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Molecular control of crop shade avoidance

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The shade avoidance response (SAR) in crops can be detrimental to yield, as precious carbon resources are redirected to stem or petiole elongation at the expense of biomass production. While breeding efforts have inadvertently attenuated this response in staple crops through correlated selection for yield at high density, it has not been eliminated. The extensive work done in Arabidopsis has provided a detailed understanding of the SAR and can be used as a framework for understanding the SAR in crop species. Recent crop SAR works point to auxin as a key factor in regulating the SAR in several crop species. These works also clearly demonstrate that one model for crop SAR will not fit all, and thus we need to move forward with studying the genetic players of the SAR in several model crop species. In this review, we provide the current knowledge of the SAR as reported at the physiological and molecular levels.

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Introduction

For plants adapted to open ranges, encroaching neighbors are perceived as competitors for light and can induce an adaptive response to escape canopy shade via the elongation of stem and petioles [1–3]. This complex phenomenon, known as the shade avoidance response (SAR), involves the modulation of transcriptional and metabolic networks to support shade-mediated growth. A classical SAR also includes reduced branching, reduced biomass, increased height, decreased leaf number, higher specific leaf area, lower chlorophyll a/b ratio, decreased photoassimilation rates, and reduction in yield per plant [4,6–9,10••,11••,12]. However, induction of the SAR in crops is not without negative consequences — resources are diverted from agronomically important tissues to support stem elongation [9,12].

Ensuring yield stability under an array of environmental conditions is a modern breeding concern in our changing environment [13–16]. While domestication has attenuated the SAR through selection for yield at high density, it has not been fully eliminated [9,11••,12,17–19]. Continuing to reduce the SAR may allow growers to increase plant density in an effort to increase harvest index, or may provide higher yield at current densities. However it has been argued that retaining some shade avoidance plasticity may be beneficial for young crop plants competing with weeds for light [13]. Currently, our knowledge of the crop SAR is limited to its negative impact on biomass or yield, with little understanding of how it is controlled at the genetic and molecular levels. Here we argue that (1) while Arabidopsis has served as an excellent model system to dissect the genetic basis of the SAR, much remains to be gained from this system to better understand how the SAR is negatively regulated and (2) we also must strive to expand our knowledge into important crop species with distinct plant architectures. In this manuscript, we review the current understanding of the molecular control of the SAR in Arabidopsis and in several agronomically important crops.

Arabidopsis as a framework: neighbor perception and signal integration

Plants detect the proximity of their neighbors via alterations in ambient light spectra. In a canopy layer, red-light (R) is absorbed preferentially by chlorophyll. Thus as light passes through the leaf, R is depleted and the spectrum becomes enriched in far-red (FR) light. This alteration of R:FR is perceived by the family of photoconvertible phytochrome photoreceptors [20] with activation of phytochrome by R (~660 nm) and inactivation by FR (~730 nm). The photoconversion of phytochrome is mediated by the covalently attached bilin chromophore; exposure to R converts phytochrome to the active (Pfr) conformation, while FR reverts phytochrome it its inactive, Pr form. Thus, phytochrome exists in a dynamic equilibrium of active and inactive forms with the abundance of each determined by the relative levels of R and FR [21]. This regulation of the phytochrome pool is essential for the proper regulation of growth, as inappropriate or excessive growth can lead to stem lodging or mechanical injury and is detrimental to fitness [4,22].

Under R-rich 'sun' environments, active phytochrome translocates into the nucleus from the cytosol and interacts with and mediates the degradation of the growth promoting

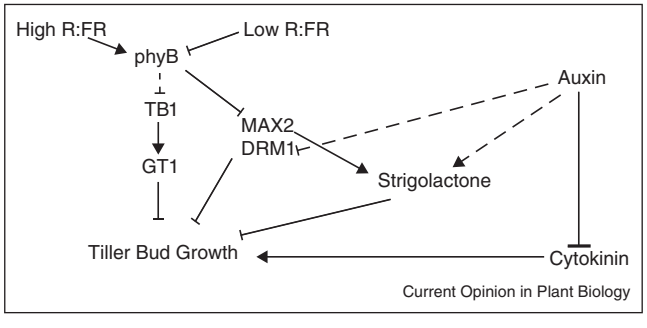
PHYTOCHROME INTERACTING FACTORS (PIFs) [23–27]. This family of bHLH transcription factors acts as the primary hub for a signaling cascade to promote cell elongation [28]. Under 'shade' the active pool of phytochrome decreases, thereby allowing for accumulation of PIFs, namely PIF4, PIF5 and PIF7; which preferentially activate E-box and G-box growth-promoting targets such as those involved in the biosynthesis and transport of auxin, gibberellins, brassinosteroids, cytokinins and ethylene [28–36,37••]. Specifically, auxin modulates cell wall remodeling and cell elongation via regulation of expansins and xyloglucan endotransglucosylase/hydrolases (XTHs) [38–40,41••]. The Arabidopsis SAR model can play an integral role in furthering our understanding of the SAR, and also learning the different mechanisms controlling the SAR employed by different species.

Crop shade avoidance response: physiological and developmental changes

Cereal crops: shoot architecture modification in SAR

In cereals, SAR reduces lateral branching and also can have a negative impact on biomass and grain production [12,42••]. Light mediated regulation of lateral branching, or tillers, is complex involving transcriptional regulators, hormone signaling pathways and cell-cycle regulation [5,42••,43–48]. Figure 1 depicts a proposed model regulating tiller bud growth under shade via phyB in sorghum, a staple crop in Africa and Asia, and a forage and bioenergy crop in North America. phyB is proposed to regulate tiller bud growth via repression of a transcriptional regulator, TEOSINTE BRANCHED 1 (TB1); TB1 activates a class I HD-ZIP transcriptional regulator, GRASSY TILLERS 1 (GT1), which represses tiller production in maize and sorghum [5,45–47]. Thus, in the shade, reduction of phyB activity allows accumulation of TB1 and then GT1, leading to reduced tiller outgrowth [5,45]. These two transcriptional regulators have been identified as major domestication QTL that have altered plant architecture in maize and sorghum [5,49]. For instance, the domestication of maize from teosinte involved selecting for plants with shorter branches and ears at the tips of branches instead of tassels [49]; as a consequence alleles of TB1 with higher expression were enriched during domestication.

Figure 1



Proposed model for tiller bud growth promotion in sorghum. Adapted from Kebrom *et al.* (2010) and Whipple *et al.* (2011). Abbreviations: phytochrome B, phyB; TEOSINTE BRANCHED 1, TB1; GRASSY TILLERS1, GT1; MORE AXILLARY BUD GROWTH, MAX; DORMANCY ASSOCIATED GENE 1 (DRM1).

Tiller bud growth is also repressed indirectly by strigolactone signaling and auxin via repression of cytokinin [45–47,50]. Additional downstream mechanisms implicated in tiller production include MORE AXILLARY BUD GROWTH 1, 2 (MAX1) and MAX2, believed to play a role either in the perception or signal transduction of strigolactones, which act downstream of auxin and upstream of DORMANCY ASSOCIATED GENE 1 (DRM1), a marker negatively correlated with bud outgrowth [46,51,52]. In sorghum, shade increases expression of MAX2. Additionally, in sorghum *phyB* mutants, MAX2 and DRM1 gene expression is elevated, suggesting that shade may also increase the expression of these two genes involved in repression of tiller bud outgrowth [45,50]. Compared to wild-type sorghum, axillary buds of *phyB* mutants show an increase in expression of a cytokinin deactivating gene, cytokinin oxidase/dehydrogenase (CKX1) and also auxin-responsive SAUR genes, suggesting that reduced cytokinin levels and increased auxin response may also regulate axillary bud outgrowth [50]. While it has not been proven in sorghum, DRM1 is negatively regulated by auxin in pea, *Pisum sativum* [45,51].

Tiller reduction under the SAR negatively impacts biomass production for bioenergy crops [42••]. To address this, it has been proposed that biomass production can be increased at high densities via a reduction in shade-induced expression of the aforementioned GT1 [5]. Warnasooriya and Brutnell [42••] argue that the inherent genome size, ploidy and generation time of major bioenergy feed-stocks poses a challenge for crop improvement and thus propose the use of a fast reproducing, diploid, wild crop progenitor, *Setaria viridis* as a model for bioenergy crops for the genetic dissection and manipulation of carbon assimilation pathways under shade. Further, some rice cultivars depend on tiller production to maintain yield potential, suggesting that the negative regulation of tillering under high planting densities has been selected against during domestication of these varieties [45]. Therefore, if we are to modify the SAR in cereals for crop improvement, modifications must be undertaken considering the architectural factors impacting yield in specific cereal crops.

Tomato: internode elongation and leaf development

Recent work in tomato has demonstrated the impact of the SAR on growth, development and leaf morphology, and how these physiological responses are integrated with gene expression [10••,11••,53–55]. Tomato displays organ-specific SAR responses, with the greatest response in the internodes [11••,55]. Cagnola and colleagues [55]

show that shade impacts gene expression patterns differently in each organ. For instance, genes upregulated in the internodes are enriched for cell wall processes while genes involved in photosynthetic translation are upregulated in the leaves. They also showed that Calvin-Cycle genes, and hence stem photosynthetic capacity, are downregulated in stem tissue in response to shade. It is also reported that stem chlorophyll, carotenoid and jasmonic acid content are also reduced in FR treated stems, suggesting that this allows for a reduction in the energetic cost of maintaining a longer stem [55]. These experiments link likely tissue-specific differences in gene expression and metabolism to developmental responses.

Bush and colleagues [11••] report that the SAR varies among wild relatives of the cultivated tomato. Analysis of the *Solanum pennellii* x M82 introgression line mapping population [56] has elucidated the genetic basis for SAR variation in these species. This work showed that the tomato SAR is regulated by both positive and negative repressors of the SAR, as some identified genotypes showed either a greater or reduced shade sensitivity phenotypic response to supplemental FR. Expression quantitative trait locus (eQTL) analysis identified a group of auxin-related genes that were correlated with the SAR. These genes were down-regulated in shade tolerant lines and up-regulated in the shade responders. This result, along with a differential weighted gene co-expression analysis showed that gene connectivity of auxin and light signaling genes were most altered under shade, suggesting that auxin plays a role in natural variation of the SAR in tomato [11••]. Cagnola and colleagues [55] also reported that auxin response genes are upregulated in the internodes compared to the leaves in response to shade, however they show that this does not translate to increased production of indole-3-acetic acid (IAA) within the respective organs. However, if auxin does in fact play a role in mediating cell elongation in the internodes compared to leaf tissue, it may be doing so by modulating organ-specific sensitivity to auxin.

Chitwood and colleagues [10••] performed a meta-analysis on the morphological consequences of short-term or long-term exposure to shade. They report that while leaf area remains plastic to shade signals throughout late development, stomatal index and chlorophyll abundance is determined early in leaf development. Further, they found that alteration of leaf shape under shade is dictated by expression of KNOX and other indeterminacy genes. This study illustrates both developmental plasticity and ultimately the long-lived impact shade can have on plant physiology.

Potato: light signaling and tuber formation

In potato (*Solanum tuberosum*) phyB mediates photoperiodic tuber induction [57,58]. Previous works determined that overexpression of *PHYB* and downregulated expression of *PHYA* results in improved yield and tuberization frequency under shade, respectively [59–61]. Potato is shade responsive, displaying increased internode and stem elongation [62]. This response is mediated by phyB and, in part, by a plasma membrane bound potato SUCROSE TRANSPORTER, (St-SUT4); whose expression is highest in sink organs such as flowers and developing tubers and is circadian regulated [62]. Under shade, St-SUT4 levels are elevated due to stabilization of the St-SUT4 transcript [63,64••]. RNA interference (RNAi) knockdown of St-SUT4 results in reduced plant height, accelerated flowering and increased tuber yield under normal conditions. Further, St-SUT4 RNAi lines were insensitive to low R:FR. In potato St-SUT4, like phyB, is known to repress early flowering and tuber development under long day conditions [59,62]. St-SUT4 RNAi lines did not demonstrate decreased phyB expression, suggesting that St-SUT4 works downstream of phyB to aid repression of early flowering and tuber development [62]. The proposed model implicates St-SUT4 to work upstream of Gibberellic Acid (GA) biosynthesis [62]. While Chinchineska and colleagues [62] did not investigate tuber yield of the RNAi St-SUT4 lines under 'shade', they did show that knockdown of St-SUT4 results in increased tuber yield under green-house conditions in spite of decreased leaf production. This work shows that modifying genes downstream of phyB may be useful in the modification of the SAR and can also improve yield characteristics in potato.

Sunflower: organ specific responses and hormone production

Under low R:FR, sunflower plants divert their carbon resources into stem elongation rather than seed yield [9]. Investigation of the effect light quality has on hormone abundance in sunflower showed that increased levels of GA and IAA phytohormones were positively correlated with stem elongation, but not leaf growth — suggesting that the leaf can act as an additional source of hormone production and that hormones are transported to areas of active stem elongation [65].

Legumes: auxin and cultivar-dependent SAR

Soybean

Soybean, *Glycine max*, mounts a classic shade avoidance response including elongated internodes, reduced branching, reduced biomass, increased height, decreased leaf number, higher specific leaf area, lower chlorophyll a/b ratio, decreased photoassimilation rates, and reduction in per-plant yield in the OAC 1-26 soybean background [6–8]. In corroboration with studies performed in maize, this reduction in yield on a per plant basis does not significantly alter the harvest-index (seed weight divided by total biomass) because both total biomass and total seed weight are reduced proportionally [9,7]. Other soybean SAR studies using the AG1631, Harosoy, and Maple Presto cultivars have shown that the SAR can be cultivar dependent. For instance, one particular study led by

Cober and colleagues [66], showed that shade delays, rather than accelerates, flowering in the tested cultivar, and Horvath and colleagues [67•] report that 'shade' decreases, rather than increases, plant height in AG1631.

Working with the AG1631 cultivar, Horvath and colleagues [67•] also investigated the effect of weed-crop competition on the mRNA expression levels of the soybean *PIF3a*, and found that *GmPIF3a* is strongly upregulated in response to weed competition, and that removal of competition reduces *GmPIF3a* levels. While this result suggests the involvement of the PIFs in the SAR in other species, it should be noted that plant stature was reduced in response to competition, suggesting that if *GmPIF3a* is functions in the light-signaling pathway, it may be a repressor of growth, contrasting with the role of PIF3 in Arabidopsis. Additionally, it should be noted that Arabidopsis PIFs are post-transcriptionally regulated; if the same is true in soybean then transcriptional abundance may not be relatable to PIF protein levels [28].

Lotus japonicus

Auxin has also been shown to be a key regulator of the SAR in the model legume species, *Lotus japonicus*. Not only does *L. japonicus* display several of the classical shade avoidance syndromes including elongated internodes, early flowering, and reduction in lateral branching, but homologs of known SAR auxin regulatory factors, an Arabidopsis homeobox domain-containing transcription factor, *ATHB2*, and *IAA29*, are upregulated under shade [32,68–70].

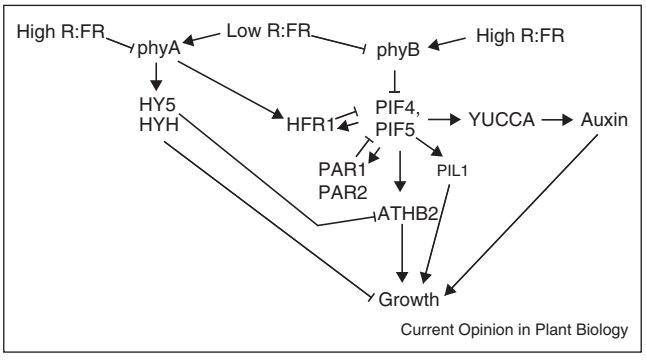
Conserved and unique manifestations of SAR across plant species

In both monocots and dicots, shade inhibition of axillary bud growth is mediated by the transcriptional regulator TB1 (monocots) and its homologs BRC1 and BRC2 (dicots) [46,71]. Similar to monocots, auxin and strigolactones inhibit axillary bud growth in Arabidopsis and play antagonistic roles with respect to growth-promoting cytokinins (Figure 1) [30,71–73]. The similarity of bud outgrowth inhibition in response to shade between these two systems shows that this genetic mechanism is organ-specific and also may be conserved across species. However, it has not been reported whether an Arabidopsis GT1 homolog is also implicated in the axillary bud growth, suggesting that this might be monocot-specific regulator involved in this process. Additionally, abscisic acid (ABA) is also involved in inhibiting bud outgrowth under shade conditions in Arabidopsis, a pathway that has not been demonstrated to date to control tiller outgrowth in monocots [50,74]. Currently, little work has demonstrated the role that the PIFs have outside of Arabidopsis. In rice, *Oryza sativa*, six PIF-like (PIL) homologs have been identified [75]. OsPIL15 has been shown to play a role in seedling photomorphogenic responses, and has also been shown to play a role in mediating red and far-red light responses [76]. However, it has not been well documented what role the PIFs, HFR1 and PAR1 and PAR2 play in crop mediated SAR responses as known from Arabidopsis studies. An example of a species-specific response is tomato. It is well accepted that Arabidopsis SAR includes an increase in the production of auxin. However, while auxin responsive genes may be differentially expressed in tomato, this is not reflective of an increase in auxin production in shade, suggesting differences in sensitivity to auxin if this hormone is in fact playing a role in mediating tomato SAR [55]. One of the challenges that we currently face as a community moving into new model systems is that we can be limited in our interpretation and understanding of species-specific responses based on Arabidopsis gene annotation or the ability to functionally test newly discovered genes within the model crop system.

Dissecting negative regulation of the SAR

One way that we can potentially increase yield through higher crop-planting densities is to finely dissect and enhance the negative regulation of the SAR, thereby reducing shade sensitivity. In Arabidopsis, the negative regulation of SAR serves as a means to prevent untimely or excessive SAR, which can negatively impact plant fitness [1,2]. PIF4 and PIF5 have been shown to activate several of their own negative regulators, including LONG HYPOCOTYL IN FAR-RED LIGHT-1 (HFR1), PHYTOCHROME RAPIDLY REGULATED-1 (PAR1) and its homolog, PAR2 [30,34,77]. Figure 2 depicts two independent modes of negative regulation of the SAR in Arabidopsis. HFR1 and PAR1, 2 homologs negatively regulate the SAR via the formation of heterodimers with PIF4, PIF5 and PIF3-LIKE1 (PIL1) that inhibit the transcriptional activators ability to bind to DNA [31,34,77–79]. The phyA signaling pathway is also involved

Figure 2



Negative regulation of the shade avoidance response in Arabidopsis. Abbreviations: ELONGATED HYPOCOTYL 5HYH; HY5 HOMOLOGHYH; PHYTOCHROME INTERACTING FACTOR, PIF; PIF3-LIKE 1, PIL1; LONG HYPOCOTYL IN FAR-RED LIGHT 1, HFR1; PHYTOCHROME RAPIDLY REGULATED (PAR); *Arabidopsis thaliana* homeobox domain 2, ATHB2; flavin monooxygynase-like enzyme, YUCCA.

in the negative regulation of the SAR in Arabidopsis, through the repression of ATHB2 via ELONGATED HYPOCOTYL 5 (HY5) and also activation of HYH, homolog of HY5, and HFR1, which also acts to repress hypocotyl growth under shade [80••,81] (Figure 2).

These negative regulatory responses are likely to be critical in multiple plant species, but it is unclear whether the PIFs or the known negative regulators are similarly implicated in mediating shade responses in the sampled crop species discussed in this review. Identification of shade tolerant lines suggest that tomato also has a means to negatively regulate the SAR, which could pose an advantageous model for other Solanaceous crops [11••]. It is possible that Arabidopsis has not been exhausted as a resource to define the genes playing a role in the negative regulation of the SAR. Shade-tolerant accessions of Arabidopsis [82] may also prove useful in determining these other factors as they may contain alternative pathways to HFR1/PAR1.

Developmental consequences of the SAR

The genetic control of the SAR can vary based on the developmental time at which SAR is induced. For instance, while auxin is implicated in the SAR during seedling, juvenile and flowering stages, jasmonic acid only affects petiole elongation and promotion of flowering under shade [83••]. Additionally, the tissues collected for gene expression as reported by Cagnola and colleagues [55] and Bush and colleagues [11••] come from two distinct developmental time points; the former study sampled mature internode and leaf tissue, whereas the latter study sampled young, expanding tissues. This may explain why the Calvin-Cycle genes were not differentially expressed in the Bush and colleagues [11••] study.

Preferred targets for plant breeding: light signaling and the SAR

Targeting the light-signaling pathway for crop improvement has been the focus of several lines of research. As reviewed in Gururani [59], one early approach was to increase expression levels of phytochrome. Ectopic expression of *PHYA* and *PHYB* increases plant's sensitivity to light and can have dramatic pleiotropic effects. For instance, over-expression of *PHYA* and *PHYB* results in dark green, dwarfed plants in several species [59]. However, overexpression of *PHYB* and down-regulation of *PHYA* has a positive effect on tuber yield in potato [59,61] Additionally, overexpression of *PHYA* improves shade tolerance in turf grass [59,84]. Overexpression of *PHYA* in other crop species like tomato leads to darker fruit pigmentation that can also alter fruit quality characteristics [59,85]. Thus, ideal targets for the attenuation of the shade avoidance response in crop species would be those that have *less pleiotropic* effects and which likely act downstream of phytochrome. For instance, specific downstream light signaling integrators such as PIF4, PIF5, HFR1 and PAR1, PAR2 homologs (Figure 2) could be attractive candidates for targeting via genetic engineering or breeding. Loss of function Arabidopsis PIF mutants are less sensitive to far-red light than wild type [86]. HFR1 is known to bind to PIF4 thereby preventing PIF4 from binding to its growth-promoting targets; as a consequence, overexpression of HFR1 in Arabidopsis results in dwarfed plants [87], illustrating the potential for HFR1 as a bioengineering or breeding target. However, overexpression of HFR1 is not without consequence; although overexpression of HFR1 does not alter developmental processes like flowering time, it does result in plants with reduced chlorophyll content [87,88•]. Additional preferable target genes for increasing crop production at high densities will be species and cultivar-dependent as well as dependent on plant architecture. For instance, Whipple and colleagues 2011 suggested that fine-tuning the expression levels of GT1 may offer an advantageous avenue for improving crop yield. For biofuel and feedstock crops, it is possible that decreasing expression of GT1 will allow for an increased production of tillers and therefore biomass production under high density planting [5].

Interaction of light signaling, the SAR and biotic stress

Not only is phyB necessary to modulate appropriate growth responses, it is also necessary for the maintenance of plant innate immunity and defense against herbivory. *phyB* mutants and FR-treated plants show that the immune response can be weakened because of the corresponding decreased response to jasmonic acid and salicylic acid [89]. Thus an added benefit of controlling the SAR can indirectly improve biotic resistance.

Is there such a thing as a 'model' organism to study the SAR?

Arabidopsis SAR studies can still enhance our understanding of the regulation of the SAR mainly because of the wealth of resources available within that particular system. To date, we have a solid framework of how the SAR promotes growth, but little knowledge of the mechanisms that confer shade tolerance. To this end, the natural variation present among Arabidopsis can be used to discover additional genes mediating shade tolerance, and provide an additional framework for studying potential shade tolerance homologues in crop species. However, finding a 'one-general model fits all' will be difficult, mainly because not all crops are grown under the same circumstances, not all plant growth traits are of equal agronomic value across several crop species, and the models we develop in crop plants must reflect that.

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- • of special interest
- •• of outstanding interest

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This study shows the developmental impact that long-term and short-term shade has on plant development and morphology. They performed a sun-to-shade, shade-to-sun swapping experiment and showed that chlorophyll accumulation and cell patterning events such as stomatal index were reduced in shade plants, even when shade was a short-term event. They performed a network analysis of expressed genes in the developing primordia, and found that the KNOX and other indeterminacy genes were implicated in establishing leaf shape of shade leaves. However, they found that leaf area was among one of the most plastic traits measured, with short-term shade bearing minimal impact on leaf area.

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This work is the first to report on the genetic basis of natural variation of the shade avoidance response in tomato. They took a quantitative trait loci mapping approach and performed phenotypic screens of several traits and also investigated gene expression profiles of the mapping population. Their work not only revealed shade sensitive or shade tolerant genotypes, but they also found organ specific responses to shade in the internodes and petioles among select genotypes. Gene expression analysis showed that regulation of auxin might be a key player in the variation of the shade avoidance response in tomato.

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