Control of Plant Growth and Defense by Photoreceptors: From Mechanisms to Opportunities in Agriculture

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ABSTRACT

Plants detect and respond to the proximity of competitors using light signals perceived by photoreceptor proteins. A low ratio of red to far-red radiation (R:FR ratio) is a key signal of competition that is sensed by the photoreceptor phytochrome B (phyB). Low R:FR ratios increase the synthesis of growth-related hormones, including auxin and gibberellins, promoting stem elongation and other shade-avoidance responses. Other photoreceptors that help plants to optimize their developmental configuration and resource allocation patterns in the canopy include blue light photoreceptors, such as cryptochromes and phototropins, and UV receptors, such as UVR8. All photoreceptors act by directly or indirectly controlling the activity of two major regulatory nodes for growth and development: the COP1/SPA ubiquitin E3 ligase complex and the PIF transcription factors. phyB is also an important modulator of hormonal pathways that regulate plant defense against herbivores and pathogens, including the jasmonic acid signaling pathway. In this Perspective, we discuss recent advances on the studies of the mechanisms that link photoreceptors with growth and defense. Understanding these mechanisms is important to provide a functional platform for breeding programs aimed at improving plant productivity, stress tolerance, and crop health in species of agronomic interest, and to manipulate the light environments in protected agriculture.

Key words: photoreceptor, phytochrome, jasmonate, growth–defense trade-off, shade, avoidance, immunity

INTRODUCTION

High plant densities are the norm in many natural and nearly all agricultural fields. Plants compete for resources with their neighbors, both above and below ground. Resource competition between individual plants is not static, and plants can adjust their physiology and architecture to optimize resource capture (Sultan, 2000; Pierik et al., 2013; Gundel et al., 2014). Depending on soil fertility and water availability, competition can be predominantly below or above ground or both (e.g., Hautier et al., 2009). Since plants harvest light in the process of photosynthesis as their sole source of energy, competition for light can be particularly fierce.

Because light is mostly unidirectional, coming from above, competition for light is typically size asymmetric: Plants with some sun-exposed leaves get a disproportionately large share of the resource as compared with plants with few or no leaves that are sun exposed (Weiner, 1990; Schwinning and Weiner,

1998). Many plant species have evolved adaptive strategies to escape from shaded zones in dense stands by adjusting their architecture. Upon detection of shade signals, plant development is adjusted such that height growth is favored over branching or tillering, improving the ability of young leaves to capture photosynthetic light (Ballaré and Pierik, 2017).

Plants harvest blue (B) and red (R) light for photosynthesis in their chloroplasts; as such, the reflection unabsorbed green (G) light is what allows us to see plants as green. In addition to G light, plants reflect and transmit most of the incident FR radiation, which is invisible to the human eye. As a consequence of this selectiveness of chlorophyll for specific wavebands, the light composition inside a vegetation canopy is different from that of sunlight. Plants are able to detect changes in the light spectrum associated with

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dense vegetation through dedicated photoreceptor molecules. In response to the detection of these signals, plants can elicit a range of developmental responses, collectively known as the shade-avoidance syndrome (SAS) (Franklin, 2008; Casal, 2013; Ballaré and Pierik, 2017; Fiorucci and Fankhauser, 2017).

Dense stands are also prone to attack by pathogens and herbivorous insects. Since inter-plant distances are small, attackers can spread very easily and their proliferation is further supported by the favorable microclimate of dense vegetation, such as increased relative humidity and shielding from weather extremes. Plants in dense stands, therefore, not only have to consolidate resource capture through adaptive growth and developmental responses, but they also need to deal with a variety of attackers. These include herbivorous insects as well as pathogenic microorganisms. There is a strong awareness in the scientific literature of the so-called growth–defense trade-off, detailing how the generation of a well-defended phenotype is often in conflict with rapid plant growth. Dense stands are probably the growth scenario under which this trade-off most prominently defines survival and yield.

In this Perspective we explain how plants perceive neighbors at high density through light cues that are detected by photoreceptors. We then discuss how plants respond to these cues by accelerating elongation growth, while becoming more vulnerable to attack by pathogens and herbivores. Next, we review the main molecular pathways and physiological mechanisms regulating these growth–defense adjustments. Finally, we discuss opportunities for translation of this basic science knowledge to agricultural production and provide ideas for future research directions on the topic.

SHADE AVOIDANCE UPON NEIGHBOR DETECTION: BRIEF HISTORY OF SIGNALS AND PERCEPTION MODULES

In the history of shade-avoidance research, SAS was traditionally viewed as a suite of responses to low R:FR ratios, perceived by phytochrome (Smith, 1995). Research in the 1990s, based on physiological experiments in real plant canopies using multiple photoreceptor mutants, suggested that other wavelengths and light signals are very important in the orchestration of the SAS (reviewed in Ballaré, 1999), an idea that it is now widely accepted (Fraser et al., 2016; Ballaré and Pierik, 2017).

Photoreceptors

The current understanding is that plants can obtain a multicolor and directional view of the canopy light environment using a variety of photoreceptor proteins (Figure 1). The primary functions of the main photoreceptors involved in shade-avoidance responses are briefly summarized below.

Phytochromes
Phytochromes (phys), particularly phyB, are responsible for detecting changes in the R:FR ratio of canopy light. This signal can be used by the plant to detect the proximity of other plants even if it is not actually shaded by them (proximity perception), as FR reflected from neighboring leaves causes a reduction in the R:FR ratio that can be detected by phyB (Ballaré et al., 1990). In caulescent plants, the internodes play a central role in detecting reflected FR (Ballaré et al., 1990). In rosette plants such as

Arabidopsis, this early FR signal can be perceived at the leaf tips, triggering rapid shade-avoidance responses, such as leaf hyponasty (Pantazopoulou et al., 2017). Together with other cues, such as mechanical signals derived from the touching of neighboring leaves (de Wit et al., 2012), perception of reflected FR provides a mechanism for the detection of competitors, which is activated in the early stages of canopy development. In addition to internode elongation and leaf hyponasty, plants respond to reflected FR with negative phototropism, which allows them to project new growth toward canopy gaps (Ballaré et al., 1992). Collectively, these responses to plant proximity are essential in competitive settings for plants to effectively forage for light and acquire the canopy space before it is occupied by competitors. When the plant is actually shaded, the strong drop in R light caused by chlorophyll absorption further reduces the R:FR ratio, causing acceleration of elongation (Smith, 1995) and even potentiating shade-avoidance responses triggered by other photoreceptors (see below).

Phototropins (phot1 and phot2)
Phototropins are light–oxygen–voltage domain-containing photoreceptor proteins that are sensitive to B/UV-A radiation (Christie, 2007). Phototropins control phototropic growth responses to gradients of B light. These B light gradients, along with reflected FR, play an important role in early neighbor detection helping the plant to orient its growth to areas of the canopy in which photosynthetic light is more available as compared with the predominantly shaded zones (Ballaré et al., 1992). Phototropins are also involved in controlling other responses that are important for plant acclimation to fluctuating light conditions in canopies, including chloroplast movement, leaf expansion, and stomatal opening (Briggs and Christie, 2002).

Cryptochromes (cry1 and cry2)
In shaded environments, not only is the R component depleted due to chlorophyll absorption, but also B and UV radiation. Cryptochromes (crys) are B/UV-A light photoreceptors that evolved from DNA-repairing enzymes (Wang and Lin, 2020). Crys can detect the attenuation of B light that occurs in closed canopies and modulates shade-avoidance responses (Ballaré, 1999; Djakovic-Petrovic et al., 2007; Keller et al., 2011; Keuskamp et al., 2011). Among the responses triggered by B light attenuation, leaf hyponasty and increased internode elongation are the ones that have been studied in the greatest detail. In addition to regulating these growth and developmental responses to density, crys also provide photoperiodic input to the biological clock (Wang and Lin, 2020).

UVR8
The UV RESISTANCE LOCUS 8 (UVR8) is a UV photoreceptor. The protein exists in a dimeric form in tissues not previously exposed to UV-B and rapidly monomerizes in response to UV-B exposure to initiate signaling. UVR8 regulates numerous aspects of plant metabolism, physiology, and morphology (Jenkins, 2017; Yin and Ulm, 2017). In particular, UVR8 is essential to activate photoprotective responses, such as the accumulation of phenolic sunscreens (Jenkins, 2009; Demkura and Ballaré, 2012; Morales et al., 2013; Coffey et al., 2017), which are important for plant acclimation to canopy gaps (Mazza et al., 2000). In terms of morphological responses, activation of UVR8 tends to inhibit elongation and counteract the shade-avoidance responses to low R:FR ratios (Hayes et al., 2014; Mazza and Ballaré, 2015) (see below). The structural basis of UVR8 function is now well characterized, as
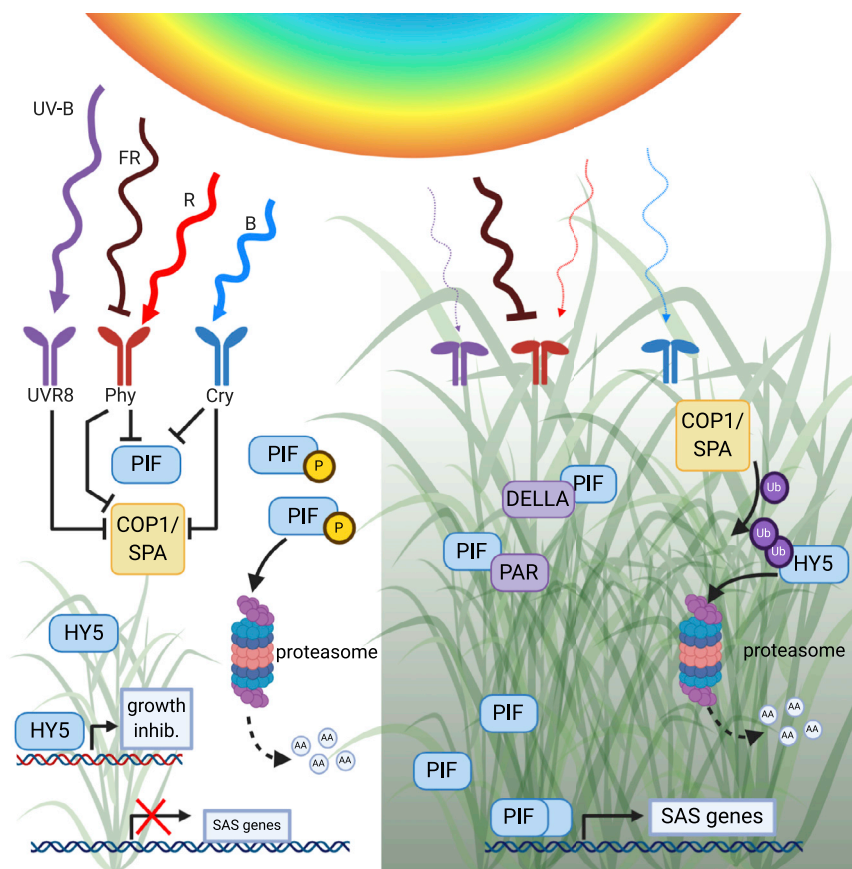
Figure 1. Shade and Proximity Are Sensed through a Combination of Light Signals That Are Detected via Different Photoreceptors.

In unfiltered sunlight, UV-B, red (R), and blue (B) light activate their respective photoreceptors: UVR8, phytochrome (phy), and cryptochrome (cry) (Franklin, 2008; Casal, 2013; Ballaré and Pierik, 2017; Fiorucci and Fankhauser, 2017). These photoreceptors directly or indirectly converge to inhibit PIFs and the Constitutively Photomorphogenic 1 (COP1)/Suppressor of Phytochrome A-105 (SPA) complex. UV-B, R, and B are depleted in shade, whereas FR is relatively abundant. As a consequence, the activity of UVR8, phy, and cry is greatly reduced, preventing the inhibitory action of these photoreceptors on COP1 and PIFs. COP1/SPA is a ubiquitin E3 ligase that targets the growth-inhibiting transcription factor HY5 for degradation (Han et al., 2020), whereas PIFs are a family of transcription factors of which a subset activates the expression of shade-avoidance-associated genes (Leivar and Monte, 2014). PIF activity is balanced by the abundance of several PIF inhibitors, such as DELLAs and PARs, whose abundance is co-regulated by shade cues (Ballaré and Pierik, 2017). Created with BioRender.com.

are the early events that initiate signaling in seedlings not previously exposed to UV-B. However, many aspects of UVR8 function under natural conditions, and the ways in which UVR8-dependent and -independent pathways interact to generate responses in the field, remain poorly understood (Ballaré and Austin, 2017; Jenkins, 2017; Liao et al., 2020). Field studies suggest that, under solar radiation, UVR8 mediates the perception of not only UV-B but also UV-A radiation (wavelengths up to 350 nm) (Rai et al., 2019). Also, the interactions between UVR8 and other photoreceptors involved in eliciting photoprotective responses under natural (polychromatic) light conditions are just beginning to be investigated (Rai et al., 2019, 2020; Tissot and Ulm, 2020).

Cooperation among Photoreceptors

Whereas the co-action among photoreceptor systems in controlling photomorphogenesis was studied in the past (Mohr, 1972), it is only recently that we have begun to understand how photoreceptors cooperate to optimize plant responses in canopies. B light attenuation caused by shading and perceived by crys can potentiate the shade-avoidance responses triggered by low R:FR (de Wit et al., 2016b) and also the phototropic responses toward canopy gaps (Boccaccini et al., 2020). These phototropic responses are also enhanced by low R:FR ratios perceived by phyB (Goyal et al., 2016). In addition, the shade-avoidance responses triggered by phyB inactivation are attenuated under high UV-B irradiances, which are perceived by UVR8 (Hayes et al., 2014; Mazza and Ballaré, 2015; Sharma et al., 2019; Tavridou et al., 2020), and retrograde signals

derived from the chloroplasts can also modulate elongation responses to phyB inactivation (Ortiz-Alcaide et al., 2019).

Collectively, these results demonstrate how plants use signals acquired by multiple photoreceptor systems to optimize their light foraging strategy in canopies. Thus, under conditions of neighbor proximity but no real shading, shade-avoidance responses are activated by reflected FR, leaf touching, and B light gradients, but these responses can be moderated by photoactivated photoreceptors and chloroplast signals. In contrast, under actual shade, the progressive inactivation of all photoreceptors and the diminished light capture by chloroplasts synergistically potentiate shade-avoidance responses. Most of these interactions are mediated via regulation of phytochrome-interacting factor (PIF) activity by PIF-interacting proteins, such as HFR1, PARs, and DELLAs, whose abundance or activity is directly or indirectly controlled by photoreceptors (reviewed in Buti et al., 2020) (see also below in the section on Molecular Mechanisms).

TRADE-OFFS ASSOCIATED WITH SHADE AVOIDANCE

Foraging for light implies the projection of new growth toward areas or strata of the canopy that are not covered by leaves and are, therefore, well exposed to sunlight. This increased exposure does not come without costs, however. On the one hand, there are *physiological* costs associated with the increased risk of photodamage and deleterious effects of solar UV radiation, increased water demand, and increased exposure to the

damaging action of wind. On the other hand, there are *ecological* costs associated with the increased exposure to grazers and other herbivores and consumer organisms, and a reduced ability to resist and tolerate defoliation and tissue damage (Ballaré and Austin, 2019). Reduced resistance to herbivores and pathogens is often associated with reduced leaf thickness and strength, which are typical responses to shade that maximize light interception per unit of carbon invested in leaf construction (Gommers et al., 2013), and also with reduced investment in defense-related specialized metabolites and changes in primary metabolism associated with the shade-avoidance program (see below). Reduced tolerance can result from diminished allocation to belowground organs and reduced branching, with both factors limiting the capacity of the plant to replace tissue losses caused by consumer organisms (Ballaré and Austin, 2019). Thus, because the growth plans that favor light gathering tend to be fundamentally different from those that reduce availability to grazers and increase resistance to herbivores and pathogens, "configurational conflicts" between the phenotypes that optimize shade avoidance and those that increase resistance to consumer organisms are often observed (Ballaré and Austin, 2019). Perhaps as a consequence of all these costs, efficient shade avoidance often trades off with tolerance and defense against herbivores and pathogens (Ballaré, 2014; Ballaré and Austin, 2019). These trade-offs are reflected in the density-dependent disease-related mortality of seedlings that is often observed in natural ecosystems (Bell et al., 2006) and in the increased susceptibility to pathogens in crops planted at high density (Burdon and Chilvers, 1982). Therefore, although shade-avoidance research has traditionally focused on elongation responses, and most of our mechanistic understanding of the signaling pathways activated by photoreceptors is derived from studies focused on elongation, increased attention is now being directed to understanding the mechanisms that plants use to find optimal solutions to the trade-offs between shade avoidance and defense. Trade-offs have been documented between shade-avoidance and defense responses against a variety of consumer organisms; here we will restrict ourselves mostly to jasmonic acid (JA)-regulated defense pathways, which fend off necrotrophic pathogens and herbivorous insects.

MOLECULAR MECHANISMS OF LIGHT SIGNALING TOWARD GROWTH AND DEFENSE

Although shade-avoidance responses are displayed by a wide variety of plant species representing a broad spectrum of growth forms, including wild and cultivated herbaceous plants (Ballaré et al., 1990; Pierik et al., 2004; Kebrom and Brutnell, 2007; Sasidharan et al., 2008; Whipple et al., 2011; Cagnola et al., 2012; Chitwood et al., 2015; Gommers et al., 2017; Molina-Contreras et al., 2019), grasses (Casal et al., 1985; Finlayson et al., 1998; Kebrom and Brutnell, 2007), vines (Izaguirre et al., 2013), and trees (Ritchie, 1997; de la Rosa et al., 1998; Li et al., 2020), in this section we focus mostly on what has been found in *Arabidopsis*, since this model provides the most advanced mechanistic insight into the topic. To maintain the focus of this review, we concentrate on the core pathways for shade avoidance that often crosstalk with defense. We direct the reader to other recent

reviews (de Wit et al., 2016a; Ballaré and Pierik, 2017) for a broader coverage of hormones and their crosstalk in shade avoidance, and to Pieterse et al. (2012), Jones et al. (2016), and Howe et al. (2018) for a broader coverage of plant immunity.

Photoreceptor Interactions

Photoreceptor Interactions with the COP1/SPA Complex
Photoactivated crys and phys suppress two major regulatory nodes for growth and development: the COP1/SPA (Constitutively Photomorphogenic 1/Suppressor of Phytochrome A-105) ubiquitin E3 ligase and PIF transcription factors (Figure 1). Suppression of COP1/SPA relieves the ubiquitination and subsequent degradation of the growth-inhibiting transcription factor HY5 (ELONGATED HYPOCOTYL 5) and is key to seedling de-etiolation (Han et al., 2020). HY5, in addition, has also been implicated in shade-avoidance inhibition during sunfleck exposure of shaded plants (Sellaro et al., 2011). HY5 may inhibit elongation by negatively regulating gibberellin signaling, as it promotes the expression of *GA2-OXIDASES*, which encode GA-inactivating enzymes (Hayes et al., 2014). HY5 also mediates lateral root development in response to shoot-detected low R:FR light (van Gelderen et al., 2018a). Loss of function of HY5 leads to severe constitutive hypocotyl elongation, whereas ectopic overexpression of HY5 inhibits hypocotyl elongation, but in both HY5 loss- and gain-of-function lines hypocotyl elongation remains clearly less responsive to R:FR (van Gelderen et al., 2018a). Another group of transcription factors that are targeted by COP1 are the so-called double B-BOX (BBX) zinc-finger transcription factors. BBX21 and BBX22 have indeed been associated with long-term shade-avoidance responses under low R:FR (Crocco et al., 2010), and loss of function of BBX25 also partially reduces low R:FR-induced hypocotyl elongation (Gangappa et al., 2013).

Photoreceptor Interactions with PIF Transcription Factors
Phytochromes in their active Pfr form translocate to the nucleus where they subsequently interact with PIFs (Figure 1). All PIFs in *Arabidopsis* contain an active phyB binding domain, whereas only two PIFs (PIF1 and PIF3) have a phyA binding domain (Leivar and Monte, 2014). PIF4, PIF5, and PIF7 are the triplet core of PIF proteins that regulates phyB- and cry1/2-mediated shade-avoidance responses, which include accelerated hypocotyl and petiole elongation (Keller et al., 2011; Hornitschek et al., 2012; Li et al., 2012; de Wit et al., 2016b), hyponasty (Keller et al., 2011; Michaud et al., 2017; Pantazopoulou et al., 2017), and early flowering (Cerdán and Chory, 2003; Galvao et al., 2019). Light foraging through phototropic bending of the hypocotyl in *Arabidopsis* in response to R:FR and B light gradients also occurs in a PIF-dependent manner (Goyal et al., 2016; Boccaccini et al., 2020).

Active phyB, upon direct interaction with PIFs, initiates their phosphorylation and subsequent inactivation (Lorrain et al., 2008; Hornitschek et al., 2012). PIF4 and PIF5 are ultimately degraded upon interaction with active phyB, whereas PIF7 is not directly degraded upon phyB-dependent phosphorylation but is nevertheless inactivated (Li et al., 2012; Huang et al., 2018). When the R:FR ratio decreases, a larger fraction of phyB is photoconverted into the inactive Pr form. As a consequence, active PIF proteins can accumulate in low R:FR. Phytochromes can also act as thermosensors under low irradiances (Jung

et al., 2016; Legris et al., 2016), and increased temperature regulates plant architecture at least in part through the canonical shade-avoidance pathway in a PIF-dependent manner (Koini et al., 2009). Interestingly, it was recently found that PIF7 translation is temperature dependent and mediated by a hairpin in the mRNA, providing an alternative mechanism for PIF7 protein control that is phytochrome independent (Chung et al., 2020).

In addition to phy, cry can also physically interact with PIFs (Ma et al., 2016; Pedmale et al., 2016). In particular, PIF4 and PIF5 are relevant for shade-avoidance responses to a depletion of B light (Keller et al., 2011; de Wit et al., 2016b; Pedmale et al., 2016), although the precise mechanisms of cry-dependent regulation of PIF activity in response to B light fluctuations are not fully elucidated yet. A recent study on phototropism indicates that *PIF4* is also transcriptionally regulated through B light-dependent activity of cry1, with active cry1 suppressing *PIF4* expression (Boccaccini et al., 2020).

PIFs Function in a Network

PIFs are a small subgroup of the large family of basic-helix-loop-helix (bHLH) transcription factors. PIFs bind to specific promoter elements, G and E boxes, and stimulate transcription of shade-responsive genes (Leivar and Monte, 2014). A wide variety of target genes for PIF transcription factors have been identified, many of which encode proteins that directly or indirectly contribute to cell growth (Hornitschek et al., 2012; Zhang et al., 2013). Although PIFs are considered a major hub for growth regulation (Leivar and Quail, 2011), it has become clear that they are part of a larger network of transcription factors now known as the BAP module (Oh et al., 2014; Chaiwanon et al., 2016; Boure et al., 2019). The BAP module consists of members from three groups of transcription factors: PIFs, ARFs (Auxin Response Factors), and BZR1 (Brassinazole Resistant 1). PIFs, ARFs, and BZR1/BES1 stimulate growth and act as light (PIF)-, auxin (ARF)-, and brassinosteroid (BZR1)-dependent transcription factors (Chaiwanon et al., 2016). Although each of these pathways alone can regulate downstream events, they enhance each other's effects when they are activated together. Although the BAP module has been convincingly shown to regulate hypocotyl elongation (Oh et al., 2014), it remains to be investigated to what extent this regulatory module can be extrapolated to other shade-avoidance responses. Nevertheless, it was recently shown that shade avoidance is modified by abiotic stress through combined BES1 and PIF action (Hayes et al., 2019). Furthermore, many of the low R:FR-induced genes detected in a transcriptome survey were found to also be direct targets of PIF4, BZR1, and ARF6 (Kohnen et al., 2016).

PIF Inhibitors

Importantly, PIF activity is co-regulated in a feedback loop by PIF-interacting proteins that are typically also transcriptionally activated by PIFs. PIF-interacting proteins with well-established roles in shade avoidance are HFR1, PAR1, and PAR2 (reviewed in Buti et al., 2020). These are atypical HLH proteins that do not directly bind DNA, but that interact with the DNA binding domain of PIFs. As a result, binding of PARs or HFR1 inhibits PIF binding to target sequences on the DNA, thereby repressing PIF transcription factor activity (Hornitschek et al.,

2009; Galstyan et al., 2011). A third layer of HLH control was recently shown: the PIF-induced, non-DNA binding protein KDR1/PRE6 was found to interact with PAR1 and PAR2, thereby likely inhibiting their PIF binding abilities and thus releasing PIF proteins to stimulate downstream events (Buti et al., 2020). Another group of PIF-interacting proteins are the so-called DELLA proteins, and, upon interaction, they render PIFs inactive (de Lucas et al., 2008; Feng et al., 2008). DELLA proteins are negative regulators of gibberellin (GA) response, and upon GA interaction with its receptor GID1, DELLAs are degraded (Daviere and Achard, 2013). An increase in GA levels under low R:FR light conditions follows from increased GA biosynthesis via GA20 oxidases (Hisamatsu et al., 2005) and leads to degradation of the DELLA protein RGA, thus releasing additional PIFs (Djakovic-Petrovic et al., 2007; Leone et al., 2014). Also, recent research demonstrates that COP1 mediates rapid, GA-independent destabilization of DELLAs in response to shade signals (Blanco-Touriñán et al., 2020). The BBX24 transcription factor, a close homolog of BBX25 mentioned earlier, can physically interact with DELLA proteins, which subsequently sequester DELLAs such that PIF4 activity is enhanced, thus promoting shade avoidance (Crocco et al., 2015).

PIFs Regulate Downstream Events to Promote Elongation

Once active PIFs bind target gene promoters (Leivar and Monte, 2014), they typically activate their transcription. Numerous transcriptome surveys have been conducted on shoots exposed to low R:FR and/or true shade (Salter et al., 2003; Li et al., 2012; de Wit et al., 2016b), and several surveys have identified a wide range of differentially expressed genes often specifically in different plant tissues (Cagnola et al., 2012; Nito et al., 2015; Nozue et al., 2015; Das et al., 2016; Kohnen et al., 2016; Pantazopoulou et al., 2017). What stands out from these many transcriptome surveys is that the auxin network is highly transcriptionally regulated under low R:FR and in a PIF-dependent manner.

Auxin

Low R:FR-induced PIFs typically regulate auxin at the levels of biosynthesis, transport, and signaling (reviewed in Iglesias et al., 2018; Ma and Li, 2019). The overall picture that has emerged for young seedlings is that a reduced R:FR ratio sensed in the cotyledons triggers *de novo* auxin synthesis through enhanced expression of *YUCCA* auxin synthesis genes (Procko et al., 2014; Kohnen et al., 2016), mostly in a PIF7-dependent manner (Li et al., 2012). The amino acid tryptophan is converted into indole-pyruvic acid, which is subsequently converted into indole acetic acid (IAA) (active auxin) via YUCCA enzymes (reviewed in Mashiguchi et al., 2011; Zhao, 2012). Consistently, mutants for this auxin synthesis pathway, such as higher-order *yuc* mutants and *sav3/wei8/taa1*, have reduced or even absent low R:FR-induced hypocotyl elongation (Tao et al., 2008; Won et al., 2011; Kohnen et al., 2016; Muller-Moule et al., 2016). IAA is then transported from the cotyledons to the hypocotyl, where it is distributed laterally toward the epidermis where it promotes cell elongation (Keuskamp et al., 2010; Procko et al., 2016). This polar auxin transport from the cotyledons to the hypocotyl and from the inner tissues to the epidermis is regulated by PIN-FORMED (PIN) auxin transport

proteins PIN3, PIN4, and PIN7 (Keuskamp et al., 2010; Kohnen et al., 2016; van Gelderen et al., 2018a). Bioactive auxin levels can, in addition, also be controlled in the hypocotyl itself through conjugation/de-conjugation via the GH3.17 (GRETCHEN-HAGEN 3.17) protein, independently of the auxin pool in the cotyledons (Zheng et al., 2016).

In plants at the rosette stage, low R:FR-induced auxin synthesis occurs in the FR-exposed leaf tips and auxin is then transported to petioles and ultimately into the root system. Local FR-induced auxin synthesis in the leaf tip-only is sufficient and necessary for the upward movement of the petiole of that very leaf (Michaud et al., 2017; Pantazopoulou et al., 2017), and this occurs primarily through PIF7-dependent regulation of *YUC8* and *YUC9* (Pantazopoulou et al., 2017). IAA is then transported from the leaf tip to the petiole via PIN3, 4, and 7. Subsequent elongation of the petiole is stimulated if FR light is sensed by the petiole itself (Pantazopoulou et al., 2017). Interestingly, *pif4 pif5* double mutants appear to be less sensitive to leaf tip-derived IAA than the wild type, implying the involvement of *PIF4* and *PIF5* in auxin responsiveness (Pantazopoulou et al., 2017; see also Hornitschek et al., 2012; Hersch et al., 2014). Indeed, PIFs regulate transcription of several *AUX/IAA* and *ARF* genes that regulate auxin response (Hornitschek et al., 2012). AUX/IAA proteins interact physically with ARF transcription factors, thus modulating their DNA binding ability (Leyser, 2018). This is a highly complex network, and this complexity is further increased by the fact that within the ARF family (Roosjen et al., 2017) there are both auxin repressors and activators. A recent study, for example, identified how PIFs inhibit the expression of *ARF18*, which encodes a transcription factor that inhibits auxin signaling (Jia et al., 2020), whereas other ARFs promote auxin signaling and growth (Reed et al., 2018). Active phyB and cry1 have also been proposed to directly interact with auxin signaling-promoting ARF proteins, such as ARF6 and ARF8, to repress their DNA binding ability (Mao et al., 2020), as well as with specific AUX/IAA proteins where photoreceptor interaction stabilizes AUX/IAAs (Xu et al., 2018).

Cell Wall Remodeling

Auxin signaling controls growth via regulation of cell wall remodeling components: under low R:FR conditions the cell acidifies rapidly (Sasidharan et al., 2010), a process that typically occurs through SAUR19 (SMALL AUXIN-UPREGULATED)-dependent activation of plasmamembrane proton ATPases (Spartz et al., 2014; Fendrych et al., 2016). This low pH is needed for cell wall modifying proteins (CWMPs) to be active, and SAUR19 activity thus indirectly activates these proteins in the apoplast. Several families of CWMPs exist and include XTHs (xyloglucan endotransglucosylase/hydrolases), Expansins, EGases (endo-β1,4 glucanases), and PMEs (pectin methylesterases), which have been associated with various plant responses to environmental parameters (reviewed in Sasidharan et al., 2011). Low B light-induced hypocotyl elongation in *Arabidopsis* is associated with increased *EXPANSIN*, *EXTENSIN*, and *XTH* gene expression in a strongly PIF-dependent manner (Pedmale et al., 2016), and this occurs in part through auxin and brassinosteroid action (Keuskamp et al., 2011). In shaded petioles, *XTHs* are also induced (Sasidharan et al., 2010) in a partially auxin-dependent manner (Sasidharan et al., 2014), and the *xth15* mutant lacks a clear petiole elongation response to low R:FR (Sasidharan et al., 2010).

Phytochrome Control of Jasmonate-Dependent Defense

Jasmonates (JAs) are lipid-derived molecules that play a central role in orchestrating the accumulation of defense-related metabolites and proteins (Howe et al., 2018; Heitz, 2020). Simultaneously, JAs are potent growth inhibitors that deplete growth-limiting resources (Havko et al., 2016; Guo et al., 2018) and inhibit cell division (Zhang and Turner, 2008) and cell expansion (Noir et al., 2013). JAs are synthetized in response to stress or internal signals from polyunsaturated fatty acids released from membrane lipids by a complex set of phospho- or galactolipases (reviewed in Heitz, 2020; Koo, 2018; Wasternack and Feussner, 2018). The conjugate jasmonyl-L-isoleucine (JA-Ile) is generally recognized as the major, conserved bioactive member of the JA family in angiosperms, and it is synthesized from JA and the amino acid isoleucine. JA-Ile is perceived by co-receptors formed by the F-box protein CORONATINE INSENSITIVE 1 and a series of JASMONATE-ZIM DOMAIN (JAZ) repressor proteins. These JAZ proteins bind to and repress the action of various transcription factors that control the physiological responses to JAs, including members of the MYC family. JA-Ile acts as a ligand that promotes the interaction of JAZ proteins with COI1, facilitating their recruitment to the E3 ligase SCF^{COI1}. Once ubiquitinated, JAZ proteins are degraded by the proteasome, thereby releasing their target transcription factors from repression (Browse, 2009; Howe et al., 2018; Heitz, 2020).

Given the configurational conflicts between shade avoidance and defense (Ballaré and Austin, 2019), it is not surprising that intense dialogue exists between the signaling pathways triggered by JA-Ile and those elicited by the photoreceptors that monitor the proximity of competitors and the degree of leaf shading (Ballaré, 2014) (Figure 2). High doses of exogenously applied JAs (Cipollini, 2005) or genetic hyperactivation of the JA pathway (Major et al., 2020) can suppress shade-avoidance responses; in turn, low R:FR ratios and phyB inactivation attenuate JA signaling and the expression of defenses against herbivores and pathogens (Moreno et al., 2009; Cerrudo et al., 2012, 2017; de Wit et al., 2013; Campos et al., 2016; Courbier et al., 2020; Fernández-Milmanda et al., 2020). Although the suppression of JA responses by phyB inactivation has been documented primarily in *Arabidopsis*, the available evidence suggests that this is a very general phenomenon that occurs over a broad range of shade-intolerant species, including many important crops (reviewed in Ballaré et al., 2012). In nature, the crosstalk between light and JA signaling allows the plant to optimize its configuration and allocation decisions as a function of the pressures imposed by competitors and consumers. However, for cultivated species, downregulation of defenses in response to proximity signals (sometimes known as FR-induced susceptibility) may have important negative effects on crop health (see section From Basic Knowledge to Increased Agricultural Production).

phyB Inactivation Attenuates JA-Mediated Defenses

Recent research has uncovered the mechanisms that mediate the effects of phyB inactivation on JA signaling (Figure 2). Downstream of JA-Ile, FR impinges on the antagonism between DELLA and JAZ proteins (Hou et al., 2010; Yang et al., 2012) to suppress JA signaling. As DELLAs are degraded in response to
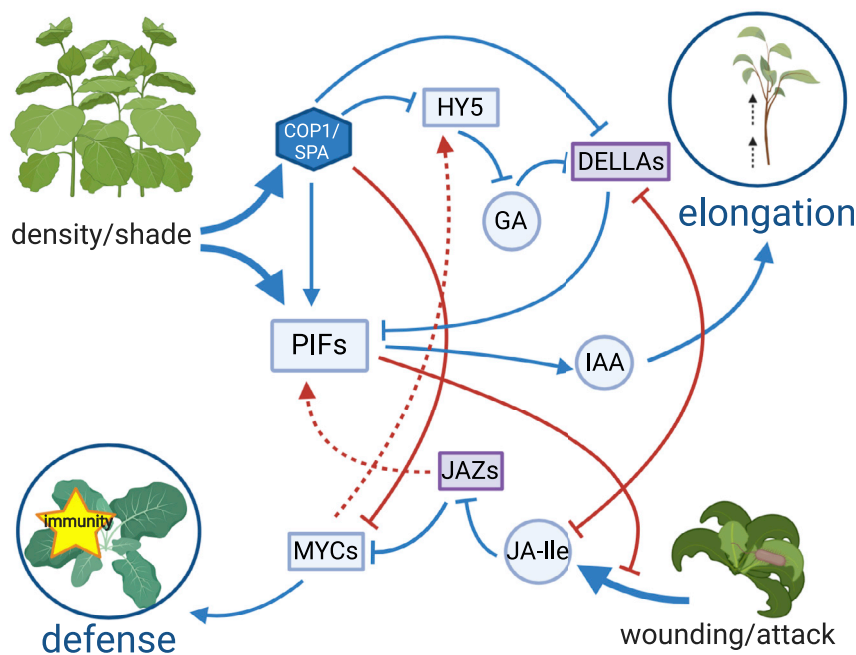
Figure 2. Crosstalk between the Light- and JA-Signaling Pathways Fine-Tunes Plant Metabolic and Configurational Responses to Competitors and Consumer Organisms.

Shade and proximity signals increase the activity of PIFs and the COP1/SPA complex, with COP1/SPA having positive effects on PIF activity when both pathways are triggered by multiple shade signals (de Wit et al., 2016b; Sharma et al., 2019). PIFs trigger shade-avoidance responses using the canonical PIF-IAA pathway (Li et al., 2012). GA accumulation can also be promoted, in part in response to reduced expression of *GA2ox* genes, which are regulated by HY5 and related transcription factors (e.g., Hayes et al., 2014). Increased GA levels promote elongation by inducing the proteolysis of DELLAs, which are negative regulators of PIFs (de Lucas et al., 2008; Feng et al., 2008). DELLAs can also be degraded in response to shading via a COP1-dependent, GA-independent mechanism (Blanco-Touriñán et al., 2020). Wounding and attack by herbivores and necrotrophic pathogens promote JA-Ile biosynthesis, which activates defense and growth inhibition by triggering the degradation of JAZ repressors and allowing MYCs and other transcription factors to activate their target genes (Howe et al., 2018). Critical points of crosstalk between the SAS and JA pathways (solid red lines) include the direct effects of PIFs, which reduce the formation of bioactive JA conjugates via the ST2a pathway (Fernández-Milmanda et al., 2020); the negative interactions between DELLA and JAZ proteins (Hou et al., 2010; Yang et al., 2012; Leone et al., 2014); and the COP1-dependent destabilization of MYCs under simulated shade light conditions (Chico et al., 2014). In addition, in seedlings (dashed red lines), MYCs can activate *HY5* transcription, leading to reduced elongation (Ortigosa et al., 2020), and JAZ can indirectly increase PIF activity, promoting elongation when the JA pathway is not activated (Liu et al., 2019). Note the central role of PIFs in regulating the reciprocal antagonism between SAS and defense responses. Arrows indicate promotion or activation; truncated connectors indicate repression or negative effects. Created with BioRender.com.

phyB inactivation (Djakovic-Petrovic et al., 2007; Leone et al., 2014), JAZ proteins are more available to suppress their target transcription factors in plants grown under low R:FR ratios, thereby attenuating JA responses (Leone et al., 2014). Genetic evidence suggests that JAZ10 plays a critical role in the repression of plant defenses under conditions that inactivate phyB (Cerrudo et al., 2012, 2017). In addition, mutant studies indicate that phyB inactivation can reduce MYC stability in a *COP1*-dependent manner, but the biochemical details of the mechanism are still not fully understood (Chico et al., 2014).

In a more direct way, FR can act upstream of JA-Ile, suppressing the formation of bioactive JA conjugates by favoring the inactivation of hormone precursors. FR strongly upregulates *ST2a* (Fernández-Milmanda et al., 2020), a gene that encodes a JA sulfotransferase that catalyzes the sulfation of hydroxy-JA (OH-JA) to form the inactive molecule hydrogen sulfate-JA (HSO$_4$-JA) (Gidda et al., 2003). When phyB is inactivated, PIFs bind to and activate the *ST2a* promoter, triggering the accumulation of HSO$_4$-JA and reducing the abundance of other JA metabolites (Fernández-Milmanda et al., 2020). The reaction defined by ST2a diverts the flux of hormone precursors away from JA-Ile biosynthesis, and reduces subsequent signaling (Fernández-Milmanda et al., 2020). Reduced production of JA-Ile under low R:FR ratios might explain the observations (Chico et al., 2014; Leone et al., 2014) of increased stability of JAZ proteins under conditions that inactivate phyB. Mutations that eliminate this PIF-driven metabolic shift in the JA pathway result in plants that

do not display the FR-induced attenuation of resistance to herbivores and fungal pathogens (Fernández-Milmanda et al., 2020).

Attenuation of JA signaling by phyB inactivation leads to reduced accumulation of glucosinolates, which are critical defense compounds in members of the mustard family (Cargnel et al., 2014; Fernández-Milmanda et al., 2020), and reduced accumulation of phenolic compounds (Moreno et al., 2009; Cerrudo et al., 2012). In addition, work in tomato demonstrates that decreased JA signaling results in reduced expression of genes that encode proteins involved in antiherbivore defense, such as THREONINE DEAMINASE and PROTEINASE INHIBITOR II (Cortés et al., 2016), and causes accumulation of soluble sugars, which in turn promote the activity of necrotrophic pathogens, such as *Botrytis cinerea* (Courbier et al., 2020). Consequently, reduced JA signaling, while allowing the plant to fully express a shade-avoidance phenotype (Fernández-Milmanda et al., 2020), results in metabolic changes that strongly impair its capacity to fend off attacking organisms.

JA Signaling Attenuates Shade-Avoidance Responses

Just as competition signals attenuate JA-mediated responses to prioritize shade avoidance, signaling elements of the JA pathway can modulate the expression of components of the SAS, at least in seedlings (Figure 2). In one mechanism, JAZ proteins can inhibit the expression of PAR1 and PAR2 (Liu et al., 2019), which are negative regulators of PIF activity, as mentioned previously (Galstyan et al., 2011). Therefore, when JAZ proteins are degraded, PARs inhibit PIF binding to their cognate

promoters, limiting the expression of shade-avoidance responses (Liu et al. 2019). In addition, MYC2 and MYC3 can directly bind to the promoter of *HY5* and inhibit elongation responses by increasing the expression and protein abundance of this negative regulator of the SAS (Ortigosa et al., 2020).

FROM BASIC KNOWLEDGE TO INCREASED AGRICULTURAL PRODUCTION

As mentioned previously, most research on shade avoidance and defense, as well as their crosstalk has been carried out in *Arabidopsis*. However, two pertinent questions arise: how much do we understand about this topic in species of agronomic interest and how can we use *Arabidopsis* knowledge for improving agricultural production?

Shade Responses in Crops

During the Green Revolution in the middle of the past century cereal crops in particular were selected that displayed significantly reduced height growth. The semi-dwarf growth form allowed these plants to carry the heavy grains that resulted from extensive breeding and high input of fertilizer. These shorter plants were much less prone to lodging as compared with the older, more elongated lines, and resources that were previously invested in stem growth, were now available for harvestable organs (reviewed in Hedden, 2003; Sakamoto and Matsuoka, 2004; Pingali, 2012). This testifies to the huge potential of crop architecture improvement for increased yield. Interestingly, many of the Green Revolution mutations that were selected for turned out later to be GA pathway components, including GA biosynthesis genes and DELLAs (Hedden, 2003). Nevertheless, many of our current crops still express a robust SAS, and thus display elongation, leaf angle, tillering, and flowering responses to density (Ballaré and Casal, 2000). Some of these traits may be desirable in specific cropping systems, but many are not. This strongly depends on, for example, the crop species and agronomic scenario: tillering can be undesirable in some cases, and an increased sensitivity to low R:FR ratios that suppress branching could be beneficial for crop yield (Casal, 1988), but tillering may promote yield in other species or conditions, such as in rice (Yan et al., 1998; Li et al., 2003), and thus different decisions may be made for such an SAS-associated characteristic. Nevertheless, height growth appears to be a rather universal SAS trait to select against in crops. Despite the strong selection against height growth during the Green Revolution, density-induced elongation remains present in many species—for example, in seedlings of modern maize hybrids (Dubois et al., 2010) and certain rice cultivars (Panigrahi et al., 2019).

Maize is a particularly well-studied species with respect to shade-avoidance responses and it is among the world's most important crops. *phyB1* mutants in maize are constitutively elongated and early flowering (Sheehan et al., 2007), similar to that observed in *Arabidopsis* (Franklin et al., 2003), and FR enrichment accordingly stimulates shoot elongation (Dubois et al., 2010; Shi et al., 2019). Inspired by knowledge from *Arabidopsis* research, parts of the signaling pathway in maize were also elucidated. Transcriptome surveys indicated differential expression of maize homologs for many of the

known regulators of shade-avoidance growth (Wang et al., 2016; Shi et al., 2019). These include *TAA1, YUCCA, AUX/IAAs,* and *SAURs* (auxin biosynthesis and response); *GA2OXs, GA1,* and *GA5* (gibberellin pathway); *PIFs* (phyB targets); *HFR1* and *PAR* (PIF interactors); and *BBX* and *HD-ZIP* transcription factor-encoding genes, including a homolog for *ATHB4* (Wang et al., 2016; Shi et al., 2019). In a recent study, maize was reported to contain seven *PIF* genes and, when expressed heterologously in *Arabidopsis*, all seven *ZmPIFs* could rescue hypocotyl length in dark-grown seedlings of the *Arabidopsis pif* quadruple mutant (Wu et al., 2019). Consistent with these findings, maize CRISPR-Cas9 knockouts for independent *pif*s had reduced mesocotyl length in darkness and mildly reduced responsiveness to FR enrichment in light-gown seedlings (Wu et al., 2019). *ZmPIF4* overexpression in *Arabidopsis* elicits a constitutive shade-avoidance response (Shi et al., 2018; Wu et al., 2019), and ZmPIF4 was shown to physically interact with the *Arabidopsis* DELLA protein RGA when expressed in yeast and transiently in tobacco leaves (Shi et al., 2018). Low R:FR light conditions in maize also suppress tillering (Finlayson et al., 2010) by alleviating the active phyB-induced suppression of *GRASSY TILLERS 1* (*GT1*), an HDZip transcription factor (Whipple et al., 2011). This regulation of *GT1* in maize is dependent on the major domestication locus *teosinte branched 1* (*tb1*) (Whipple et al., 2011). Finally, genes associated with defense were shown to also be shade regulated in maize, including upregulation of *JAZ1* (Wang et al., 2016), which is reminiscent of the upregulation of some *JAZ* genes in *Arabidopsis* (Moreno et al., 2009; Fernández-Milmanda et al., 2020). Collectively, these comprehensive studies in maize confirm that the fundamental understanding of the core SAS pathways, obtained in *Arabidopsis*, has the potential to be indeed highly translatable to distantly related crop species.

Although SAS research mostly focusses on light-exposed plant parts, belowground organs also should be taken into account when thinking about crop improvement at high planting density. *Arabidopsis* main root elongation and lateral root development are inhibited upon exposure of the shoot to FR-enriched light (Salisbury et al., 2007; van Gelderen et al., 2018a). Phytochromes can be active in the root system itself but light responses are most likely mediated through mobile molecular components (Van Gelderen et al., 2018b), making this in an interesting target for crop improvement. An extensive review of the literature, based mostly on research carried out in cultivated species, indicates that plant exposure to low R:FR ratios negatively affects root growth and interactions with beneficial soil microorganisms (Gundel et al., 2014). These effects of light quality could have large effects not only on the efficiency with which crops capture resources below ground, but also on the carbon inputs to the soil. Furthermore, belowground organs other than roots are often the reason why many species are cultivated, and the growth of these organs can also be greatly affected by shading and proximity cues. For example, low R:FR ratios perceived by the shoots can result in reduced tuber yield in potato (Boccalandro et al., 2003). Interestingly, there is evidence that the effects of R:FR ratios on root interactions with symbionts involve changes in JA metabolism and/or signaling (Suzuki et al., 2011; Nagata et al., 2015); these light-mediated changes in JA signaling might also have consequences for root interactions with root herbivores and pathogenic soil

microorganisms, but this possibility has, to the best our knowledge, not been investigated. Clearly more work is needed to understand the mechanisms by which photoreceptors control growth and development of belowground plant parts.

Ectopic Overexpression of Phytochrome: An Early Case Study

An early attempt to genetically engineer shade-avoidance characteristics and overall yield was made by the late Harry Smith and coworkers in tobacco more than 25 years ago. The *PHY* gene family had been studied rather extensively, and ectopic overexpression of phyA was known to antagonize phyB-mediated shade-avoidance responses (McCormac et al., 1992). By overexpressing an oat *PHYA* cDNA in tobacco they expected to suppress shade avoidance and improve photoassimilate allocation. The transgenic lines indeed had strongly suppressed proximity-induced stem elongation, and an up to 20% increased harvest index (Robson et al., 1996). Harvest index indicates harvestable biomass/total biomass, which in the case of tobacco means leaf biomass/total biomass. This advance could probably be extrapolated to leafy vegetables, where leaf biomass also constitutes yield, but not necessarily to cereals where it is not the leaves but the grains that are harvested. Being in the UK, Smith's initiative stalled due to the anti-GM sentiments of Europe. Importantly, this endeavor showcased the huge potential for crop improvement through targeting phytochrome and SAS signaling components. Importantly, as exemplified above with tillering responses, the direction in which shade avoidance should be manipulated to increase yield may depend strongly on the crop species and production context. Blunt suppression of SAS can be beneficial to increase harvest index and reduce lodging in some species, but it could also have negative effects such as reducing crop light interception and size uniformity (Ballaré et al., 1994; Ballaré and Casal, 2000).

Modifying the SAS–Defense Balance: From *Arabidopsis* to Crops

Since our understanding of SAS and defense signaling pathways have massively advanced over the past 25 years, more sophisticated interventions with fewer side effects are now possible. Furthermore, as mentioned above, the signaling pathways toward different SAS components have been elucidated to some extent, which in theory could allow us to engineer specific SAS traits while leaving others untouched. Using a combination of local expression systems driven by tissue-specific promoters with modulators targeting plasticity rather than the core components, promises to hold great potential in crop improvement. Rather than ectopically overexpressing photoreceptor genes, which will likely interfere with a plethora of light-driven processes all over the plant body, we might now be able to alter shade-avoidance responses in a specific organ, for example, the internode. Early work demonstrated that manipulation of photoreceptor genes in specific organs could be used to obtain transgenic plants in which certain organs or tissues are made insensitive to phytochrome-perceived signals of canopy density, but whose general shade-avoidance behavior is not greatly disturbed (Rousseaux et al., 1997). Our improved understanding of the molecular connections between photoreceptors and physiological responses also allows us to

manipulate specific elements of the signal-transduction cascade to create precise changes in the plant phenotype. For example, we could target a specific component in FR-induced susceptibility, thus preventing the FR-mediated suppression of plant defenses against insects and pathogens. The demonstration that some specific *JAZ* genes are important for connecting phyB inactivation with the attenuation of JA responses suggests potential targets for manipulation of plant health in high density crops. In fact, Cerrudo et al. (2017) demonstrated that genetic inactivation of *JAZ10* results in *Arabidopsis* plants that display largely normal morphological responses to shade signals but that are nevertheless resistant to infection by *B. cinerea* under conditions that inactivate phyB. Manipulation of defense-related transcription factors whose stability is compromised under FR radiation (such as MYCs) (Chico et al., 2014) might also provide ways to improve defenses. In addition, our growing understanding of JA metabolism (Koo, 2018; Heitz, 2020) and its regulation by light signals (Fernández-Milmanda et al., 2020) could hint to ways in which crop immunity could be enhanced. The recently discovered regulation of JA metabolism by the sulfotransferase ST2a that is controlled via the phyB-PIF transcription module in *Arabidopsis* (Fernández-Milmanda et al., 2020), represents an obvious target for genetic interventions when orthologs in crops are identified.

The SAS–Defense Balance in Crops: Tomato as an Example

Although we mentioned above that most of our mechanistic understanding of shade-avoidance and immune response regulation, and particularly their interaction, has been obtained in *Arabidopsis*, there has also been preliminary work done in crops, especially tomato. Tomato is well studied for its phytochrome photoreceptors and shade avoidance (Chitwood et al., 2015; Schrager-Lavelle et al., 2016). Although it appears that wild relatives of cultivated tomato, such as *Solanum penellii*, have stronger elongation responses to FR enrichment than, for example, cultivated *S. lycopersicum* cv. M82, the cultivated lines also display robust shade-avoidance responses (Chitwood et al., 2015). Similar to *Arabidopsis*, tomato also appears to pair shade-avoidance responses under low R:FR conditions with suppressed defense. It was found that the constitutively shade-avoiding *phyB1phyB2* mutant has increased sensitivity to herbivorous insects, such as thrips and *Spodoptera eridania* caterpillars (Izaguirre et al., 2006) and reduced expression of typical JA markers (Cortés et al., 2016). Furthermore, resistance against the fungal pathogen *B. cinerea* is reduced in tomato when phyBs are genetically or physiologically inactivated (Courbier et al., 2020). Similar to *Arabidopsis*, this effect of phyB inactivation is at least partially JA dependent. It turns out that, in tomato, inhibition of JA response in low R:FR allows leaf soluble sugar levels to increase, which likely promotes fungal growth and perhaps pathogenicity (Courbier et al., 2020). In many areas of the world, tomato cultivation takes place indoors in greenhouses or other protected facilities. Although such systems are very energy intensive, they also offer opportunities. One important opportunity is the possibility of precisely controlling the light environment. LED technology offers greatly improved energy efficiency for lighting, as well as control over the light spectral composition (Pattison et al., 2018). A recent example shows how supplemental FR light not only boosts

stem elongation and suppresses tomato plant defense, but can also promote partitioning of dry mass to fruits under greenhouse conditions (Ji et al., 2019). Indeed, the observed promotion by supplemental FR of sugar metabolism (Ji et al., 2020) and soluble sugar levels (Courbier et al., 2020) leads to increased tomato fruit sink strength (Ji et al., 2020). The precise mechanisms of these FR-induced changes in sugar metabolism and partitioning remain to be elucidated. Although this is in part related to the reduced JA signaling in FR-enriched light, there may also be a photosynthetic component that contributes to increased yield (Zhen and Bugbee, 2020). It will be interesting to see if and how such beneficial effects of FR on fruit production can be balanced against its detrimental effects on defense.

Photoreceptors Regulate Crop Quality

As mentioned above, photoreceptors not only regulate plant biomass and form, but also plant defense against attackers. These defense pathways often include the accumulation of specialized metabolites, many of which are important to define the quality of the harvest or have applications in the food and pharmaceutical industry. For example, R and FR wavelengths have been shown to regulate the accumulation of glucosinolates (Engelen-Eigles et al., 2006; Cargnel et al., 2014), terpenes (Kegge et al., 2013; Carvalho et al., 2016; Cortés et al., 2016), alkaloids (Matsuura et al., 2016), anthocyanins, and other phenolic compounds (Kitazaki et al., 2018) that are often, but not always, co-regulated by the JA pathway. As discussed in other recent reviews, there is huge potential for improving crop quality by manipulating the light environment (Vänninen et al., 2010; Johansen et al., 2011; Huché-Thélier et al., 2015; Demotes-Mainard et al., 2016; Holopainen et al., 2018; Neugart and Schreiner, 2018), and some of these manipulations could be even extended during transport and storage of the produce (Campbell et al., 2020).

CONCLUDING REMARKS AND FUTURE DIRECTIONS

We review how plant neighbor detection involves the action of a multitude of light cues that are detected by several photoreceptors. These different signals are integrated over spatial and temporal scales (Küpers et al., 2018) to result in a coordinated output that enables plants to forage for light in dense and heterogeneous canopies. We are starting to understand the very detailed control of transcription factor networks in interaction with hormonal networks in their respective spatial (organs, cell types) and temporal scales. Photoreceptor-mediated regulation of molecular networks also allows plants to modulate their immune systems in ways that are presumably adaptive in the wild, but with potentially negative consequences for crop health in intensive agriculture (Ballaré et al., 2012). Although our mechanistic understanding of growth–defense trade-offs is relatively limited, major progress has been made in the past decade and it has already become possible to genetically separate SAS and defense regulation in response to low R:FR. CRISPR-Cas9 genome-editing technologies (Zhang et al., 2018; Manghwar et al., 2019) present a spectacular opportunity to translate detailed mechanistic insights from *Arabidopsis* to crops. Progress in this direction will require comparative studies

between *Arabidopsis* and crops to validate to what extent our detailed understanding of SAS–defense mechanisms can be translated to other species. These comparative studies can cherry-pick from the vast *Arabidopsis* knowledge base, which in turn will have to keep expanding to sustain the translational research needed to feed the world, now and in the future.

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