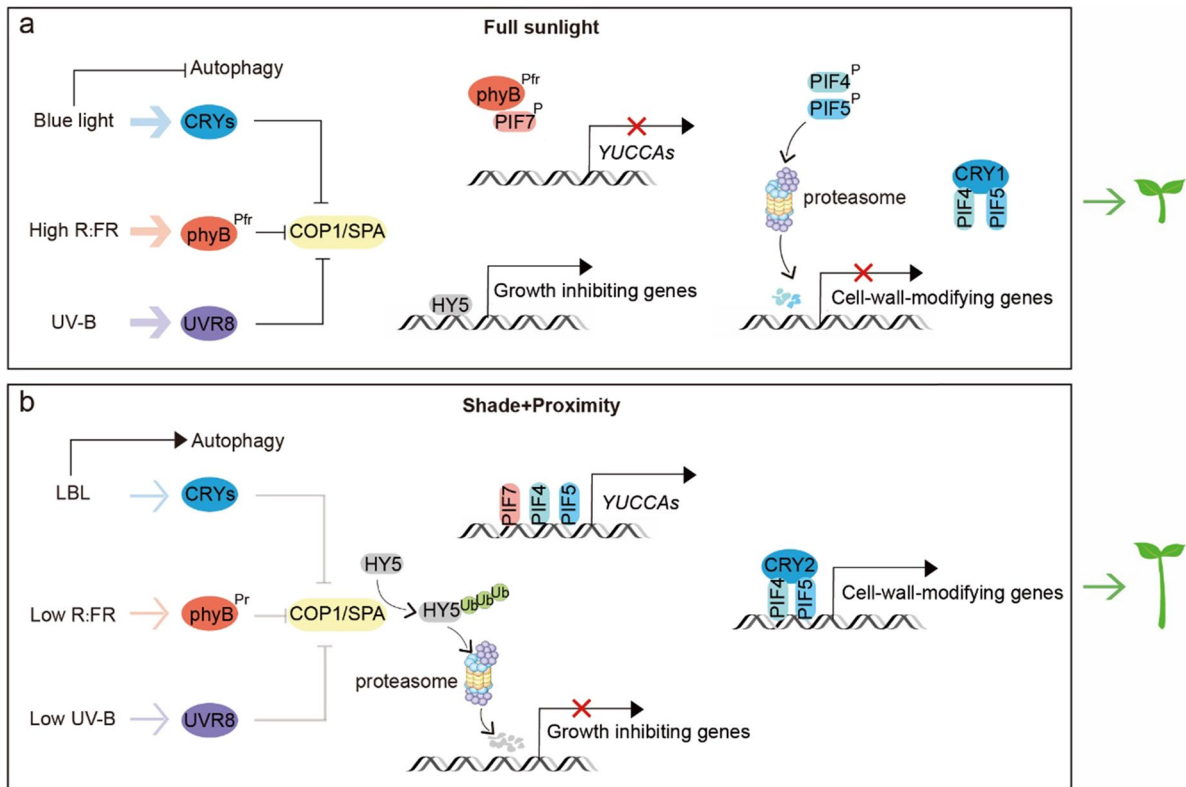
**Fig. 2** Models for hypocotyl elongation under sunlight and shade conditions through integration of light signals in *Arabidopsis thaliana.* **a** Under sunlight conditions, the UV-B light, red light, and blue light active respective photoreceptors (UVR8, phyB$^{Pfr}$, and CRYs) inhibit the activity of ubiquitin E3 ligase COP1/SPA complex and induce the phosphorylation and degradation of the bHLH transcriptional factor PIFs. The bZIP transcriptional factor HY5 accumulates to a high level to activate the expression of genes for photomorphogenesis and inhibit hypocotyl elongation. In addition, autophagy remains at the basal level under normal blue light. **b** Under shade conditions, the flux intensity of UV-B, red and blue light markedly decreases which reduces the activity of respective photoreceptors to release the degradation of HY5 proteins by the COP1/SPA complex. While PIFs accumulate to a high level and activate the expression of genes promoting hypocotyl elongation. In addition, LBL promotes autophagy-mediated recycling

expansion, which trigger stem elongation in response to LBL. Additionally, CRY2 and PIF4/5 bind to common promoter regions under LBL conditions (Fig. 2a, b), suggesting that these proteins directly regulate transcription of genes involved in SAS (Pedmale et al. 2016). In the presence of blue light, CRY1 interacts with both GID1 and DELLA proteins to repress GA signaling (Zhong et al. 2021), indicating that DELLA may also play a role in LBL-induced shade avoidance response. Recently, Ince et al. demonstrated that majority of LBL-induced genes do not depend on PIFs or auxin pathway. Instead, LBL induces starvation responses and promotes autophagy (Fig. 2a, b), which are essential for enhancing hypocotyl growth under the limited availability of newly fixed carbon (Ince et al. 2022).

The COP1 and SUPPRESSOR OF PHYA-105 (SPA) ubiquitin E3 ligase complex is a key regulator of shade avoidance response, ubiquitinating and promoting the degradation of positive regulators of photomorphogenesis, such as ELONGATED HYPOCOTYL 5 (HY5), HY5-HOMOLOG (HYH), LONG AFTER FAR-RED LIGHT 1 (LAF1), LONG HYPOCOTYL IN FAR-RED (HFR1), and PHYTOCHROME RAPIDLY REGULATED1/2 (PAR1/2) (Fig. 2a, b) (Liu et al. 2011; Bhatnagar et al. 2020; Zhou et al. 2014; Holm et al. 2002; Seo et al. 2003). The *cop1* mutants showed greatly reduced hypocotyl elongation under shade conditions, indicating a vital role for COP1 in mediating the shade-avoidance response (Pacín et al. 2013).

Simulated shade by reduced blue light or the ratio of R:FR caused the nuclear re-accumulation of COP1 and degradation of HFR (Pacin et al. 2016; Pacín et al. 2013). Furthermore, the *bbx21bbx22* double mutations restored the response of shade-induced hypocotyl elongation in the *cop1* background. These studies highlight the importance of HFR, BBX21 and BBX22 as downstream components of COP1, as well as their roles in the SAS in natural environments (Crocco et al. 2010). In addition to *COP1*, the *SPA* genes have been found to have redundant functions in regulating the SAS in seedlings (Rolauffs et al. 2012). The *spa* tripe mutants (*spa1 spa3 spa4* and *spa1 spa2 spa4*) or the *spa* quadruple mutant (*spa-Q*) lack the hypocotyl elongation response triggered by low R:FR. The COP1-SPA complex enhances hypocotyl elongation in low R:FR by degradation of HFR and promotion of shade-induced auxin biosynthesis (Rolauffs et al. 2012). Taken together, these findings emphasize the complex and multifaceted nature of the regulatory pathways involved in *Arabidopsis* shade avoidance response.

Soybean and *Arabidopsis* exhibit some comparable responses to shade signals. For example, in *Arabidopsis*, auxin metabolism and transport have a key role in shade avoidance responses. Similarly, a defect in *GmIAA27* leads to dwarf phenotypes, and *Gmpin1abc* and *Gmpin1bc* mutants displayed reduced petiole angles (Su et al. 2022; Zhang et al. 2022), indicating that auxin may also be of critical importance in shade avoidance syndromes in soybean. Therefore, the detailed mechanism studies of SAS in *Arabidopsis* provide valuable insights into exploring the shade avoidance response in soybean.

On the other hand, recent studies have highlighted notable differences in phenotypic changes and molecular regulations between soybean and *Arabidopsis*. For instance, *Arabidopsis* displays both hypocotyl elongation and main stem elongation in response to low R:FR (Roig-Villanova and Martinez-Garcia, 2016). In contrast, soybean exhibits elongation of bottom internodes (epicotyl and hypocotyl) with inhibition of the middle and upper internodes elongation under the same conditions (Lyu et al. 2021). Consistent with this, soybean plants competing with weeds in canopy closure (low R:FR) are shorter than those of weed-free plants (normal conditions) (Horvath et al. 2015). Furthermore, RNA-seq data also indicated that *GmPIF3a* is highly up-regulated in response to

weed competition, and its removal reduced *GmPIF3a* levels, suggesting that *GmPIF3a* may act as a growth repressor. Additionally, a constitutive overexpression of *GmPIF4b* also reduced the soybean plant height (Arya et al. 2021). These finds suggest that PIF transcription factors, which usually act as growth enhancers in *Arabidopsis*, may play an oppositive role in soybean. In addition, the LBL signal has been observed to play a more prominent role in promoting stem elongation compared to low R:FR signal, but does not affect leaf hyponasty (Fig. 1b, c) (Lyu et al. 2021). The regulation of stem elongation in response to blue light signals involves GmCRY1s, which enhance the protein abundance of STF1/2 possibly by inhibition in the activity of the ubiquitin ligase GmCOP1 (Lyu et al. 2021; Shin et al. 2016). Interestingly, the *Gmcop1a1b* double mutant exhibited extreme dwarfism and completely abolished shade-induced stem elongation, suggesting that GmCOP1s are key regulatory nodes for the shade-induced stem elongation in soybean (Ji et al. 2022).

The research on the molecular mechanism of shade avoidance response in *Arabidopsis* and soybean has revealed important potential target genes for soybean shade tolerance and lodging resistance breeding. Notably, the gibberellin (GA) signaling pathway plays an essential role in the regulation of soybean shade avoidance responses. Intriguingly, many of the genes involved in the "Green Revolution" in rice and wheat were subsequently identified as components of the GA biosynthesis or signalling pathways (Peng et al. 1999; Sasaki et al. 2002). Therefore, it is likely that modulating the soybean GA pathway could potentially increase soybean yield. Additionally, manipulating the genes involved in the soybean shade avoidance response, such as *GmPIFs*, *GmCOP1s*, *GmSPAs*, and their downstream target genes, may also aid in the development of soybean varieties with improved lodging resistance and high yield under dense planting and intercropping conditions.

## Trade-offs between SAS and yields

Shade avoidance syndrome (SAS) in plants involves a reallocation of resources from storage organs to stems and petioles, which provides a competitive edge over neighboring plants and is considered as a "selfish behavior" (Weiner 2019). While SAS increase the

fitness of wild plants, it can have negative impacts on domesticated crops, which are typically grown at high densities in human-influenced environments.

In soybean plants, shade avoidance responses, such as increased height growth, can lead to lodging and reduce yield. Lodging during the R4 to R6 period interrupts light penetration, increasing the risk of pod and stem diseases and reducing yield by up to 22% (Woods and Swearingin 1977; Hussain et al. 2020; Noor and Caviness 1980). Lodging at a later stage reduces harvest efficiency and yield by 5 to 12% (Weber and Fehr 1966). In addition, shade reduces the number of flowers per plant, stimulates flower and pod abscission, and negatively affects the number of pods per plant (Jiang and Egli 1993; Egli and Bruening 2005). Research has shown that both the number of branches and nodes per branch are inversely proportional to the timing of shade exposure from stage V1 to V6 (Green-Tracewicz et al. 2011).

Considering these findings, it has been suggested that shade-induced plasticity of plant height can be disadvantageous to crop production. C.M. Donald proposed the concept of "communal ideotypes", which optimizes competition between individual plants to avoid the "tragedy of the commons" (where success in competition comes at the expense of community performance) and achieve maximum plant population uniformity at high planting densities (Donald 1968). This concept was applied during the "Green Revolution" in the selection of semi-dwarf wheat and rice plants. Therefore, crop breeding often reduces "selfish behavior" and encourages interplant cooperation to maximize population yield, making it a form of "group selection."

On the other hand, some changes in agronomic traits induced by shade can benefit total yield in domesticated crops. For instance, the domestication of highly branched wild species into less-branched cultivated plants has improved yield (Studer et al. 2017). In maize and sorghum, genes such as *teosinte branched 1* (*TB1*) and *grassy tillers 1* (*GT1*) regulate apical dominance and tiller bud dormancy, and their expression is sensitive to a low R:FR ratio (Studer et al. 2011; Whipple et al. 2011). In shade, PfrB senses a low R:FR, which promotes *TB1* and *GT* expression to suppress lateral bud outgrowth (Whipple et al. 2011; Kebrom et al. 2010). This implies that humans may have unconsciously utilized natural variations to domesticate plants with constitutive

shade-avoidance phenotypes to adapt to high planting densities (Chen et al. 2021b). Furthermore, reduced leaf angle (hyponasty) is an important shade avoidance response in crops growing in dense populations, which can improve light perception, photosynthetic efficiency, and ventilation, and contribute to yield increases in high-density plantings. To sum up, engineering shade avoidance syndrome pathways to address fitness-versus-yield trade-offs is crucial for soybean improvement.

## Strategies to reduce the negative impacts of SAS

To maximize yield, various techniques such as field management practices, chemical formulations, genetic breeding, and biotechnological tools have been employed to mitigate the deleterious impacts of SAS on agricultural output (Noor and Caviness 1980; Carriedo et al. 2016; Liu et al. 2017; Cober et al. 2005).

Field management practices

Weed-induced crop yield decline is commonly attributed to a combination of direct resource competition and the response of crops to the presence of weed (Korav et al. 2018). Studies have shown that weed competition reduces soybean yield and growth in monocropping systems (Deiss et al. 2017), and that weed density has a more significant impact on soybean yield than species compositions (Pagnoncelli et al. 2017). Soybean responds to the presence of weeds by altering its growth in response to changes in light quality (Green-Tracewicz et al. 2012). Green-Tracewicz et al. used weed addition/removal to create two light quality treatments, low R:FR and high R:FR ratio, and observed that the growth of soybean between the first trifoliate (V1) stage and third trifoliate (V3) stage was particularly sensitive to low R:FR, which was similar to the Critical Period for Weed Control (CPWC) previously defined in field studies (Van Acker et al. 1993; Halford et al. 2001; Knezevic et al. 2003; Green-Tracewicz et al. 2012). In another study, RNAseq revealed weed-induced up-regulated expression of PIF3-like genes, indicating a low R:FR response in soybean (Horvath et al. 2015). Weed-free control during CPWC and manipulating weed tolerance by modulating candidate target genes such as

PIF3 are two strategies to reduce weed stress response in soybean.

A novel maize-soybean strip intercropping model is currently being developed, aiming to minimize the negative impact of SAS on soybean yield through optimized layout and variety selection to simultaneously achieving additional soybean harvest while maintaining corn yield like under monoculture conditions. This model includes three innovative features compared to traditional intercropping methods: (1) Expand row spacing. Narrowing the maize strip while widening the soybean strip to increase the light utilization of soybean. Additionally, the minimum distance between the outer rows of maize strips and soybean strips is increased from the traditional 40–50 cm to 60–70 cm. This not only ensures high light transmittance for soybean but also enhances the edge advantage of maize; (2) Optimal cultivar screening. It is important to select soybean varieties that are both shade-tolerant and resistant to lodging. In addition, semi-dwarf maize can be used to further reduce the shading rate of soybean; (3) Reduce in-row planting spacing. To achieve a high yield of both crops, it is recommended to increase the planting density by appropriately reducing plant spacing. The use of semi-dwarf and lodging-resistant plants is also conducive to further reducing planting distances (Du et al. 2018).

Moreover, the shade tolerance of soybean seedlings can be improved by providing fertilizers such as $NH_4^+$ and $NO_3^-$, which are the basic sources of nitrogen. According to researchers, providing an optimal ratio of $NH_4^+/NO_3^-$ (25:75 and 50:50) can promote growth and photosynthesis, ultimately enhancing the shade tolerance ability of soybean (Raza et al. 2021).

### Chemical control

Recent studies have investigated the effects of various plant growth regulators on mitigating the negative effects of shade stress on soybean growth. These findings provide valuable insights for developing effective strategies to reduce the negative impact of shade on soybean growth and yield. For instance, the application of 1-N-naphthylphthalamic acid (NPA), an auxin transport inhibitor, was found to reduce cytokinin levels and the mitotic frequency during early stage of cell expansion in shade, implying that cytokinin may inhibit shade-induced leaf area decrease (Gong et al. 2021). Additionally, other compounds such as IAA biosynthesis inhibitors 5-(4-chlorophenyl)-4H-1,2,4-triazole-3-thiol (yucasin) and L-kynurenine (kyn), the auxin transport inhibitor 2,3,5-triiodobenzoic acid (TIBA), the GA biosynthesis inhibitor paclobutrazol (PAC), the BR biosynthesis inhibitor brassinazole (BRZ) have been shown to inhibit hypocotyl elongation in shade, indicating their potential to inhibit stem elongation induced by shade (Jiang et al. 2020; Bawa et al. 2020; Lyu et al. 2021). Moreover, the treatment of soybean seeds with appropriate concentrations of uniconazole powder can promote soybean seedling growth, enhance lodging resistance, and increase yield under maize-soybean intercropping systems (Yan et al. 2010). Furthermore, the utilization of Si on soybean leaves has been demonstrated to effectively mitigate the detrimental effects of shade stress in intercropping situations, by enhancing soybean's photosynthetic efficiency and stem durability (Hussain et al. 2021). Similarly, applying lower concentrations of Ti has been shown can improve root morphological parameters, increase biomass accumulation, and enhance photosynthetic efficiency in soybean plants under both normal and shade conditions (Hussain et al. 2019a). These findings provide valuable insights for developing effective strategies to reduce the negative impact of shade on soybean growth and yield.

### Molecular breeding

Molecular breeding is a powerful tool to combat soybean SAS, one of the strategies is the conscious introgression of the desired alleles with the help of marker-assisted selection (MAS) (Vogel et al. 2021; Collard and Mackill 2008). A recent study showed that a total of 75 markers associated with low-light resistance were identified using association mapping, which holds potential for breeding shade-tolerant soybean (Hou et al. 2022). Transgenic technology is another molecular breeding strategy, whereby genes of interest, such as insect resistance or herbicide resistance genes, are introduced into the recipient genome to obtain the desired traits (Kumar et al. 2020). For example, overexpression of the blue light receptor *GmCRY1b* can significantly improve shade tolerance and yield of soybean under high-density planting conditions (Lyu et al. 2021). Another study reported that overexpression of *GmMYB14* resulted in a semi-dwarf phenotype and an increased number of nodes and yield under dense planting conditions (Chen et al. 2021a). Additionally, CRISPR-Cas9 technology can

be utilized to modify genes associated with shade avoidance responses and create shade-tolerant soybean (Yin et al. 2017; Hsu et al. 2014). For instance, knocking out negative components of the blue light signaling pathway in soybean, such as *GmBICs* and *GmCOP1s*, can mitigate or even eliminate the ESE induced by LBL (Ji et al. 2022; Mu et al. 2022).

## Ideotype toward shade-tolerant soybean

Since the mid-twentieth century, breeders have achieved a "Green Revolution" in yield through the use of semidwarf mutants to create dense and lodging-resistant grass crops, including wheat and rice (Peng et al. 1999; Sasaki et al. 2002). However, a similar "Green Revolution" has yet to be achieved for soybean crops due to their more complex and flexible architecture when exposed to light variations in comparison to cereal crops, which only bear one panicle per tiller (Liu et al. 2020). The yield of soybean cannot be readily enhanced by density planting using semidwarf cultivars, which generally have lower node numbers and bear fewer pods (Liu et al. 2020). Given the complexity of soybean yield components, an ideal plant architecture of soybean suitable for high-density planting should possess but not be limited to the following characteristics (Fig. 3):

(1) A strong main stem with shorter internode lengths, higher node number, and insensitive to the fluctuation of light. Notably, a reduction in the light fluence rate, especially blue light, can induce ESE syndrome in soybean (Raza et al. 2019). A stable plant height is required to avoid lodging and ensure an increase in yield with increasing planting density.
(2) Reduced branches, short leaf petioles, small petiole angle and erect leaves to ensure a compact plant stature, good ventilation, and higher light capture efficiency.
(3) Delayed leaf senescence ensures continuous photosynthesis and resistance to disease and supports the growth of pods at the bottom position.
(4) Steeply angled root systems prevent lodging and increase the absorption of water and nutrients.
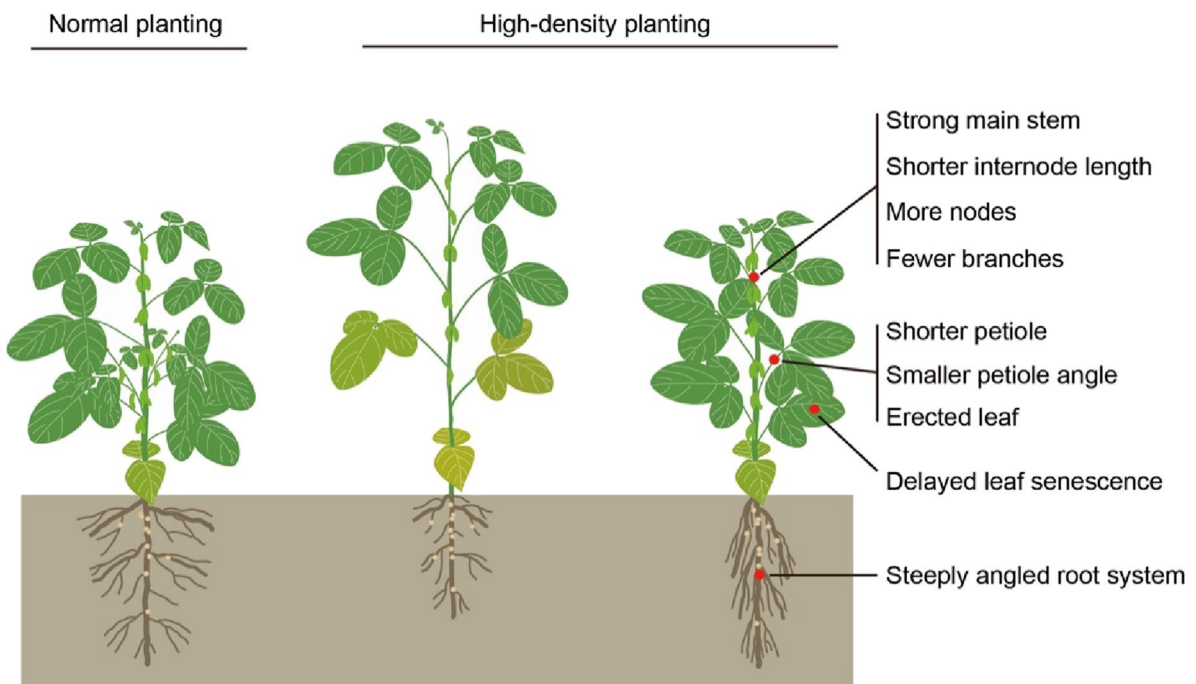


**Fig. 3** Ideal plant architecture of soybean suitable for high-density planting

Comparison of soybean architecture growing at normal (left) and high-density (middle) conditions. A proposed ideal architecture suitable for high-density planting (right)

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