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Review

Multiple pathways in the control of the shade avoidance response

Giovanna Sessa[1], Monica Carabelli[1], Marco Possenti[2], Giorgio Morelli[2] and Ida Ruberti[1*]

[1] Institute of Molecular Biology and Pathology, National Research Council, P.le A. Moro 5, 00185 Rome, Italy; giovanna.sessa@uniroma1.it, monica.carabelli@uniroma1.it, ida.ruberti@uniroma1.it

[2] Research Centre for Genomics and Bioinformatics, Council for Agricultural Research and Economics (CREA), Via Ardeatina 546, 00178 Rome, Italy; marco.possenti@crea.gov.it, giorgio.morelli.crea@gmail.com

*Correspondence: ida.ruberti@uniroma1.it; +39 06 49912211

Abstract: Plants have evolved two opposing strategies in response to competition for light: shade tolerance and shade avoidance. To detect the presence of neighboring vegetation, shade-avoiding plants have evolved the ability to perceive and integrate multiple signals. Among them, changes in light quality and quantity are central to elicit and regulate the shade avoidance response. Here, we describe recent advances in the understanding of photoperception and downstream signaling mechanisms underlying the shade avoidance response, focusing on Arabidopsis because most of our knowledge derives from studies conducted in this model plant. Shade avoidance is an adaptive response, resulting in phenotypes with high relative fitness in natural dense communities. However, it contributes to reduction in crop plant productivity, and the design of new strategies aimed at attenuating shade avoidance in a stage- and/or organ- specific manner in high-density crop plantings is a major challenge for the future. For this reason, in this review, we also report on recent advances in the molecular description of the shade avoidance response in crops, such as maize and tomato, and discuss similarity and differences with Arabidopsis.

Keywords: Arabidopsis; auxin; HD-Zip transcription factors; light environment; photoreceptors

1. Introduction

To grow and develop appropriately, all organisms need to perceive and elaborate information from their environment, and to respond accordingly. As sessile organisms, plants have evolved complex and sophisticated mechanisms to sense and respond to the presence of neighboring vegetation. Plants have evolved two opposing strategies in response to competition for light: shade tolerance and shade avoidance. Shade-tolerant plants have adapted their photosynthesis to function optimally under Low-light conditions, and are therefore able of long-term survival and reproduction under a canopy shade [1-3]. To detect the presence of neighbors, shade-avoiding plants use multiple cues [4]. However, among them, changes in light quantity and quality play a central role in the regulation of the shade avoidance response. Light reflected or transmitted through vegetation is depleted in blue (B), red (R) and UV-B wavelengths which are absorbed by photosynthetic tissues. Hence, the reflected or transmitted light is enriched in green (G) and far-red (FR), resulting in reduced ratios of R/FR light and B/G light. Plants sense these differences through multiple photoreceptors, which in turn trigger signaling cascades to regulate plant growth under suboptimal light environments [5-8].

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In Arabidopsis, a typical shade-avoiding plant, the shade avoidance response at the early stage of seedling development consists of hypocotyl elongation, reduction of cotyledon and leaf lamina growth, and diminution of root development (Figure 1). Here, we describe key pathways underlying the shade avoidance response focusing mainly on Arabidopsis, because most of the molecular mechanisms regulating this response have been identified in this model plant.

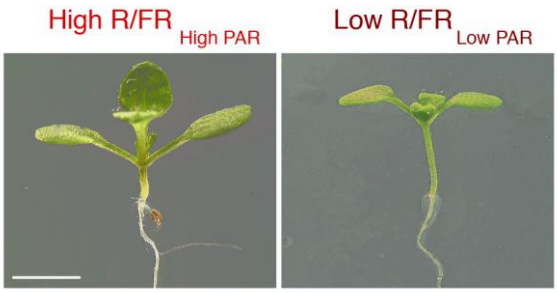

Figure 1. Shade avoidance phenotypes in Arabidopsis seedlings. Seedlings were grown for 4 days in High R/FR $_{\text{High PAR}}$ and then maintained in High R/FR $_{\text{High PAR}}$ or transferred to Low R/FR $_{\text{Low PAR}}$ for 6 days in 16 h light/8 h dark photoperiod to simulate, respectively, sunlight and shade. Light outputs in High R/FR $_{\text{High PAR}}$ and Low R/FR $_{\text{Low PAR}}$ were as previously reported [9]. Scale bar, 2 mm.

2 Perception of Shade Light Signals by Photoreceptors

The R/FR ratio is a highly accurate indicator of plant proximity, and probably for this reason, for many years shade avoidance research mostly focused on phytochrome signaling of changes in the R/FR ratio. However, an ever-increasing body of evidence highlights the significance of the reduced irradiance and the blue/green ratio as signals which play important roles in activating plant responses to canopy light [5-8].

2.1 Phytochromes

Phytochromes are photochromic biliproteins that exist in two photo-convertible isoforms: a R-light-absorbing form (Pr) and a FR-light-absorbing form (Pfr). They exist as dimers with each monomer consisting of an apoprotein covalently attached to a tetrapyrrole chromophore, phytochromobilin. Phytochromes are synthesized in the dark in their inactive Pr form. Upon absorption of red light, Pr is converted into the biological active Pfr form which can absorb FR light and switch back to Pr, resulting in a dynamic photoequilibrium between the two forms of phytochrome. Following conversion to the Pfr form, phytochromes translocate to the nucleus [5, 10].

The phytochrome apoproteins are encoded by a small gene family in most plant species. In Arabidopsis, they are encoded by five genes, *PHYA-PHYE*. *PHYE* likely originated from a duplication within the *PHYB* lineage at early stages of dicots evolution. *PHYD*, which encodes a protein closely related to *PHYB*, presumably emerged from a gene duplication within the Brassicaceae [11]. *PHYC* probably arose from a duplication within the *PHYA* lineage [11]. phyA is rapidly degraded in its Pfr form and signals during photoconversion between Pr and Pfr form. phyB-E are relatively stable in the Pfr form, and control several growth and developmental responses [5, 10, 12].

Among the light-stable phytochromes, phyB has a predominant role in the control of the shade

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avoidance response. However, evidence exist that phyD and phyE act redundantly with phyB in promoting shade-induced elongation [12, 13] (Figure 2). By contrast, phyA attenuates the elongation response induced by Low R/FR light [9, 14-16] (Figure 2).

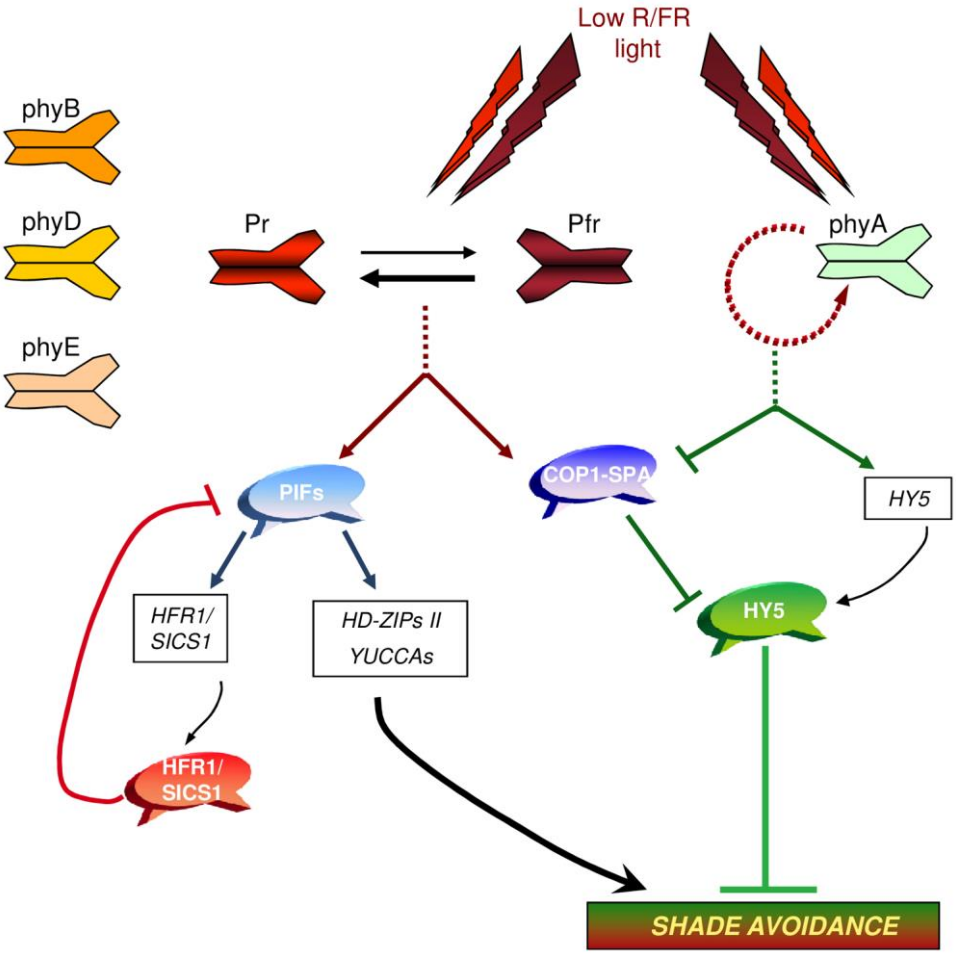

Figure 2. Regulatory networks in the shade avoidance response. Changes in the R/FR ratio are perceived by multiple phytochromes (phyB, phyD, and phyE) and result in a shift of the photoequilibrium between the Pr and Pfr forms toward Pr which, in turn, leads to an increase in the level and/or activity of several PIF proteins. These changes in PIFs rapidly induce the transcription of genes encoding positive (HD-Zips II and YUCs) and negative (HFR1/SICS1) regulators of the shade avoidance response. By forming non-functional heterodimers, HFR1/SICS1 inhibits PIF activity avoiding an exaggerated response to Low R/FR. Shade avoidance is further attenuated by phyA which positively regulates *HY5*, a central regulator of de-etiolation. phyA and phyB oppositely affect the activity of COP1/SPA complexes.

In the nucleus, phytochromes physically interact with a subfamily of basic helix-loop-helix (bHLH) proteins, the PHYTOCHROME-INTERACTING FACTORS (PIFs), controlling several aspects of plant growth and development [17-19]. The Arabidopsis genome encodes eight PIF/PIF-like proteins – PIF1, PIF3-8, PIL1/PIF2 –, all containing a conserved Active Phytochrome B Binding (APB) domain, required for the interaction with the Pfr form of phyB. PIF1 and PIF3 also contain an Active Phytochrome A Binding (APA) domain, necessary and sufficient for binding the Pfr form of phyA. Most of the PIFs promote growth whereas PIF6 and PIL1/PIF2 seem to have an

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opposite function [20]. PIF proteins have both redundant and distinct functions at different stages of plant development, and coherently only a subset of target genes is regulated by multiple PIFs (PIF1, PIF3-5) [20]. PIFs bind to promoter regions enriched in the DNA motif G-box (CACGTG) and the E-box variant (CACATG and CATGTG), called the PBE-box (PIF binding E-box) [18]. However, the mechanisms by which different PIFs bind distinct set of target genes is largely unknown. Interestingly, it has been recently shown that the promoters of PIF1 target genes are enriched with G-box coupling elements (GCEs), which bind PIF1-interacting transcription factors (PTFs). These interactions may contribute to the targeting of PIF1 to specific sites in the genome [21].

In most cases, the interaction of PIFs with phyB in the nucleus leads to PIF's phosphorylation, ubiquitination, and degradation via the 26S proteasome, with degradation half-times in the range of 5 to 20 min [17]. PIF3, PIF4 and PIF5 protein levels increase rapidly in green seedlings upon exposure to Low R/FR light [22, 23]. Interestingly, PIF7 is not rapidly degraded upon interaction with phyB in High R/FR light but accumulates in a phosphorylated form. Exposure to Low R/FR results in a rapid decrease of the amount of phosphorylated PIF7 with a concomitant increase in the level of dephosphorylated PIF7 [24]. PIF1, PIF3, PIF4, PIF5, and PIF7 have all been directly implicated in the shade avoidance response [22-25]. Shade-induced elongation response is indeed significantly attenuated in *pif4 pif5*, *pif1 pif3 pif4 pif5* quadruple (*pifq*) and *pif7* loss-of-function mutants [22-24].

Interestingly, PIF proteins directly control the expression of both positive and negative regulators of the shade avoidance response [5-8, 26] (Figure 2).

Among the positive regulators is the Homeodomain-Leucine Zipper (HD-Zip) *ARABIDOPSIS THALIANA HOMEOBOX2* (*ATHB2*) transcription factor gene, functionally implicated in the elongation response provoked by light quality changes [27, 28]. The transcript levels of the *ATHB2* gene increase within a few minutes of Low R/FR exposure and fall very rapidly upon transfer from Low R/FR to High R/FR [29]. phyB, phyD, and phyE are all involved in the regulation of *ATHB2* by light quality changes [30]. *ATHB2* induction by Low R/FR does not require *de novo* protein synthesis [31] and is significantly reduced in loss-of-function *pif* mutants (*pif4 pif5*; *pifq*) [22, 32]. Furthermore, there is evidence that *ATHB2* is recognized *in vivo* by PIF5 [25]. Relevantly, among the positive regulators are also several auxin biosynthesis *YUCCA* (*YUC*) genes, thus directly linking the perception of light quality changes to plant growth [24].

Among the negative regulators of shade avoidance controlled by PIF proteins is LONG HYPOCOTYL IN FAR RED 1/SLENDER IN CANOPY SHADE 1 (HFR1/SICS1), an atypical bHLH protein. *HFR1/SICS1* is rapidly induced by Low R/FR, and there is evidence that it is a direct target of PIF5 [25, 33, 34]. Prolonged exposure to Low R/FR leads to the accumulation of HFR1/SICS1 and the formation of non-active heterodimers with PIF4 and PIF5 [33, 34]. Consistently, several genes rapidly and transiently induced by Low R/FR are up-regulated in loss-of-function *hfr1/sics1* mutants under persistent shade [33, 35]. Moreover, *hfr1/sics1* plants display an exaggerated shade avoidance response whereas transgenic seedlings overexpressing a stable HFR1/SICS1 protein have suppressed elongation [33, 36]. Another atypical bHLH protein gene, *HELIX LOOP HELIX1/PHYTOCHROME RAPIDLY REGULATED1* (*HLH1/PAR1*) [31, 33], also acts as a negative regulator of the shade avoidance response. It is rapidly regulated by Low R/FR light, and its induction does not require de novo protein synthesis. HLH1/PAR1 has been proposed to act as a dominant-negative antagonist of bHLH transcription factors including PIF4 [36-39].

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Attenuation of shade avoidance responses also involves Low R/FR stimulation of phyA signaling [9, 40, 41] (Figure 2). The *PHYA* gene is early induced by Low R/FR, and phyA is required for the up-regulation of the basic leucine zipper (bZIP) transcription factor gene, *ELONGATED HYPOCOTYL 5 (HY5)*, a central regulator of photomorphogenesis [42]. HY5, on one hand, down-regulates genes early induced by Low R/FR light and, on the other hand, positively regulates photomorphogenesis-promoting genes upon prolonged exposure to shade [9]. Evidence exists that HY5 interacts with PIF proteins [43, 44].

phyA in its active form directly interacts with SUPPRESSOR OF PHYA-105 (SPA) proteins and inhibits their interaction with CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1) [45]. The COP1/SPA complexes are part of the CULLIN 4-DAMAGED DNA BINDING 1 ubiquitin E3 ligase complex (CUL4–DDB1$^{COP1/SPA}$) and are required for substrate recognition [46]. Several positive regulators of photomorphogenesis, including HY5 and HFR1/SICS1, are targeted for 26 proteasome-mediated degradation by CUL4–DDB1$^{COP1/SPA}$ [41]. The active form of phyA also interacts with COP1, and it has been recently proposed that binding of phyA to SPA proteins results in rearrangement of the interactions within the COP1/SPA complex rather than in its dissociation [45]. Evidence exist that direct interaction of COP1 and SPA proteins is relevant for the activity of CUL4–DDB1$^{COP1/SPA}$, and it has been therefore proposed that binding of phyA to SPA proteins inactivates CUL4–DDB1$^{COP1/SPA}$ which in turn results in the stabilization of positive regulators of photomorphogenesis [41] (Figure 2). phyB in its active form has also been shown to bind to SPAs and inhibit their interaction with COP1 [45] (Figure 2). The analyses of loss-of-function *cop1* and *spa1-4* mutants in Low R/FR indicate that the COP1/SPA complex is essential for shade-induced elongation [47, 48]. It has been suggested that in Low R/FR, reduced levels of the active form of phyB indirectly enhance PIF activity increasing COP1/SPA-mediated degradation of negative regulators of shade avoidance response [48, 49]. Together the data indicate that phyA- and phyB-mediated control of COP1/SPA activity oppositely affects the levels of negative regulators of shade avoidance such as HY5, HFR1/SICS1, PAR1 and members of the BBX transcription factor family [50-52].

2.2 Cryptochromes

Cryptochromes are flavoprotein photoreceptors first identified in Arabidopsis, and subsequently found in prokaryotes, archaea, and many eukaryotes [53]. Cryptochromes (CRY) are structurally related to photolyases that catalyze light-dependent DNA repair [54]. The Arabidopsis genome encode two cryptochromes, CRY1 and CRY2. They consist of two domains, the PHR (photolyase-homologous region) domain, required for photoperception and dimer formation, and the CCE (cryptochrome C-terminal extension) domain, involved in signal transduction to downstream factors. It has been proposed that cryptochromes are activated by blue light through conformational changes, mostly in CCE domains [55]. CRY2 is rapidly degraded by the 26 proteasome system subsequent to blue light activation, whereas CRY1 is stable [54].

Both CRY1 and CRY2 are involved in Low Blue Light (LBL)-induced shade avoidance response [56-58]. Interestingly, it has been recently demonstrated that PIF4 and PIF5 activity is required for LBL-induced hypocotyl growth, and evidence has been provided that these PIFs physically interact with CRY1 and CRY2 [58, 59]. Furthermore, CRY2 has been shown by chromatin immunoprecipitation sequencing to bind to PIF4 and PIF5-regulated gene promoters [58]. Transcriptomic analysis revealed different expression profiles in Low R/FR- and LBL-treated

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seedlings. Relevantly, LBL, differently from Low R/FR, does not involve changes in auxin levels and sensitivity, further supporting the proposal that phy and CRY photoreceptors control plant responses to shade via largely independent pathways [56-58].

Analogously to the active form of phyB, photoexcited CRY1 has been shown to bind SPA1, resulting in suppression of the SPA1–COP1 interaction. This in turn reduces COP1 activity, leading to increased levels of transcription factors such as HY5 [60].

2.3 UVR8

UV-B light is strongly filtered by plant canopies, thus providing further information on plant density [6, 61]. In Arabidopsis, inhibition of hypocotyl elongation by UV-B light depends on the UV-B receptor UVR8 [62, 63]. UVR8 in its dimeric form perceive UV-B light; absorption of UV-B induces instant monomerization of the photoreceptor and interaction with COP1. This, in turn, promotes accumulation of HY5 and its close relative HY5 HOMOLOGUE (HYH) [64-66]. UVR8 promotes gibberellic acid (GA) degradation in a HY5/HYH-dependent manner, contributing to stabilization of DELLA proteins and consequent formation of inactive DELLA-PIF complexes [67]. Furthermore, evidence exist that UV-B also enhances the degradation of PIF4 and PIF5 [67]. Together the data indicate that UV-B light inhibits PIF function, thereby attenuating plant responses to canopy shade [67, 68].

3 Auxin in the Control of the Shade Avoidance Response

There is a large body of evidence showing that plant responses to shade involve changes in hormonal pathways. Here we focus on auxin whereas for other hormones involved in the shade avoidance response we recommend recent reviews [69, 70]. Auxin has a key role in many aspects of the shade avoidance response, such as increased elongation of stem-like organs (including hypocotyl and petioles), reduced leaf and root growth. Auxin homeostasis, transport and signaling are all regulate in response to shade [35, 71]. Interestingly, it has been shown that whereas the increase in auxin synthesis is a major event at the early stages of shade avoidance, persistence of shade mainly result in modulation of auxin sensitivity [25, 72-74].

3.1 Auxin Homeostasis

The levels of auxin in the shoot upon exposure to Low R/FR light increase rapidly [24, 25, 75]. New auxin is synthesized in cotyledons from tryptophan (Trp) through TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS 1 (TAA1), an enzyme encoded by the *SHADE AVOIDANCE3* (*SAV3*) gene [75, 76]. Trp is converted to indole-3-pyruvic acid (IPA), and IPA is converted to indole-3-acetic acid (IAA) through the action of a family of flavin monooxygenases encoded by the *YUCCA* (*YUC*) gene family [77-80]. *YUC2*, *YUC5*, *YUC8*, and *YUC9* are induced by Low R/FR in a PIF-dependent manner [24, 75]. Furthermore, the *sav3* mutant and the quadruple *yuc2 yuc3 yuc8 yuc 9* mutant are impaired in Low R/FR-induced responses [75, 81, 82].

Low R/FR further controls auxin levels by regulating auxin inactivation. Several auxin-inducible genes of the Gretchen Hagen 3 (GH3) family have been shown to be early up-regulated by Low R/FR [14, 83]. GH3 proteins are known to promote the conjugation of free IAA to different amino acids, likely reducing the pool of free IAA [84], and it has been reported that plants with altered levels of GH3 proteins display defects in light-mediated hypocotyl elongation responses [85, 86]. Furthermore, it has been recently shown that loss-of-function of *VAS2*

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[*IAA-amido synthetase* (*GH3.17*)] results in an increase in free IAA at the expense of IAA-glutamate in the hypocotyl epidermis. Interestingly, the *vas2* mutants display longer hypocotyls in response to Low R/FR light largely independently of the novo IAA biosynthesis in cotyledons, demonstrating the relevance of local auxin metabolism to modulate IAA homeostasis in an organ-specific manner in response to shade [87].

The relevance of local responses is also demonstrated by the recent finding that alteration of the R/FR ratio at the leaf tip induces a hyponastic response (upwards leaf movement) that is restricted to the leaf perceiving the light signal. Evidence have been provided that this response is mediated by auxin synthesized in the leaf blade and transported to the petiole [88a, 88b].

3.2 Auxin Transport

It has been proposed that auxin synthesized in the cotyledons through the TAA1/YUC pathway upon Low R/FR exposure is transported to hypocotyls, leading to promotion of cell elongation [75]. Consistent with this proposal, blocking auxin transport with chemical inhibitors abolishes Low R/FR-induced elongation, highlighting the relevance of auxin distribution for the shade avoidance response [27, 75].

A large body of evidence indicate that polar auxin transport is actively regulated during the shade avoidance response. Low R/FR has been shown to regulate the expression of PIN-FORMED (PIN) auxin efflux carriers PIN1, PIN3, PIN4 and PIN7 [14, 25, 83, 89, 90]. Moreover, it has been observed that the triple loss-of-function *pin3 pin4 pin7* mutant does not elongate under simulated shade [81]. Regulation of ATP-binding cassette B (ABCB) auxin transporters is also required for proper auxin distribution in the hypocotyl in simulated shade [91].

In the hypocotyls Low R/FR also regulates the localization of PIN3 [89], known to play a central role in tropic responses [92, 93]. By analogy to tropic responses, it was proposed almost twenty years ago that elongation growth induced by shade is the result of a laterally symmetric redistribution of auxin [27, 94, 95]. In accordance, it has been subsequently found that Low R/FR promotes PIN3 lateral localization in the endodermal cells toward the outer cells of the hypocotyl [89]. This shade-induced relocalization of PIN3 redirects auxin efflux toward the cortical and epidermal cells of the hypocotyl, promoting cell elongation [89].

Interestingly, it has been recently demonstrated that the regulation of auxin fluxes has a key role in coordinating shoot and root growth in response to light cues [90, 96]. *PIN1* is expressed at low levels in the hypocotyls of dark-grown Arabidopsis seedlings, and it is significantly up-regulated upon light exposure, thus suggesting that light may control shoot-to-root polar auxin transport in the hypocotyl mainly through regulation of *PIN1* expression. Accordingly, it has been shown that *pin1* loss-of-function mutants have reduced root length and defects in the root apical meristem (RAM) analogous to those of plants treated with polar auxin transport inhibitors. Remarkably, the light-mediated regulation of *PIN1* expression in the hypocotyl depends on the action of COP1, which can thus tune shoot-derived auxin levels in the root. This influences root elongation and adapts auxin transport and cell proliferation in the RAM through modulation of PIN1 and PIN2 intracellular distribution in the root in a COP1-dependent manner [96]. In shade conditions, a strong down-regulation of PIN1 in the hypocotyl, along with a concomitant decrease in auxin levels in the RAM, has also been observed, suggesting that Low R/FR light might activate a PIN1-dependent mechanism, analogous to that observed in dark-grown seedlings, to partition auxin between shoot and root [90, 96]. Together the data reveal a dual role for COP1 in the regulation of

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light-mediated root growth, as it regulates both long-distance transport and local RAM fluxes of auxin through different mechanisms [96]. As for the first mechanism, it has been suggested that HY5, one of the best characterized targets of COP1-mediated degradation, might directly regulate *PIN1* transcription in the hypocotyl [96]. Notably, recent work has shown that HY5 is a shoot-to-root mobile signal that mediates light promotion of root growth [97, 98]. Perception of Low R/FR in the shoot also results in a decrease in lateral root (LR) emergence, and it has been proposed that HY5 regulates this process by inhibiting the auxin efflux carrier PIN3 and the influx carrier LIKE-AUX1 3 (LAX3) auxin transporters, which act in concert in the process of LR emergence [98, 99].

3.3 Auxin Signaling

Auxin regulates gene expression through physical interaction with the TRANSPORT INHIBITOR RESPONSE 1/AUXIN SIGNALING F-BOX (TIR1/AFBs) proteins. TIR1/AFBs are auxin receptors and constitute the F-box subunits of the SKP1 CULLIN–FBOX (SCF)-type E3 ligase, $SCF^{TIR1\text{-}AFBs}$. Auxin binding to $SCF^{TIR1AFBs}$ determines the ubiquitination and degradation of the AUXIN/INDOLE-3-ACETIC ACID (Aux/IAA) proteins. Aux/IAAs function as repressors by forming dimers with AUXIN RESPONSE FACTORs (ARFs), and their degradation releases the inhibition on ARF transcription factors [100, 101].

Relevantly, it has been shown that Low R/FR light rapidly and transiently reduces the frequency of cell division in young Arabidopsis leaf primordia through a non-cell-autonomous mechanism that requires the action of TIR1. Consistent with the role of HFR1/SICS1 in the shade avoidance response, the leaf primordium phenotype is enhanced in loss-of-function *hfr1*/*sics1* mutant seedlings in Low R/FR light (Figure 3). The auxin increase perceived through TIR1 induces *CYTOKININ OXIDASE/DEHYDROGENASE 6* (*CKX6*), a gene encoding an enzyme involved in cytokinin degradation [102, 103], which in turn promoting cytokinin breakdown diminishes cell proliferation in developing leaf primordia [83, 104]. Further studies are needed to identify the specific ARF(s) involved in the up-regulation of the *CKX6* gene by Low R/FR.

A number of studies have identified auxin-related genes over-represented among the genes up-regulated by shade in young seedlings [14, 33, 23, 24, 9, 49 81, 105]. Interestingly, a large proportion of these genes are induced simultaneously in cotyledons and hypocotyl, thus indicating that shade-induced elongation depends not only on the cotyledon-derived auxin but also on local hypocotyl signals [81]. Among the auxin-related genes rapidly induced by Low R/FR are several early auxin response genes, particularly members of the *Aux/IAA* and the *SMALL AUXIN UP RNA* (*SAUR*) gene families, thus indicating that a number of ARF proteins contribute to the shade avoidance response. Recent work provided indeed evidence that three ARF proteins, ARF6, NPH4/ARF7 and ARF8, together play a major role in the control of hypocotyl elongation in a Low R/FR environment as well as in response to other signals, including high temperature [106].

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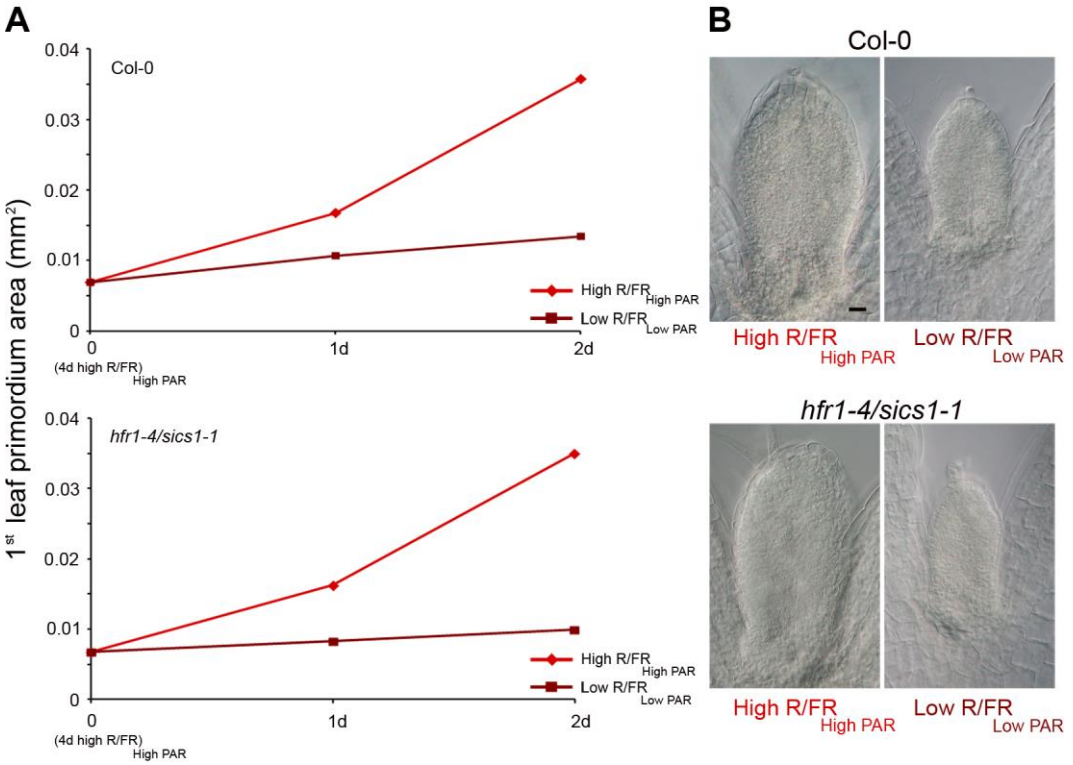

Figure 3. ***hfr1/sics1*** **mutation causes an exaggerated leaf primordium phenotype in shade.** (A) Col-0 and *hfr1/sics1* seedlings were grown for 4 days in High R/FR $_{\text{High PAR}}$, and then maintained in High R/FR $_{\text{High PAR}}$ or transferred to Low R/FR $_{\text{Low PAR}}$ for the indicated times. The mean area of the first/second leaf primordium was determined measuring 50 samples in each condition. (B) Leaf primordia of Col-0 and *hfr1/sics1* grown for 4 days in High R/FR $_{\text{High PAR}}$, and then maintained in High R/FR $_{\text{High PAR}}$ or transferred to Low R/FR $_{\text{Low PAR}}$ for 2 days, observed under DIC optics. Light outputs in High R/FR $_{\text{High PAR}}$ and Low R/FR $_{\text{Low PAR}}$ were as previously reported [9]. Scale bar, 10 μm.

4 HD-Zip Transcription Factors in the Control of the Shade Avoidance Response

The HD-Zip class of transcription factors is unique to plants [107]. HD-Zip proteins bind to DNA exclusively as dimers recognizing dyad symmetric sequences [108-111], and act as positive or negative regulators of gene expression [112]. On the basis of sequence homology in the HD-Zip DNA-binding domain, Arabidopsis HD-Zip proteins have been grouped into four families, HD-Zip I–IV [113]. Each protein family can also be distinguished by the presence of additional conserved motifs, and specific intron and exon positions [114-118]. Phylogenetic and bioinformatics analysis of *HD-Zip* genes using transcriptomic and genomic datasets from a wide range of Viridiplantae species indicated that the HD-Zip class of proteins was already present in green algae [119].

All the four HD-Zip protein families can be further divided into subfamilies containing paralogous genes that have likely arisen through genome duplication, considering their association with chromosome duplicated regions in Arabidopsis and rice [115-118]. Interestingly, members of both the HD-Zip II and HD-Zip III protein families have been implicated in the regulation of the shade avoidance response [112, 120].

Relevantly, HD-Zip II and III binding sites share the same core sequence [AAT(G/C)ATT] [108, 114], thereby suggesting that members of the two families may regulate common target genes [121]. HD-Zip II proteins contain an LxLxL type of ERF-associated amphiphilic repression (EAR) motif [117, 122] and there is evidence that they function as negative regulators of gene expression [27, 121,

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123, 124]. On the contrary, HD-Zip III proteins act as positive regulators of gene expression [111, 121, 125-127].

4.1 HD-Zips II

The HD-Zip II protein family includes *ATHB2*, the first gene shown to be rapidly regulated by changes in the R/FR [29]. Multiple phytochromes are involved in the regulation of *ATHB2* by Low R/FR [29, 30], and it has been demonstrated that *ATHB2* is a direct target of PIF5 [25]. Lack of ATHB2 function results in reduced hypocotyl elongation in Low R/FR whereas the phenotype of seedlings with elevated levels of ATHB2 in High R/FR resembles that of wild type in Low R/FR [27, 28]. The expression of ATHB2, as deduced by the GUS pattern observed in ATHB2::ATHB2:GUS seedlings, is rapidly and strongly induced by shade in all the cell layers of the elongating region of the hypocotyl [28]. Taken together the data indicate that ATHB2 acts as a positive regulator of the shade-induced elongation response.

The HD-Zip II family consists of 10 genes, five of which [*ATHB2*, *HOMEOBOX ARABIDOPSIS THALIANA* (*HAT1*), *HAT2*, *ATHB4*, and *HAT3*] are regulated by changes in the R/FR ratio light [117]. In the *hat3 athb4* double loss-of-function mutant hypocotyl elongation is impaired [128] whereas overexpression of HAT1, HAT2, HAT3, and ATHB4 results in phenotypes similar to those caused by elevated levels of ATHB2 in High R/FR [26, 35, 117, 124, 128], further highlighting the redundancy of these transcription factors in the regulation of the shade avoidance response. Relevantly, homologue genes have been shown to be induced in monocotyledonous and dicotyledonous plants upon exposure to Low R/FR, indicating a conserved function of HD-Zip II transcription factors through evolution [129-131].

Very recent work has shown that prolonged shade results in early exit from proliferation in the first and second leaves of Arabidopsis and that this process requires the HD-Zip II proteins ATHB2 and ATHB4 (Figure 4) [132]. Furthermore, evidence has been provided that the ATHB2 and ATHB4 proteins function as a complex in the regulation of leaf development during shade avoidance, likely forming heterodimers as suggested by yeast two-hybrid assays [132, 133]. Together the data provide new insights on the mechanisms regulating leaf development in shade. However, further work is needed to understand how ATHB2 and ATHB4 transcription factors interact with known regulators of leaf cell proliferation [134, 135].

Links between HD-Zip II transcription factors and auxin have been established [35, 112]. However, how HD-Zip II proteins interact with auxin machineries remains to be investigated.

Interestingly, a growing body of evidence demonstrates that, apart from their function in shade avoidance, HD-Zip II transcription factors control key developmental processes in a sunlight simulated environment, including embryo patterning, shoot apical meristem (SAM) function, leaf polarity and gynoecium development [112, 121, 136-139]. These studies highlight that developmental processes and shade avoidance responses share common transcription factors. Connections between developmental and shade avoidance regulatory networks is further indicated by the recent finding that under shade PIFs directly suppress the expression of multiple *miR156* genes, resulting in increased expression of the *SQUAMOSA-PROMOTER BINDING PROTEIN-LIKE* (*SPL*) family of genes [140], known to play a role in the regulation of several aspects of plant development, including leaf initiation rate, branching, vegetative phase change and flowering time [141].

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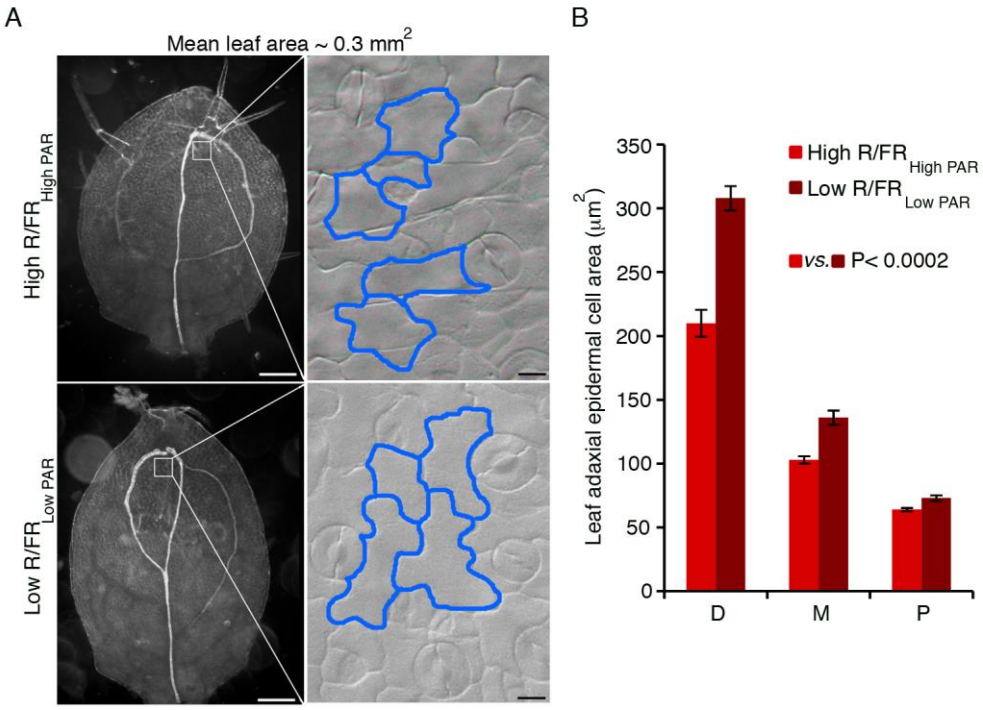

Figure 4. Shade affects adaxial epidermal cell expansion in the Arabidopsis leaf. (A) Dark-field images of cleared first/second leaves of Col-0 seedlings grown for 8 days in High R/FR $_{\text{High PAR}}$ (High R/FR $_{\text{High PAR}}$), or for 4 days in High R/FR $_{\text{High PAR}}$ and subsequently for 5.5 days in Low R/FR $_{\text{Low PAR}}$ (Low R/FR $_{\text{Low PAR}}$), respectively. The insets show a paradermal view of adaxial epidermal cells; the borders of a few cells have been highlighted manually with a blue line. Light outputs in High R/FR $_{\text{High PAR}}$ and Low R/FR $_{\text{Low PAR}}$ were as previously reported [9]. Scale bars: (A), 100 µm; insets, 10 µm. (B) The graph shows the mean epidermal cell area at three positions along the proximo-distal leaf axis, distal (D), median (M) and proximal (P) in High R/FR $_{\text{High PAR}}$ and Low R/FR $_{\text{Low PAR}}$. At least 100 adaxial epidermal cells in 10 leaves were measured for each condition. T-test statistical analysis was performed using QuickCalcs Online Calculators for Scientists (GraphPad Software, Inc. http://graphpad.com/quickcalcs/).

4.2 HD-Zips III

The HD-Zip III protein family consists of five members: ATHB8, CORONA (CNA), PHABULOSA (PHB), PHAVOLUTA (PHV), and REVOLUTA (REV). Several evidence indicate that HD-Zip III transcription factors act as regulators of embryonic apical fate [142], and are required to maintain SAM activity and to establish lateral organ polarity [143, 144]. The expression pattern of the HD-Zip III genes largely coincides with the pattern of auxin distribution [145-151]. Furthermore, HD-Zip III genes are post-transcriptionally regulated by the microRNAs miR165/166, which repress these genes through mRNA cleavage [143, 152].

Interestingly, there is evidence that REV directly regulates the auxin biosynthetic genes *TAA1* and *YUC5*, indicating that at least part of its role in several developmental processes implies the regulation of auxin biosynthesis [111, 153]. Furthermore, it has been recently shown that genes involved in auxin transport, including the influx carriers *LIKE AUXIN RESISTANT 2* (*LAX2*) and *LAX3*, and response are also directly regulated by REV [127, 151, 153, 154].

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Among the gene targets of REV are also *HAT3*, *ATHB4*, ATHB2, and *HAT2*, and there is evidence that *HAT3* is regulated by PHB and PHV [111, 121]. Coherently, the expression pattern of HAT3 and ATHB4 in sunlight essentially coincides with that of PHB, PHV, and REV in the adaxial domain of cotyledons and young leaf primordia, in the vasculature, and in the SAM. The expression of *ATHB2* is restricted to procambial cells at the early stages of embryo and leaf development; however, *ATHB2* is expressed in the domains of *HAT3* and *ATHB4* in *hat3 athb4* double loss-of-function mutants, compensating at least in part for the function of HAT3 and ATHB4 [121].

The direct regulation of *HD-Zip II* genes by HD-Zip III transcription factors and the finding that the phenotypes of multiple loss-of-function *HD-Zip II* mutants (*hat3 athb4 athb2*) in sunlight resemble those of *rev phb phv* indicate that HD-Zip II and HD-Zip III proteins function in the same pathways under a sun simulated environment [112, 120]. Considering that HD-Zip II proteins work as repressors of gene expression [27, 121, 123], it was proposed that, among other possibilities, they may negatively regulate molecules that restrict HD-Zip III expression [112]. Interestingly, it was recently shown that REV, whose expression is restricted to the adaxial side of the leaf through the activity of miR165/166, physically interacts with HAT3 and ATHB4 to directly repress MIR165/166 expression in the leaf adaxial domain [155].

The analysis of HD-Zip III loss- and gain-of function mutants has uncovered the involvement of REV in shade-induced elongation growth. *rev* loss-of-function mutants as well as plants ectopically expressing *MIR165a* display reduced elongation growth under simulated shade, whereas REV gain-of-function mutants (rev10D) have slightly elongated hypocotyls under sunlight conditions [111, 120]. It will be of interest in the future to investigate whether HD-Zip II and HD-Zip III transcription factors act together in the regulation of gene expression under a simulated shade environment.

5 From Arabidopsis to Crops

The yield of a crop somehow depends on its radiation use efficiency and capacity of light interception. At high planting density, the light interception depends on plant architecture, the degree of mutual shading among plants and the genetically defined ability of the plant to react to shading, i.e. producing new leaves or reorienting the leaves towards open light [5]. Indeed, several of the effects of perception of Low R/FR signals appear to be negative for yield. Interestingly, despite breeding programs resulted in new cultivars with increased performance under high planting density, many crops still retain the ability to sense and react to canopy shade. For instance, the sensing and reactions to Low R/FR, including elongation responses, are present in modern commercial hybrids of maize [156-158]. Similarly, the analysis of ten modern Argentinian wheat cultivars revealed that the selection for yield did not reduced the ability to respond to Low R/FR ratio and to diminish the impact of the negative control of productivity [159]. The reduction of these responses may allow to increase plant productivity at higher density or may provide higher yield at current densities. This could be realized through selection of natural variants or mutants, as well as by generation of mutations in critical factor genes by new breeding techniques (NBT) or production of transgenic plants (a.k.a. GMO) expressing specific regulators. The latter two approaches require the identification of key regulatory factors. Arabidopsis is an excellent model system to uncover and dissect mechanisms regulating the shade avoidance response, some of which are likely to be conserved during evolution. However, some important differences are emerging from the analysis of other plant species, recently described in several excellent reviews [160-162]. It

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is clear that we have to expand our knowledge of other plant species, especially those representing crop model plants, both for food and energy production. Effective approaches for studying the dynamics of shade avoidance and for the identification of critical regulators are genome-wide transcriptional analyses, also taking advantage from the genetic diversity of wild and cultivated species and introgression line (IL) populations produced by their crossing. Here, we briefly review the main results obtained in maize and tomato, two economically important mono- and di-cotyledonous crops, respectively.

5.1 Maize

The genome of maize encodes three types of phytochromes (phyA, phyB and phyC) [163]. *PHYB* is encoded by two genes (*PHYB1* and *PHYB2*) derived from an ancient tetraploidization event, and both phytochromes contribute differently to distinct physiological aspects of the shade avoidance response [164]. The *phyB1 phyB2* double mutant exhibits many of the characteristics of a constitutive shade avoidance response, including increased plant height, increased internode length, reduced tillering, and early flowering [164]. Studies in hybrid maize and teosinte using end-of-day far-red (EOD-FR) light treatments suggested that mesocotyl elongation responses were of the same magnitude [158]. However, a comparison between a modern and an old variety suggested that hybrids that are more productive under high density plantings may have a reduced auxin response to changes in light quality [157]. Recent data of a genome-wide expression analysis using the maize B73 elite inbred line support this hypothesis [131]. Interestingly, light conditions mimicking canopy shade identical to those utilized by Ruberti and co-workers to study the process in Arabidopsis [9] were used for the analysis of the shade avoidance response in maize [131]. Consistently, under this light condition, maize seedlings showed an elongated phenotype typical of the shade avoidance response. Thereby, the authors were able to compare the dynamics of the transcriptional reprogramming in the two plant species. Two major important differences, among several others, came out from this analysis. First of all, the *YUC* genes, strongly induced by Low R/FR light in Arabidopsis, were not found regulated in maize. Conversely, *TAA1* was slightly up-regulated in maize seedlings whereas it is down-regulated to some extent in Arabidopsis. Coherently, the Gene Ontology (GO) analysis revealed the lack of an enrichment in auxin response genes among those induced by Low R/FR light. Furthermore, a genome-wide expression analysis in rice also revealed the lack of induction of auxin response genes when the seedlings were exposed to Low R/FR light [165]. Therefore, it seems possible that the auxin response may have a less important role in monocots, or be a peculiarity of the shade avoidance response in dicotyledonous plants, as confirmed by the large amount of data collected [71, 76, 166]. A confirmation of such a hypothesis will require a more systematic analysis of monocotyledonous plant species and their undomesticated ancestors, including teosinte. In addition, the comparison of maize and Arabidopsis transcriptional responses also revealed a very little overlap between the early response genes despite the fact that hundreds of genes are regulated by Low R/FR [131]. In particular, only 20 up-regulated and 11 down-regulated maize genes have orthologous genes similarly regulated by shade in Arabidopsis. In addition, 19 orthologous gene pairs displayed contrasting regulation in response to Low R/FR light. Among the up-regulated orthologous pairs there are *ATHB2* and *GIGANTEA* (*GI*). GI has been implicated in the induction of shade-mediated rapid flowering in Low R/FR [167]. The role of ATHB2 in the shade avoidance response has been discussed earlier in this review and, of interest, it is induced by Low R/FR light in other plant species [130, 165, 168, 169].

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The Arabidopsis *ATHB2* gene is a direct target of PIF proteins [25, 170], and the maize genome encodes for homologs of the Arabidopsis PIF proteins. The overexpression of either ZmPIF4 or ZmPIF5 partially rescues the reduced hypocotyl elongation of the quadruple *pif1 pif3 pif4 pif5* Arabidopsis mutant, and the overexpression of ZmPIF5 in Arabidopsis exhibited a constitutive shade avoidance phenotype [171]. Further studies should clarify if the ZmPIFs have any role in the shade avoidance response, including the up-regulation of *ATHB2*-like maize genes.

5.2 Tomato

Physiological and molecular studies have begun to dissect the effects of neighbor detection and shade avoidance in tomato [130, 168, 172, 174]. As other plant species, tomato plants exposed to Low R/FR elongate more both internodes and petioles. Differently from other species, tomato plants increase the size of the SAM and incipient leaf primordia, and of the leaf blade when exposed to shade. The alteration of leaf morphology has been observed both in cultivated [130] and wild species [175]. Molecular studies have begun to highlight specific patterns of gene expression in leaf and stem. Particularly significant is the differential regulation of genes involved in photosynthesis in leaf and stem, being up- and down-regulated, respectively [168]. As in the case of maize, the domestication of tomato results in plants which exhibit a reduced shade avoidance response compared to wild tomato species. By mean of the introgression analysis of a population arising from a cross between the cultivated tomato M82 and the wild relative *Solanum pennellii*, several loci have been found to affect the strength of shade avoidance, either positively or negatively. The expression analysis of the introgressed lines (ILs) confirmed and extend the molecular data obtained by Casal and coworkers [168]. In particular, this analysis identified a group of auxin-related genes whose expression correlates with the strength of the shade avoidance response, being up-regulated in strong responding and down-regulated in tolerant lines, respectively [172]. However, prolonged exposure to shade, still producing shade avoidance responses, results in normal levels of auxin both in leaf and stem, although auxin-responsive genes are found up-regulated [168]. Similar results are also found in Arabidopsis and soybean [74, 176, 177] indicating that part of the responses to prolonged exposure to shade are produced by an increased sensitivity to auxin [177]. The analysis of ILs also revealed a very limited number of transcription factor genes regulated by shade; among these genes only 3 homologs of *ATHB2* and the homolog of *ETHYLENE AND SALT INDUCIBLE 3* (*ESE3*) [172] are induced by shade in Arabidopsis, whereas ESE3 is not regulated in maize [131]. Expression profiling studies in the first emerging leaf primordium exposed to shade light for 28 hours also revealed a significant up-regulation in the expression of the tomato ortholog of *SHOOTMERISTEMLESS* and other *KNOX*-related genes known to promote indeterminacy, and a down-regulation of genes involved in leaf differentiation [130].

5. Conclusions

Dose-dependent responses to transient and/or persistent stimuli are very common in nature. Generally, a transient behavior with very steep initial up-regulation and a subsequent decay region is observed. The overall shape of the response depends on the magnitude of the stimulus received, i.e. it shows a dose-dependent behavior, likely as the product of negative feedback(s). The persistence or the extinction of the response depends on the permanence of the stimulus.

Recent data in Arabidopsis and tomato strongly suggest that the strength of the shade avoidance response depends on auxin. Studies at the molecular level conducted mainly in Arabidopsis have

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highlighted two distinct molecular programs operating in the shade avoidance response. The first one, defined as neighbor detection, is characterized by a strong induction of auxin biosynthesis, its accumulation and transport, and transduction of the auxin signal, together with the up-regulation of several transcription factor genes and expression of multiple hormone pathways with distinct and/or overlapping programs taking place in different organs [81]. This molecular response is rapid and transient, a "warning signal" comparable to a defense response, with the auxin biosynthesis quickly turned off by the intensity of the light reaching the plant that affects the stability of the negative regulator HRF1/SICS1 [73]. The second program (canopy shade) takes place later on, in part overlaps with the first one, and persists even when the plant is unable to escape shade by the need of the plant to acclimate to the new environmental conditions characterized by a less efficient photosynthetic light. It has been proposed that auxin signaling is also involved in the regulation of this program, likely by a change in the sensitivity to auxin rather than an increase in the concentration of this hormone [25, 72-74, 176, 177]. However, intriguingly, the data accumulating in monocotyledonous plant species seem to indicate a reduced or even the lack of auxin response(s), in spite of the presence of a characteristic shade avoidance response [131, 157, 165].

It is worth to remind that neighbor detection and canopy shade are both under strict control of the phytochrome systems through the PIF proteins and that the whole processes are rapidly reversed by High R/FR light, eventually just by increased irradiance and/or altered spectral composition of sunflecks perceived through the canopy [105]. Consistently, ATHB2, being a direct target of PIF proteins, is rapidly and reversibly regulated by changes in R/FR light ratio [29] and it is fully induced even by local irradiation [178]. Evidences are accumulating that ATHB2 and its homologs are key regulators of the shade avoidance response, at least in Arabidopsis. Indeed, the overexpression of different members of the HD-Zip II family phenocopies the effect of shade light on distinct organs and flowering even when the plants are grown in High R/FR [26, 27, 35, 117, 124, 128]. On the contrary, single and double loss-of-function HD-Zip II mutants display altered growth responses to shade both in the hypocotyl and in the leaf [28, 128, 132]. In agreement, expression of a dominant-negative *athb2* mutation in transgenic Arabidopsis and tomato plants results in phenotypic alterations suggestive of an overall attenuation of the shade avoidance response [179]. Unfortunately, multiple loss-of-function HD-Zip II mutants are difficult to test in shade, since they are strongly altered in embryo, SAM activity, leaf polarity, gynoecium and fruit development under simulated sunlight conditions [121, 136, 138], implying a fundamental role of these proteins in the regulation of plant growth and development. Indeed, there are evidences that alteration of selected HD-Zip II proteins affects at least a regulatory circuit between HD-Zip II and HD-Zip III transcription factors [111, 117, 121, 136, 155] and hormones signal transduction pathways [139, 180]. In addition, evidence exists that a PIF/HD-Zip II genetic module was recruited to carpel development in Arabidopsis [137].

In evolutionary terms, the shade avoidance response appears to be a relatively recent invention, since it is predominantly found in angiosperms. Although the transcriptional program(s) that regulate the developmental responses to shade may be different in distant evolutionary species, it is relevant to emphasize that ATHB2 and its homologs are the only transcription factor genes regulated by Low R/FR light in all the species analyzed up to today, including the poplar [181].

Further work is needed to establish whether ATHB2 and ATHB2-like proteins, together with the PIF proteins, may be considered as the "core regulatory module" recruited to escape and/or adapt to canopy shade.

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Conflicts of Interest

The authors declare no conflict of interest.

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