The shade avoidance syndrome: Multiple signals and ecological consequences

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ABSTRACT

Plants use photoreceptor proteins to detect the proximity of other plants and to activate adaptive responses. Of these photoreceptors, phytochrome B (phyB), which is sensitive to changes in the red (R) to far-red (FR) ratio of sunlight, is the one that has been studied in greatest detail. The molecular connections between the proximity signal (low R:FR) and a model physiological response (increased elongation growth) have now been mapped in considerable detail in Arabidopsis seedlings. We briefly review our current understanding of these connections, and discuss recent progress in establishing the roles of other photoreceptors in regulating growth-related pathways in response to competition cues. We also consider processes other than elongation that are controlled by photoreceptors and contribute to plant fitness under variable light conditions, including photoresponses that optimize the utilization of soil resources. In examining recent advances in the field, we highlight emerging roles of phyB as a major modulator of hormones related to plant immunity, in particular salicylic acid and jasmonic acid (JA). Recent attempts to manipulate connections between light signals and defense in Arabidopsis suggest that it might be possible to improve crop health at high planting densities by targeting links between phyB and JA signaling.

Summary statement

During the last four decades, there has been an enormous increase in our understanding of how plants sense shading and the proximity of neighbors, and how they activate adaptive morphological and physiological responses. Important elements of the signal transduction pathways that connect informational photoreceptors with functional responses have been elucidated, and shade avoidance has become a textbook example of adaptive plasticity. It is now becoming clear that proximity perception leads to a complete reconfiguration of plant function. This reconfiguration allows the plant to optimize the deployment of leaves into light gaps, balance resource allocation between shoots and roots, optimize leaf gas exchange and nutrient uptake as a function of the degree of shading, and adaptively regulate interactions with herbivores, pathogens and beneficial microorganisms. In this review, we describe the progress in understanding shade avoidance mechanisms and highlight the diversity of plant processes and functions that are controlled by canopy light signals.

INTRODUCTION

During the last four decades there has been an enormous increase in our understanding of how plants sense shading and the proximity of neighbors, and how they activate adaptive morphological and physiological responses. Research in the field has moved from working on simple morphological responses (e.g., internode elongation) to a single light cue (low R:FR ratio) to the discovery of multiple responses elicited by a broad spectrum of neighbor proximity signals. Important elements of the signal transduction pathways that connect informational photoreceptors with functional responses have been elucidated, and shade avoidance has become a textbook example of adaptive plasticity. In this review, we describe the progress in understanding shade avoidance mechanisms, summarize our current view of the roles of different photoreceptors in the perception of competition, and highlight the diversity of plant processes and functions that are controlled by canopy light signals. We also consider future challenges and opportunities in this multidisciplinary research field. Other reviews on this topic have been published recently, and provide additional perspectives on the mechanisms and functional implications of shade avoidance responses (Casal, 2013, Ballaré, 2014, Pierik & de Wit, 2014, Pierik & Testerink, 2014, de Wit *et al.*, 2016a, Fraser *et al.*, 2016, Viczian *et al.*, 2016).

PHYTOCHROME PERCEPTION OF CHANGES IN THE R:FR RATIO

Connecting shade with phytochrome

As early as 1971, studies on cultivated tobacco revealed that the ratio between Red (R, $\lambda \sim 650$ nm) and Far-Red (FR, $\lambda \sim 730$ nm) radiation was lower under the canopies than in direct sunlight, and that plant treatment with FR radiation could promote stem elongation (Kasperbauer, 1971). These studies inspired the pioneering work of H. Smith in the 1970's, describing the basics of shadelight perception and responses. Using a FR supplementation approach, it was found that the R:FR ratio was a key determinant of elongation growth in shade-intolerant species such as *Chenopodium album* and *Sinapis alba*. R light is absorbed by plants for photosynthesis, whereas FR radiation is mostly reflected or transmitted. Elegant studies revealed that internode elongation was strongly accelerated at low R:FR ratios (e.g., Morgan & Smith, 1978), a response that could be considered adaptive because it would allow the plant to position its leaves in higher, better-lit strata of the canopy (Fig. 1A). These effects of light quality on elongation were attributed to phytochrome, a R:FR-reversible protein discovered in the 1950s by scientists working at the U.S. Department of Agriculture in Beltsville, MD (Hendricks & Borthwick, 1959) (for historigraphical accounts, see Sage, 1992, Lindblom, 2015). Typically, phytochrome occurs in a photoequilibrium between the active (Pfr) and inactive (Pr) states. Absorption of R light converts Pr to Pfr, whereas FR absorption by the active

Pfr form reverts it to the inactive Pr state. In addition to this R:FR photoreversibility, Pfr can spontaneously revert to the inactive Pr state by a slow non-photoinduced reaction (Li *et al.*, 2011). Internode elongation rates of light-grown *Chenopodium album* and *Sinapis alba* seedlings were found to correlate very tightly with the phytochrome photoquilibrium, defined as Pfr/Ptotal (Morgan and Smith, 1978; Child and Smith, 1983). The early work of Smith and co-workers provided three key pieces of evidence to support the concept that the main function of phytochrome was to promote stem elongation under shade: i) the R:FR ratio was an excellent signal of canopy cover; ii) within the natural range of variation [between 1.2 (full sunlight) and 0.1 (deep shade)], changes in R:FR ratio are linearly related with changes in the estimated phytochrome photoequilibrium; and iii) under experimental conditions, the rate of internode elongation is inversely related to the calculated Pfr/Ptotal ratio established by the light sources (Smith, 1982). This work was followed by outdoor experiments in several systems that began to address the role of phytochrome in the perception of leaf shading and the ecological implications of plant responses to light quality under field conditions (Deregibus *et al.*, 1985, Ballaré *et al.*, 1987, Schmitt *et al.*, 1995, Schmitt *et al.*, 1999).

A particularly important aspect of R:FR dynamics during the growth of a plant stand is that the R:FR ratio of horizontally-propagated light decreases before true shading among neighboring plants occurs, owing to the backscattering of FR radiation by green leaves (Ballaré *et al.*, 1987). This reflection signal allows plants to remotely detect their neighbors and activate elongation responses before the onset of competition for resources (Ballaré *et al.*, 1987, Ballaré *et al.*, 1990). Laboratory experiments with linear variable displacement transducers indicated that internode elongation responses to FR-enrichment can occur very rapidly, within minutes upon FR exposure (Child & Smith, 1987), and canopy studies demonstrated that the internodes themselves are important sites of perception for reflected FR (Ballaré *et al.*, 1989, Ballaré *et al.*, 1990).

Subsequent research on shade avoidance demonstrated that not just internode or hypocotyl elongation are controlled by R:FR ratio, but in fact a suite of responses, including petiole elongation, upward leaf movement (hyponasty), inhibition of branching and acceleration of flowering are commonly co-expressed when phytochrome is inactivated. This suite of responses is collectively known as the Shade Avoidance Syndrome (SAS) (Smith, 1995).

Multiple phytochromes sense changes in R:FR ratio (discussed in Smith & Whitelam, 1997) and although phytochrome B (phyB) is the predominant phytochrome controlling SAS in response to low R:FR ratio (Franklin & Quail, 2010) and neighbor proximity (Ballaré, 1999), phyD and phyE seem to have partially redundant functions in Arabidopsis (Franklin & Quail, 2010). In young seedlings phyA partially antagonizes low R:FR-induced hypocotyl elongation, due to its activation by FR radiation. Since phyA is light-labile, its involvement in fully de-etiolated, more mature plants is rather modest (Franklin & Quail, 2010).

The signaling network downstream of phytochromes

A number of transcriptome surveys have been conducted on shade avoidance responses in Arabidopsis. The first ones were published more than a decade ago, using the aerial parts of young Arabidopsis seedlings (Devlin *et al.*, 2003, Salter *et al.*, 2003), and were followed by studies that focused on more mature, rosette-stage plants and sampled specific organs (Kozuka *et al.*, 2010, de Wit *et al.*, 2013, de Wit *et al.*, 2016b). Very recently, transcriptome surveys have been published that include detailed time series and between-organ comparisons of gene expression profiles (Das *et al.*, 2016, Kohnen *et al.*, 2016), and experiments that compare multiple light quality treatments (de Wit *et al.*, 2016b). These transcriptome surveys have been useful to generate models of regulatory networks. Nevertheless, functional proof for causal involvement of specific regulators has come from dedicated physiological and gene functional studies, which in some cases were combined with transcriptome profiling of genotypes with perturbed expression or activity of the proposed signaling components (e.g., Tao *et al.*, 2008, Hornitschek *et al.*, 2012, Leivar *et al.*, 2012, Li *et al.*, 2012, Ciolfi *et al.*, 2013, Pedmale *et al.*, 2016, Procko *et al.*, 2016).

An impressive variety of regulators downstream of phy photoconversion has been elucidated, mostly by studying the elongation response of Arabidopsis hypocotyls to supplemental FR irradiation under white light conditions (Fig. 1B). We will classify these regulators according to function and discuss them briefly.

Phytochrome-interacting factors (PIF)

Phytochrome, upon activation by R light, migrates from the cytosol to the nucleus where it interacts with Phytochrome Interacting Factors (PIFs), a group of subfamily 15 of bHLH transcription factors (Leivar & Quail, 2011, Leivar & Monte, 2014). Although this family contains 7 members that can physically interact with phytochrome, only three of these phy-interacting proteins are unambiguously involved in SAS control: PIF4, PIF5 and PIF7. PIFs contain an Active Phytochrome-

Binding (APB) domain with which they interact specifically with the biologically-active Pfr form of phyB, although PIF1 and PIF3 have been shown to also interact with Pfr from phyA through a motif called active phytochrome A-binding (APA) (Li *et al.*, 2011). Upon interaction with phyB Pfr, PIFs typically are phosphorylated and in the case of PIF4 and PIF5 they are subsequently ubiquitinated and degraded (Lorrain *et al.*, 2008). In the case of PIF7, phosphorylation occurs but no subsequent degradation was observed, even though PIF7 ability to regulate transcription of target genes was inhibited (Li *et al.*, 2012).

Other transcriptional regulators

Several other transcriptional regulators are controlled at the transcriptional level by phytochrome inactivation in low R:FR ratios (Fig. 1). Among these are other members of the bHLH family, such as HFR1, PAR1 and PAR2 (Sessa *et al.*, 2005, Roig-Villanova *et al.*, 2007). These three proteins are negative regulators that lack a typical basic domain to interact with promoters of target genes. Instead, they interact with the DNA binding domain of PIF proteins, preventing PIFs from interacting with the promoters of their target genes (Hornitschek *et al.*, 2009, Galstyan *et al.*, 2011). These regulators are thought to keep the strength of elongation responses in check. Indeed, *hfr1* knockout mutants have exaggerated low R:FR-induced hypocotyl elongation, whereas an over-expressor of a stable HFR1 protein has suppressed elongation (Galstyan *et al.*, 2011). These studies have been limited to young seedlings and the functionality of these negative regulators in mature plants remains to be verified. Other bHLH proteins whose gene expression is induced upon low R:FR ratio, but that are positive regulators of SAS, include BEE1 and BIM, which are PAR1-interacting factors (Cifuentes-Esquivel *et al.*, 2013).

Transcription factors from families other than bHLHs that are induced upon exposure to low R:FR ratios include homeodomain-leucine zipper (HD-ZIP) proteins encoded by *ATHB2, ATHB4, HAT1, HAT2* and *HAT3* (Steindler *et al.*, 1999, Sorin *et al.*, 2009). *ATHB2* diurnal expression under short day conditions has been shown to be PIF4 and PIF5 dependent (Kunihiro *et al.*, 2011). *ELONGATED HYPOCOTYL 5* (*HY5*) encodes a bZIP transcription factor that is up-regulated in response to low R:FR ratio (Ciolfi *et al.*, 2013, de Wit *et al.*, 2016b) [although HY5 protein stability is reduced by end-of-day FR (Toledo-Ortiz *et al.*, 2014)] and that can interact with PIFs (Chen *et al.*, 2013), thereby inhibiting their function in a way that is similar to HFR1.

Hormones

The above-described transcription factor network is highly interconnected, and novel components and interactions are still being elucidated. This network, largely centered around PIFs (Fig. 1), is now known to target some major physiological regulatory components, particularly hormones. Upon exposure to low R:FR ratios, the biosynthesis of at least three growth-associated hormones is stimulated: gibberellins (GA), auxin, and ethylene. In addition, low R:FR desensitizes plants to defense-associated plant hormones, such as jasmonic acid (JA) and salicylic acid (SA), which leads to a crosstalk between shade avoidance and plant immunity that will be discussed in sections "Effects on biotic interactions" and "Growth-defense balance".

Auxin is now known as the dominant physiological regulator activated by PIF proteins when they accumulate in low R:FR light. Low-R:FR-induced auxin is derived from tryptophan through the TAA1 pathway (Tao *et al.*, 2008) and involves PIF-mediated transcription of *YUCCA* genes that encode rate-limiting enzymes in auxin biosynthesis (Hornitschek *et al.*, 2012, Li *et al.*, 2012). This low R:FR-induced de novo synthesis of auxin in seedlings occurs mostly in the cotyledons (Procko *et al.*, 2016) and drives expression and localization of the auxin efflux-associated protein PIN3 to transport auxin towards the hypocotyl epidermis (Keuskamp *et al.*, 2010). In the epidermis auxin induces both brassinosteroid (BR) responses, as well as BR-independent responses (Procko *et al.*, 2014). Auxin signaling through the receptor TIR1 and related Auxin Signaling F-Box Proteins (AFBs) leads to degradation of AUX/IAA proteins, which in turn relieves repression of Auxin Response Factors (ARFs) that control transcription of auxin response genes, ultimately leading to cell growth (reviewed in Dünser & Kleine-Vehn, 2015).

Low R:FR conditions also stimulate the biosynthesis of another group of growth-promoting hormones: GA. This occurs at least in part through transcriptional up-regulation of genes encoding the GA biosynthetic enzymes GA20ox1 and GA20ox2 (Hisamatsu *et al.*, 2005). Bioactive GA, upon interacting with its receptor GID1, leads to ubiquitination and subsequent proteasomal degradation of DELLA proteins, GRAS domain proteins that lack direct DNA binding properties (Harberd *et al.*, 2009). Interestingly, DELLAs are direct interactors of PIFs (de Lucas *et al.*, 2008, Feng *et al.*, 2008) and their binding to PIFs prevents PIF proteins from binding DNA and thus controlling the expression of growth-promoting genes. Low R:FR ratios promote DELLA degradation(Djakovic-Petrovic *et al.*, 2007, Leone *et al.*, 2014), and proteins that physically interact with DELLAs, such as BBX24, were shown to modulate DELLA-mediated repression of PIF activity and shade avoidance responses (Crocco *et al.*, 2015).

Finally, biosynthesis of the volatile hormone ethylene is accelerated upon phytochrome inactivation in low R:FR light (reviewed in Kegge & Pierik, 2010). Cultivated tobacco plants expressing the dominant negative mutant receptor *etr1-1* from Arabidopsis are ethylene-insensitive and show delayed shade avoidance responses to plant neighbors at high density (Pierik *et al.*, 2004a). Although there is an interaction with R:FR signaling (Pierik *et al.*, 2004a), the delayed leaf movement and stem elongation responses to neighbors seem to be particularly associated with other canopy signals (Pierik *et al.*, 2004b), which will be discussed below.

Actuators in growth control

The above-described plethora of transcription factors, transcriptional co-regulators, hormone biosynthesis enzymes and hormone signaling components ultimately target the cell growth machinery. Shade avoidance research has mostly focused on cell expansion as the driving force of organ elongation. For plant cells to expand, they need to loosen their cell walls so they can yield to the existing turgor pressure from the vacuoles. Indeed an established shade avoidance marker gene that is under R:FR control is *XTH15/XTR7* (Hornitschek *et al.*, 2009, de Wit *et al.*, 2012). XYLOGLUCAN ENDOTRANSGLUCOSYLASE/HYDROLASE (XTH) proteins are cell wall modifying enzymes that can modify the load-bearing xyloglucan-cellulose cross links in the cell wall. Cleavage through hydrolase activity results in wall loosening, whereas transglucosylation can strengthen the cell wall, thus giving these proteins the potential to control cell growth (Rose *et al.*, 2002, Sasidharan *et al.*, 2011). It has been shown that PIFs can directly target the expression of for example *XTH15* in Arabidopsis seedlings under low R:FR ratios (Hornitschek *et al.*, 2009). Furthermore, coordinated auxin production and polar auxin transport has also been shown to be important for enhanced expression of different XTHs (e.g. *XTH17, XTH19*) in Arabidopsis petioles under shade (Sasidharan *et al.*, 2014). Interestingly, auxin involvement in shade-induced XTH expression intersects with another component of cell growth: cortical microtubules (CMTs) (Yu *et al.*, 2015). CMTs rearrange their subcellular localization in shade, facilitating unidirectional cell growth in Arabidopsis petioles, and disrupting CMT polymers with the drug oryzalin inhibits shade-induced petiole elongation. CMT disruption also minimizes shade-induced expression of some XTHs and this can be rescued by exogenous application of auxin (Sasidharan *et al.*, 2014). Finally, the classic mode of action for auxin-induced cell growth is the acid growth theory: auxin regulates activity of proton pumps in the plasma membrane, leading to acidification of the apoplast, thereby increasing, among others, the activity of cell wall modifying proteins (reviewed in Dünser & Kleine-Vehn, 2015).

MULTIPLE SIGNALS FOR SHADE AND NEIGHBOR DETECTION

The R:FR ratio is an incredibly reliable indicator of plant proximity since very few objects other than green plants absorb R light so efficiently, and FR barely at all. Perhaps because the signal appeared to be so good, shade avoidance research has focused for many years almost exclusively on phytochrome signaling of changes in R:FR ratio (Ballaré, 1999). Nevertheless, there is now strong evidence that other signals play an important role activating shade avoidance responses in plant canopies. Most of these signals are generated from the spectral properties of leaves, which include strong absorption of R, blue and ultraviolet (UV) radiation and reflection and transmission of green and especially FR radiation. The emerging picture is that different light signals interactively control shade avoidance, thus adjusting the magnitude of response to the severity of competitive threat.

Light intensity

Although dismissed as "essentially irrelevant" in an influential *Commentary* in this journal (Smith & Whitelam, 1997), attenuation of overall light intensity is now known to indeed induce shade avoidance responses. One reason for the initial dismissal of light intensity (irradiance) as a shade signal could be that, under conditions in which light is limiting for photosynthesis (as was the case in many growth-chamber studies), the trophic effects and the photomorphogenic effects of light attenuation could have been confounded. Consistent with this hypothesis, in studies where shading was applied from the side, simulating the proximity of other plants but without affecting the light received by the leaves, attenuation of the light received by the internodes caused strong elongation responses (Ballaré *et al.*, 1991). Another reason for not considering total irradiance as a shade signal was that shade avoidance research at that time was rather "elongation-centered", whereas especially leaf angles are highly responsive to changes in light intensity (Pierik *et al.*, 2004b, Mullen *et al.*, 2006, Millenaar *et al.*, 2009). The effects of light intensity promoting shoot elongation are partially mediated by cryptochromes (as discussed in the following section). However, early studies have shown that attenuation of R and FR radiation (without affecting blue light or the R:FR ratio) is sufficient to promote stem elongation in some species (Ballaré *et al.*, 1991). The available evidence suggests that this irradiance response is mediated by phyB in Arabidopsis (Trupkin *et al.*, 2014).

Interestingly, leaf responses that may contribute to shade tolerance, rather than avoidance, including the increase in specific leaf area (SLA), are strongly sensitive to changes in the intensity of photosynthetically active radiation (PAR) (Björkman, 1981), but poorly responsive to changes in R:FR ratio (Poorter et al., 2011). Essentially, a higher SLA indicates a larger area to intercept solar

radiation per unit carbon invested in the construction of leaf tissue, often coinciding with a thinner leaf through formation of fewer mesophyll cell layers.

Blue light

Blue light depletion can trigger shade avoidance responses in many plant species. Perhaps the best studied shade avoidance response controlled by blue light is phototropism, which is mediated by phototropins (phot1 and phot2 in Arabidopsis) (Briggs & Christie, 2002). Positive phototropism to blue light, along with negative phototropic responses to reflected FR radiation (Ballaré *et al.*, 1992), can help plants to direct their growth toward canopy gaps in patchy canopies (Ballaré *et al.*, 1995b, Ballaré, 1999). Interestingly, in Arabidopsis seedlings, phot-mediated phototropism is enhanced by low R:FR ratios (Goyal *et al.*, 2016).

Internode and petiole elongation in species such as tobacco, jimsonweed, mustard and Arabidopsis is also stimulated by the attenuation of blue light (Ballaré *et al.*, 1991, Pierik *et al.*, 2004b, Sellaro *et al.*, 2010, Keller *et al.*, 2011, Keuskamp *et al.*, 2011). Exposure of light-grown Arabidopsis seedlings to light deprived of the blue component leads to a very strong elongation response of the hypocotyl, even larger than that induced by low R:FR (Pierik *et al.*, 2009). This and other elongation responses to blue light depletion are triggered through the photoreceptors crytochrome 1 and 2 (cry1 and cry2) in Arabidopsis (Pierik *et al.*, 2009, Keller *et al.*, 2011, Pedmale *et al.*, 2016). Low blue and low R:FR signaling recruit partially similar physiological regulators to control hypocotyls elongation, including auxin, brassinosteroids and XTHs (Keuskamp et al., 2011) (Fig. 1). Interestingly, also upstream of the hormones, low blue and low R:FR signaling were recently shown to converge in their requirement of transcriptions factors PIF4 and PIF5 (Keller *et al.*, 2011). Pedmale *et al.* (2016) showed that cry1 and cry2 interact physically with PIF4 and PIF5, thereby modulating their transcriptional output and hence growth, involving XTHs. The main difference between low R:FR ratio and low blue light seems to be that low R:FR-mediated hypocotyl elongation involves a dominant role for PIF7, with the *pif7* knockout being essentially irresponsive to low R:FR (Li *et al.*, 2012), whereas the *pif7* mutant still shows pronounced low blue-mediated elongation (Pedmale *et al.*, 2016). Although blue light depletion induces shade avoidance responses, depletion of blue light will not occur alone in dense vegetation (Ballaré *et al.*, 1991). The functional relevance of blue light signaling in the control of shade avoidance seems to be that low blue levels enhance the elongation responses induced by low R:FR ratios, thus allowing plants to attune their shade avoidance phenotype to the severity of competitive threat. This enhancement appears to occur through

suppression by blue light depletion of negative SAS regulators, such as HFR1, which are induced by low R:FR conditions (de Wit *et al.*, 2016b).

UV-B radiation

Plant canopies effectively filter out UV radiation, including the UV-B (290-315 nm) component (Flint & Caldwell, 1998), and changes in UV-B levels can affect plant growth. Inhibition of hypocotyl elongation by UV-B radiation involves the UV-B receptor UVR8 in Arabidopsis (reviewed in Jenkins, 2009, Ulm & Jenkins, 2015). UVR8 binds to CONSTITUTIVELY PHOTOMORPHOGENIC 1 (COP1), thereby promoting accumulation of HY5 and HY5 HOMOLOGUE (HYH) (Brown & Jenkins, 2008, Favory *et al.*, 2009). HY5/HYH promote GA degradation, leading to stabilization of growth-repressing DELLA proteins and inhibiting PIF function. UV-B also enhances the degradation of PIF4 and PIF5 (Hayes *et al.*, 2014). Consequently, PIF and auxin-dependent elongation responses to low R:FR ratio can be antagonized by the UVR8-dependent signaling of UV-B radiation (Hayes *et al.*, 2014, Mazza & Ballaré, 2015).

Non-light cues

Although canopy-generated light cues probably dominate neighbor detection and shade avoidance, some complementary signaling mechanisms have been described. It was found in Arabidopsis canopies that the flat lying rosette leaves do not generate a strong FR-reflection signal, due to the absence of a vertical structure. As a consequence, these plants detect neighbors through touching of neighboring leaf tips. In response to this biomechanical detection, Arabidopsis leaves move upward, thereby creating a vertical structure that generates horizontal FR reflection, thus triggering low R:FR responses in the stand, such as petiole elongation (de Wit *et al.*, 2012). The regulatory (sensing) mechanisms underpinning these responses are currently unknown, but seem to differ from other established thigmomorphogenic responses (Chehab *et al.*, 2009, Chehab *et al.*, 2012).

Plants in high density stands can be close enough to communicate via volatile compounds. Much has been written about volatile organic compounds (VOCs) and their potential for carrying information about neighbor identity and physiological status. As mentioned above, ethylene emissions are largely increased under low R:FR light and it has been shown that ethylene can accumulate to physiologically meaningful concentrations in dense stands of cultivated tobacco (Pierik *et al.*, 2004b). Although the emission of several other volatiles from Arabidopsis (Kegge *et al.*, 2013), barley (Kegge *et al.*, 2015) and tomato (Cortés *et al.*, 2016) are affected by low R:FR ratios, it remains to be studied if these changes in VOC profiles are involved in neighbor detection and shade avoidance responses.

Nevertheless it has been shown that the changes in VOC emissions induced by low R:FR in barley can alter carbon allocation in neighboring plants (Kegge *et al.*, 2015).

FROM MORPHOLOGY TO MULTIPLE RESPONSES

The initial focus on stem elongation responses led to a detailed mechanistic understanding of the molecular connections between photoreceptors, particularly phyB, and growth-related signaling pathways (Fig. 1). Photoreceptors provide information on neighbor proximity and spatial distribution, thereby allowing the plant to "forage" for light in complex canopies. It is now becoming clear that proximity perception leads to a complete reconfiguration of plant function. This reconfiguration allows the plant to optimize the deployment of leaves into light gaps, balance resource allocation between shoots and roots, optimize leaf gas exchange and nutrient uptake as a function of the degree of shading, and adaptively regulate interactions with herbivores, pathogens and beneficial microorganisms (Fig. 2).

Optimizing resource capture and economy

The roles of phyB and other photoreceptors, including phototropins and cryptochromes, as modulators of morphological responses that are important for the optimization of leaf placement in patchy canopies are now well documented and have been summarized in previous sections of this review. Field studies have shown that mutants impaired in R:FR perception are less efficient than the corresponding wild types at foraging for light in heterogeneous light environments, providing direct evidence for the adaptive value of phytochrome-mediated shade avoidance (Ballaré *et al.*, 1995b, Schmitt *et al.*, 1995, Schmitt *et al.*, 1999). More recent work has suggested that, in addition to the main functions of phytochromes, cryptochromes and phototropins in controlling shoot architecture and foraging for light in patchy canopies, the UV-B photoreceptor UVR8 may contribute to attenuate shade-avoidance responses when the plant meets well-illuminated areas in canopy gaps (Hayes *et al.*, 2014, Mazza & Ballaré, 2015).

Besides optimizing light interception, evidence is emerging that photoreceptors play a key role adjusting plant structure, hydraulics and nutrient uptake. In this section, we provide examples of the role of informational photoreceptors in controlling plant functional acclimation to open or shaded conditions. Transition between sun and shade are often associated with sharp variations in exposure to mechanical stress from exposure to wind, evaporative demand, nutrient requirements, and need of photoprotection.

Structural acclimation

Early work in cucumber demonstrated that, in canopy openings, activation of phyB promotes morphological and anatomical changes that increase plant fitness (Casal *et al.*, 1994). Thus, when phyB is activated under sunlight conditions, Pfr promotes the formation of thicker and mechanically more resistant stems, with increased cross-section of xylem vessels and higher water conductivity compared with plants under shade. These responses were shown to be essential for plant survival in canopy gaps (Casal *et al.*, 1994). Effects of phyB on structural properties of the stems likely complement the specific effects of mechanical stress on internode architecture and mechanical resistance (Anten *et al.*, 2005).

Root function, uptake of soil resources, and nutrient metabolism

Root growth (Casal *et al.*, 1994), gravitropism (Galen *et al.*, 2007, Boccalandro *et al.*, 2008), and development (Salisbury *et al.*, 2007, Tong *et al.*, 2008) are known to be affected by photoreceptors. Some of the effects of photoreceptors on root growth, particularly during de-etiolation, are thought to be mediated by changes in photoassimilate supply from the cotyledons, which is affected by photoreceptor signals that trigger cotyledon expansion and the establishment of photosynthetic competence in the shoot as it emerges from soil (Kircher & Schopfer, 2012). The adaptive value of root responses to photoreceptor signals has seldom been tested in the field (Gundel *et al.*, 2014). However, there is some evidence that root foraging for soil resources can be influenced by photoreceptors. For example, Galen *et al.* (2007) demonstrated that the ability of Arabidopsis roots to forage for water in the field was impaired in a *phot-1* mutant. Root cells have photoreceptors, but aside from the case of very young seedlings, where physiologically significant amounts of light can be piped from shoot to roots (Lee *et al.*, 2016), or under certain types of substrates, such as very sandy soils (Tester & Morris, 1987), the vast majority of root cells will grow in the dark under field conditions. Therefore, most effects of light on root function are likely to depend on light perception by shoot cells and mobile signals traveling from shoot to roots. Recent research (Chen *et al.*, 2016) demonstrated that HY5, a transcription factor involved in the signal transduction pathways of nearly all photoreceptors, is a signal that moves from shoot to root and mediates light promotion of root growth and nitrate uptake in Arabidopsis seedlings. Thus shoot-derived HY5 activates *HY5* expression in the root and promotes nitrate uptake by activating *NRT2.1*, a gene that encodes a high-affinity nitrate transporter. In the shoot, HY5 promotes the expression of genes involved in carbon assimilation and translocation to roots (Toledo-Ortiz *et al.*, 2014, Chen *et al.*, 2016), whereas in the root, HY5 activation of *NRT2.1* expression and nitrate uptake is potentiated by increased sucrose levels (Chen *et al.*, 2016). HY5 function is irradiance-dependent, and this regulation appears

to play an important role, along with shoot-derived sugar signals (e.g., Kircher & Schopfer, 2012), in coupling nitrogen and carbon assimilation under variable light conditions (Chen *et al.*, 2016). Photoreceptors also modulate nutrient metabolism and redistribution, for example during shade-induced leaf senescence. The activity of nitrate reductase, a key enzyme in nitrogen assimilation, is regulated by phytochrome (Whitelam & Johnson, 1980) and this regulation, among other metabolic changes, such as chlorophyll degradation, may contribute to optimize the redistribution of nutrient assimilation and photosynthetic capacity throughout the plant, so as match the vertical light gradient in high density crops (Rousseaux *et al.*, 1996, Rousseaux *et al.*, 1997).

Regulation of stomatal conductance

Gas exchange per unit leaf area is also regulated by photoreceptors, presumably contributing to optimize CO_2 fixation under fluctuating light conditions. phyB controls stomatal differentiation (Casson *et al.*, 2009, Kang *et al.*, 2009), increasing stomatal density under open conditions (Boccalandro *et al.*, 2009). This developmental response helps to minimize epidermal resistance to CO_2 diffusion between the atmosphere and the mesophyll in leaves exposed to high irradiance (where light is not limiting for photosynthesis). However, the increased number of stomata could also make the plant more vulnerable to desiccation. This is, however, prevented by a positive effect of phyB on stomatal sensitivity to abscisic acid (González *et al.*, 2012). Blue light photoreceptors, including phot1 and phot2 and cry1 and cry2, may also be important to optimize photosynthesis under high irradiance, acting through mechanisms that are dependent or independent of stomatal responses (Boccalandro *et al.*, 2012).

Optimizing leaf photoprotection

Adjusting photoprotection as a function of light exposure is also an important function of photoreceptors. Positioning of leaves in well illuminated areas of the canopy during shade avoidance increases the availability of energy for photosynthesis, but at the same time increases the potential for harmful effects of UV radiation. Accumulation of protective phenolic sunscreens in the field is sensitive to small variations in the UV-B region of the solar spectrum (Barnes *et al.*, 2000, Mazza *et al.*, 2000), and the UV-B photoreceptor UVR8 has been shown to regulate the expression of numerous genes involved in the biosynthesis of these protective compounds (reviewed in Jenkins, 2009, Ulm & Jenkins, 2015). Under field conditions, other photoreceptors, besides UVR8, are likely to participate in the control of UV photoprotection (Morales *et al.*, 2013). The accumulation of epidermal sunscreens is coordinated with growth inhibition responses (Ballaré *et al.*, 1995a), and

dynamically adjusted under fluctuating light conditions to maximize photoprotection (Barnes *et al.*, 2016a, Barnes *et al.*, 2016b).

Effects on biotic interactions

Recent studies have demonstrated that plant functional responses to proximity signals can impact plant interactions not only with other plants (i.e. competition), but with a variety of other organisms, including herbivores, pathogens, symbionts and herbivore predators.

Interactions with enemies

A flurry of recent research has demonstrated that low R:FR ratios down-regulate defense responses in shade-intolerant species (reviewed in Ballaré, 2014). Inactivation of phyB leads to increased susceptibility to insect herbivores and microbial pathogens of various lifestyles. This increased plant susceptibility to pathogens and herbivores has been linked to reduced expression of defense-related traits, including phenolic compounds (Izaguirre *et al.*, 2006, Moreno *et al.*, 2009); glucosinolates (Engelen-Eigles *et al.*, 2006, Cargnel *et al.*, 2014); latex (Agrawal *et al.*, 2012), and extrafloral nectar (Izaguirre *et al.*, 2013).

The observed reduction of defense responses can be explained by simultaneous attenuation, under low R:FR ratios, of the two major hormonal pathways that orchestrate plant defense, namely the SA and JA signaling pathways (reviewed in Ballaré, 2014). The mechanisms that mediate the effects of phyB inactivation on SA signaling are not well understood. Reduced induction of SA synthesis (Griebel & Zeier, 2008) and response to SA (de Wit *et al.*, 2013) have been documented under conditions of phyB inactivation, and attenuation of SA under low R:FR ratios correlated with reduced levels of phosphorylation of the SA-signaling component NONEXPRESSOR of PATHOGENESIS-RELATED GENE 1 (NPR1) (de Wit *et al.*, 2013). In the case of JA responses, shading has been shown to reduce herbivory-induced JA accumulation (Agrawal *et al.*, 2012), and inactivation of phyB consistently reduces plant sensitivity to exogenous JA (Moreno *et al.*, 2009, Cerrudo *et al.*, 2012, de Wit *et al.*, 2013). Sensitivity to JA under low R:FR ratios is attenuated as a consequence of increased turnover of DELLA proteins (presumably in response to increased GA activity) (Leone *et al.*, 2014), and increased stability of jasmonate ZIM domain (JAZ) repressor proteins (Chico *et al.*, 2014, Leone *et al.*, 2014). Destabilization of MYC transcription factors in response to low R:FR may also contribute to attenuating defense responses (Chico *et al.*, 2014). Physical interaction (and mutual interference) between the growth-repressing DELLA proteins and defense-repressing JAZ proteins is thought to be critical in the regulation of resource allocation between growth and immunity (Hou *et al.*, 2010, Yang

et al., 2012). Therefore, the ability of phyB to affect the stability of members of these two protein families represents a critical link between the photoperception of neighbor proximity and the transcriptional programs that optimize resource allocation between shade avoidance and defense responses under variable conditions of competition (Ballaré, 2014, Mazza & Ballaré, 2015).

Interactions with beneficial microorganisms

There is growing evidence that photoreceptors, particularly phyB, can regulate plant interactions in the rizosphere. Plant nutrition is often dependent on associations between roots and beneficial microorganisms, such as nitrogen-fixing bacteria, and mycorrhizae. Early studies have demonstrated that these symbiotic associations are modulated by light quality (reviewed by Gundel *et al.*, 2014). For example, supplemental FR radiation perceived by the shoots reduces nodulation in legumes (Kasperbauer *et al.*, 1984, Kasperbauer & Hunt, 1994). Similarly, simulated canopy shade reduces mycorrhizal colonization in several plant species (de la Rosa *et al.*, 1998, Skálová & Vosátka, 1998, Pecháčková, 1999). The development of symbiosis and the subsequent maintenance of the symbiont represent a metabolic cost to the host plant, and the exchange of carbon for nutrients between plants and root symbionts is tightly regulated (Helber *et al.*, 2011). Therefore, it is reasonable to expect that photoreceptors that inform the plant about the prevailing light conditions (and hence the conditions for carbon assimilation) have a role modulating the establishment and symbiotic interactions. Recent work suggests that the positive effects of phyB on legume-*Rhizobium* interactions is mediated by enhanced JA signaling (Suzuki *et al.*, 2011). Similarly, the positive effects of high R:FR ratios and phyB on colonization of tomato and *Lotus japonicas* roots by arbuscular mycorrhizae correlate with enhanced expression of JA markers in the roots and increased concentrations in the root exudates of (+)-5-deoxystrigol, a strigolactone that functions as an inducer of fungal hyphal branching (Nagata *et al.*, 2015).

GROWTH-DEFENSE BALANCE

The demonstration that, in addition to the well-known effects on growth-related processes, photoreceptors are key regulators of plant immunity has lent support to the idea that these proteins have an important role in balancing allocation between growth and defense. When shade-intolerant plants are simultaneously challenged with competition and herbivory or pathogen attack, foraging for light through growth responses often takes priority over plant immune responses.

Short-term studies with Arabidopsis demonstrate that it is possible to genetically uncouple the effects of light on growth from the effects of light on defense. For example, the *sav3* mutant of Arabidopsis, which does not respond to supplemental FR radiation with increased leaf elongation and the classic repertoire of changes in shoot morphology, still displays a low defense phenotype in bioassays (Moreno *et al.*, 2009, Cerrudo *et al.*, 2012). Conversely, the *cry1* mutant, which shows a constitutively elongated phenotype under white light, does not display increased susceptibility to infection by the fungus *Botrytis cinerea* (Cerrudo *et al.*, 2012). More importantly, by mutating *JAZ* genes it has been possible to keep defenses at high levels in plants that express a classic SAS morphological repertoire in response to phyB inactivation (Cerrudo *et al.*, 2012, Leone *et al.*, 2014, Campos *et al.*, 2016, Cerrudo *et al.*, 2016).

The demonstration in Arabidopsis that it is possible to experimentally uncouple the effects of light on growth from the effects of light on defense indicate that, at least in the short term, plants are able to defend their tissues from consumer organisms even if they are committing resources to express shade-avoidance responses to outcompete their neighbors. At the same time, these observations beg the question of why, then, do plants normally repress their defenses when they face a high risk of competition? A possible explanation is that it is advantageous for the plant to make the decision of curtailing expenditures in defense while it still has plenty of resources. Unlike escape responses in animals, which can be very rapid, escaping from competition in plants often requires new growth, which could be slow and demanding in terms of carbon and other resources. Therefore, rapid use of information about neighbor proximity in the mechanisms that control resource allocation might be very important for plants that grow in competitive environments. It is also worth noting that plants appear to have evolved strategies to minimize the fitness costs of down-regulating defenses in response to competition signals. As explained below, these strategies take advantage of the modular nature of the plant body and the complex biotic scenario in which plants interact with their attackers.

Shrewd allocation

Plants are modular organisms, and as such they can save resources by activating defense responses only in their most valuable modules. Not all plant parts have the same importance for the capture of resources. For example, those leaves that are placed in well-illuminated strata of the plant canopy have a high potential to contribute to the carbon balance of the plant. In contrast, leaves that become shaded have a relatively low value and will eventually activate a senescence program leading to leaf abscission. Whereas the induction of defense in response to attack is generally

systemic (Ross, 1961, Green & Ryan, 1972), the repression of defense responses by photoreceptor signals appears to be localized (Izaguirre *et al.*, 2013). In *Passiflora edulis* plants, wounding and MeJA treatment activated the systemic production of extrafloral nectar (an indirect defense), and this response could be suppressed locally in individual branches by supplementing the light received by those branches with FR radiation (Izaguirre *et al.*, 2013). This suggests that, when activating a defense program in response to attack, the plant can, because of its modular organization, "sacrifice" those modules that encountered poor or not so promising light conditions, and concentrate its defense resources in the most valuable parts of the organism. The assignment of "value" to the different plant parts for this self-pruning strategy could be based on phyB status (where high Pfr levels would mean favorable light conditions), as in the *P. edulis* case. However, under natural conditions, other physiological differences between sun and shade branches may contribute to locally adjust the expression of the defense response. One of these additional signals could be the level of citokinins (discussed in Ballaré, 2014). Citokinins are positive regulators of defense and JA responses (Choi *et al.*, 2010, Dervinis *et al.*, 2010, Brütting *et al.*, 2016), and because of their higher transpiration rates, sun leaves have higher levels of cytokinins than shaded leaves (Boonman *et al.*, 2007).

Calling for help

Low R:FR ratios can alter the emission of constitutive and JA-induced VOCs in Arabidopsis, and these changes can be perceived by herbivorous insects (Kegge *et al.*, 2013). A recent study suggested that shifts in the blend of VOCs induced by phyB inactivation could play an important role in the attraction of predatory insects. Working with tomato, Cortés *et al.* (2016) found that when phyB was inactivated (by mutation or supplemental FR), leaf defenses were down-regulated, as expected; however, at the same time, phyB inactivation led the plants to produce a blend of JA-induced monoterpenes that increased their attractiveness to the predatory mirid bug *Macrolopus pigmaeus* (Cortés *et al.*, 2016). This predator can provide indirect protection to tomato plants by feeding on their insect herbivores (Lins *et al.*, 2014). If the pattern documented in tomato represents a general strategy, these results suggest that plants exposed to low R:FR ratios could minimize the cost of down-regulating direct defenses by finely adjusting the blend of volatile compounds that they emit in response to herbivory, turning themselves more attractive to prey-seeking carnivorous insects (Cortés *et al.*, 2016).

CHALLENGES AND OPPORTUNITIES

The field of plant photobiology has come a long way since the pioneering attempts to connect plant responses to shade with the activity of phytochrome. During the last decade, research on the photoresponses of Arabidopsis seedlings, using hypocotyl elongation as the principal physiological readout, has been very successful in elucidating the main signaling components that connect photoreceptors (particularly phyB) with growth responses (Fig. 1). At the same time, research in other systems and conditions has revealed that photoreceptors modulate virtually all aspects of plant acclimation to varying light conditions in canopies. This modulation includes some responses that were never thought to be connected with light signaling, such as, for example, nutrient uptake and chemical communication between plants and other organisms (Fig. 2). The future of the field is full of opportunities and interesting challenges, some which are briefly outlined below.

Dealing with complexity and signal interactions

The light environment of plant canopies is complex and includes a multiplicity of shade signals. R:FR-centered research has proven to be highly successful in elucidating the main elements of the core SAS pathway. Nevertheless, the demonstration that even mutants that fail to respond to R:FR ratio show strong shade-avoidance responses to plant proximity (Keller *et al.*, 2011) indicates that if the aim is to understand plant responses in nature, research will have to consider a broader array of light signals and photoreceptors. In addition, we know from physiological studies carried out more than four decades ago that the pathways activated by different photoreceptors often interact in the with each other (Mohr, 1972). Since the signaling components downstream of individual photoreceptors have now been studied at an appreciable depth, it is becoming feasible to include them in signaling networks, which consider several photoreceptors and plant responses to light in a more integrative way (Hayes *et al.*, 2014, Mazza & Ballaré, 2015, de Wit *et al.*, 2016b, Goyal *et al.*, 2016). This is highly important also when trying to translate knowledge on SAS control to crops in order modulate (aspects of) shade avoidance; simply selecting against R:FR responses, for example, will not necessarily eliminate responses to light intensity or other proximity signals.

Complexity is not only a matter of multiple light colors; it is also a consequence of spatial and temporal variation in these light signals. Not all parts of a plant experience the exact same combination of light cues, and these light cues can be dynamic over time. This is usually not a problem if the goal is to understand a simple system, such as the Arabidopsis seedling, where there is little room for spatial variation in light quality, and the studied responses are complete in a very short period of time. But field studies with more mature plants indicate that many important

photoresponses are locally controlled by the light environment of particular organs or parts. Examples include, among others, tillering responses in grasses (Deregibus *et al.*, 1985), stem elongation in even-height canopies (Ballaré *et al.*, 1990), leaf senescence (Rousseaux *et al.*, 1996, Rousseaux *et al.*, 1997), and reproductive abortion in soybean (Heindl & Brun, 1983). The modular nature of the plant body, and the response to local light signals are essential aspects of plant photomorphogenesis.

A successful way to deal with the evident need for understanding the increasing complexity in biological research is to include mathematical modeling. This can be achieved at many different organizational levels. Functional Structural Plant Models (FSP models) are a great tool to integrate a wide variety of physiological processes in a spatially explicit way, creating virtual plant stands in which parameters of plant growth can be modified. These parameters can include SAS in response to multiple light signals as occurring in these stands (Evers *et al.*, 2007, Bongers *et al.*, 2014). Computational models can also be used to understand interactions between light signals and resources (Hersch *et al.*, 2014), or to predict functional responses to signaling gradients (van Berkel *et al.*, 2013).

Dealing with processes other than growth responses

Given the historical focus on effects light on growth, it is not surprising that most of the efforts to elucidate downstream signaling pathways have concentrated on growth-related hormones, such as auxin, GA, and BR. However, it has recently become clear that photoreceptors are major modulators of the hormonal pathways that control plant defense, including JA and SA. This modulation is sensitive to the changes in the light spectrum associated with neighbor proximity, which may have important implications for the regulation of defense responses in crops (Ballaré *et al.*, 2012). Given the heightened interest in tradeoffs between plant growth and defense (Yang *et al.*, 2012, Leone *et al.*, 2014, Shyu & Brutnell, 2015, Campos *et al.*, 2016, Cerrudo *et al.*, 2016, Havko *et al.*, 2016, Kliebenstein, 2016, Smakowska *et al.*, 2016), and the realization that photoreceptors play a key role feeding proximity information into the signaling mechanisms that make adaptive decision in the face of these tradeoffs, we expect that a major challenge in future research will be to elucidate the mechanisms by which photoreceptors control defense signaling pathways.

Translating to crops

Whereas the mechanisms involved in the photocontrol of many important responses are now very well established, virtually nothing is known about the role of photoreceptors in controlling yield and

defense-related traits in crops under field conditions. As the amount of information on molecular responses to light signals in cultivated species continues to grow (Kebrom & Brutnell, 2007, Bush *et al.*, 2015, Horvath *et al.*, 2015, Kharshiing & Sinha, 2015, Carriedo *et al.*, 2016, Wang *et al.*, 2016), the opportunities to manipulate those responses using traditional breeding, transformation, genome editing or other technologies will obviously increase. A major challenge will be to identify which responses should be manipulated in order to have a significant impact on crop yield, yield stability, crop health and/or plant quality. For example, it could be interesting to eliminate the effects of those light proximity signals that redirect resources to stem or petiole elongation at the expense of other desirable functions, such as plant defense. However, at the same time, it would be important to retain the ability of plant shoots to phototropically locate gaps in the crop canopy, to maximize light interception, or to adjust stomatal behavior as a function of the prevailing light conditions, in order to optimize gas exchange. The recent progress in dissecting the signaling pathways that control specific decisions downstream of the photoreceptors provides an opportunity to target specific signaling elements so as to manipulate individual responses. For example, a step forward might be to uncouple defense responses from proximity perception in crop plants (Ballaré *et al.*, 2012). Recent studies in Arabidopsis show that null mutations in *JAZ* genes can reduce or eliminate the negative effect of low R:FR ratios and phyB inactivation on plant immunity against necrotrophic pathogens and chewing insects, but without affecting morphological responses to shade signals (Cerrudo *et al.*, 2012, Campos *et al.*, 2016, Cerrudo *et al.*, 2016). These findings hint at possible ways to develop crop plants that retain strong defense responses even when grown at high density. Refinement of technologies such as high-throughput sequencing and development of new model systems and genetic resources will surely help to identify targets for crop improvement. In a related vein, recent advances in artificial lighting technology, including the development of high-output LED arrays (Huché-Thélier *et al.*, 2015, Demotes-Mainard *et al.*, 2016), provide great potential for applying our increased understanding of plant photobiology to improve the yield, health and produce quality in horticultural crops.

CONFLICT OF INTERESTS

The authors have no conflicts of interest to declare.

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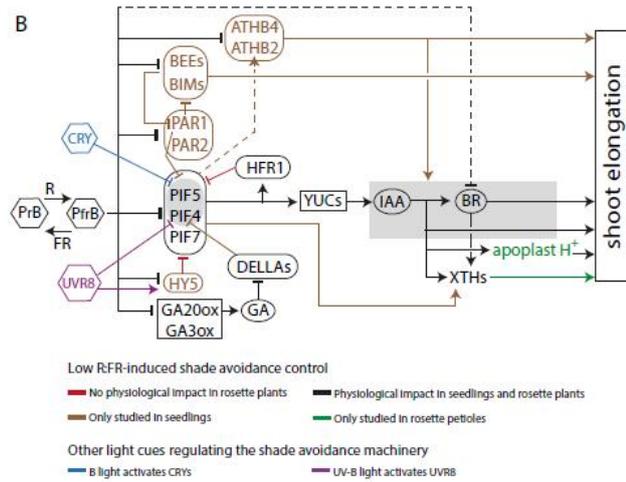
Fig. 1. Photoreceptors regulate shade avoidance responses. A. *Brassica nigra* grown for two weeks in a growth chamber under white light (R:FR = 2.1) or white light supplemented with FR (R:FR = 0.2). Low R:FR stimulates elongation of the hypocotyl, internodes and petioles, whereas the expansion of the leaf lamina is inhibited. Growth conditions: 9 h light (PAR = 150 µmol m^{-2} s^{-1}, 15 h light), RH = 70 %, 21°C). B. Schematic representation of the signal transduction network that regulates elongation responses under the control of phyB. UV-B signaling through UVR8 and blue light signaling through CRYs also feed into the core PIF signaling hub that orchestrates the majority of the downstream events. Different colors indicate study systems in which certain signal transduction components were shown to function in low R:FR-induced elongation.

Rounded boxes: transcription (co)factors, square boxes: hormone biosynthetic enzymes, ellipses: hormones, hexagons: photoreceptors. Dashed lines: hypothesized mode of action. Arrows: positive interaction, Blocked arrows: negative interaction.
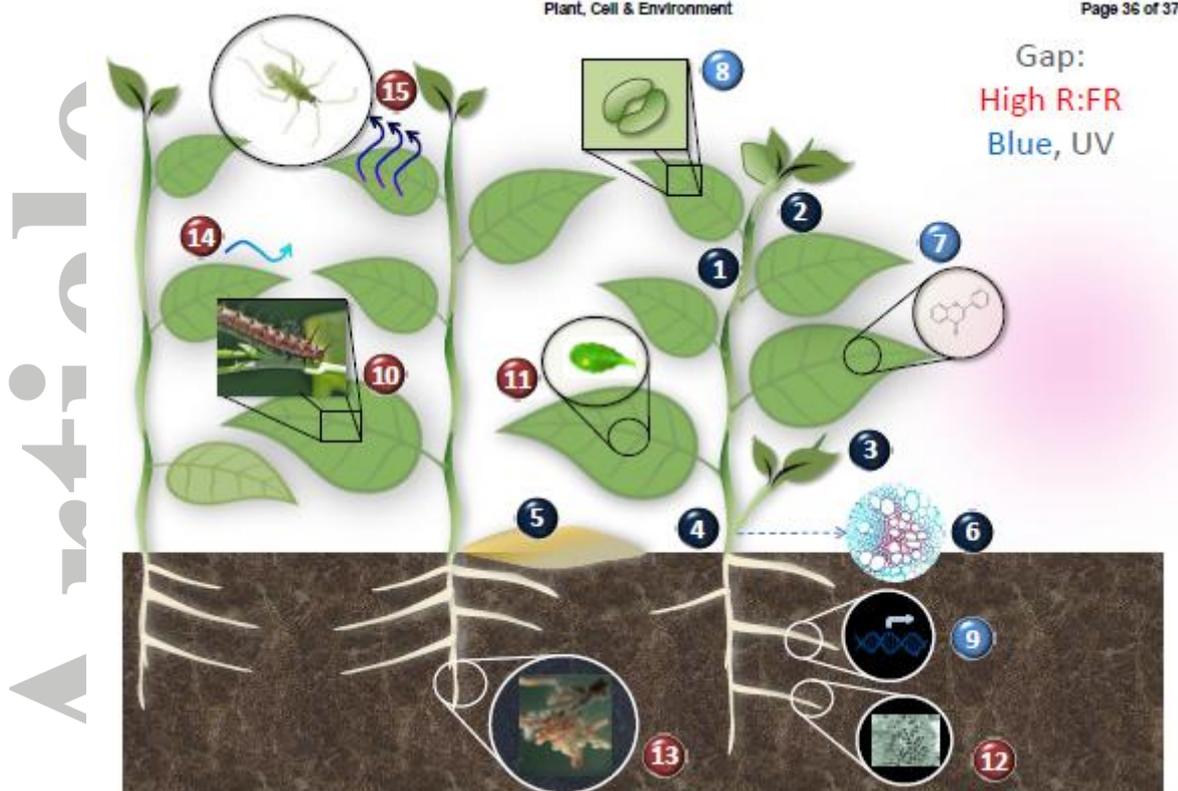
Fig. 2. Photoreceptors optimize plant structure and function in patchy canopies. As discussed in the text, proximity cues perceived by phyB and other photoreceptors are used by the plant to optimize foraging for light, as these signals regulate stem elongation (1); phototropism (2); branching (3); resource partitioning between shoot and roots (4); and leaf senescence (5). In addition to these structural changes that allow the plant to optimize the spatial distribution of its branches and leaves in the canopy light matrix, photoreceptors regulate the mechanical strength and hydraulic resistance of the stem (6), and contribute to adjust the physiology of resource-harvesting organs to the prevailing light conditions. Under high light, such in a canopy gap, photoreceptors activate leaf photoprotection (7), increase stomatal conductance and sensitivity to water stress signals (8); and activate mobile signals that increase the expression of a NO_3^- transporter in the roots (9), which presumably contributes to maintain the C:N homeostasis under changing light conditions. Proximity signals perceived by phyB also have profound effects on plant interactions with other organisms. Low R:FR ratios locally repress jasmonic acid signaling and down-regulate salicylic acid responses, which reduces plant resistance to herbivores (10) and pathogens (11). Light effects on jasmonate signaling also affect plant interactions with root simbionts, including rizhobia (12) and mycorrhyzae (13). Low R:FR ratios also promote the emission of ethylene, which may contribute to shade avoidance (14), and alter the blend of terpene compounds emitted by induced plants, which may contribute to increase indirect defense against herbivores in shaded plants (15).