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Title:

Reaching out for the sun: plant strategies enhancing access to sunlight.

Authors:

Anne-Sophie Fiorucci[1] and Christian Fankhauser[1,*].

Author affiliations:

[1] Center for Integrative Genomics, Faculty of Biology and Medicine, University of Lausanne, CH-1015 Lausanne, Switzerland.

*Correspondence: christian.fankhauser@unil.ch

ORCID IDs: 0000-0002-3254-5967 (A.-S. F.), 0000-0003-4719-5901 (C.F.).

Summary

Light is a vital resource for plants, which compete for its availability particularly in dense communities. Plants possess multiple photosensory receptors to detect the presence of competitors and thereby adjust their growth and developmental strategies accordingly. Broadly speaking plants fall into two categories depending on their response to foliar shade: shade tolerant or shade avoiding. In this review we will describe the photoperception mechanisms and the growth responses elicited by the neighboring vegetation in shade-avoiding species. As these mechanisms are best understood in *Arabidopsis thaliana*, we will focus on this species. The type of responses depends on plant density ranging from neighbor detection modulating growth in anticipation of future shading to the response to canopy shade where light resources are limiting. These diverse environments are sensed by various photoreceptors and we will describe our current understanding of signal integration triggered by distinct light cues in diverse light conditions.

Introduction

Plants perceive direct sunlight in open habitats or at the top of the canopy but have to face daily and seasonal fluctuations of light composition. While the spectral composition of solar radiation is rather constant during the day when the sun is high on the horizon, it is significantly enriched in blue and far-red (FR) wavelengths at twilight. Clouds further reduce the incoming light up to 90%, but without a major effect on the color spectrum [1]. Light composition also changes during the year, particularly at high latitudes when the sun remains low on the horizon, and it has been proposed that plants use this color information in addition to photoperiod to prepare for seasonal adaptations [2].

Once sunlight reaches plants, it is used as a source of energy for photosynthesis through absorption by chlorophyll and other pigments composing the photosynthetic apparatus. Photosynthetically active radiation (PAR) approximately corresponds to the spectrum visible to the human eye (λ=400-700 nm) but light absorption by photosynthetic pigments occurs especially in the blue (λ=400-500 nm) and red (λ=600-700 nm). In parallel a large part of FR light (λ=700-750 nm) is transmitted and/or reflected by plant tissues (Figure 1A). These spectral properties of aerial plant tissues have a great influence on light composition available to plants, particularly when considering their ecological context.

Indeed even in open habitats, plants are rarely isolated and are mostly found within communities, where competition for light between plants of equivalent height is high. This is the case in both natural situations, like meadows or clearings, and agricultural fields. In such environments plants detect the presence of neighboring competitors through an increased perception of reflected FR light leading to a low R/FR ratio, without any major drop in the global amount of light [3] (Figure 1B). In shade-avoiding plants this so-called neighbor detection triggers a suite of morphological adaptations which are thought to help outgrow competitors: elongation of stem-like structures, elevation of leaves, as well as reduced branching and acceleration of flowering. Such morphological and developmental changes are associated with an increased fitness in competitive environments but occur at the expense of biomass production [4-6]. An additional apparent cost of the shade avoidance

strategy is the reduced ability of such plants to defend themselves against a variety of pathogens [7] and to develop symbiotic interactions with micro-organisms [8].

A drop in the R/FR ratio serves as an early signal of a forming canopy indicating that plants will soon face unfavorable conditions [9]. With the closure of the canopy, light quantity decreases progressively as the leaf area index increases [10, 11]. Most of the blue, red and UV-B wavelengths are absorbed by leaf covering and the resulting filtered light is relatively enriched in green and FR (Figure 1A). These conditions are thus characterized by both a low PAR and a low R/FR ratio. In such conditions, shade-avoiding species like most crops (tomato, cereals, legumes, etc.) display elongation phenotypes, a quantitative response increasing according to plant density [12]. However, many herbaceous species living under closed canopies like forest understory cannot outcompete tall trees and have developed strategies of shade-tolerance helping to cope with dim light and to optimize light capture [13]. For example, a Begonia species living under a tropical canopy has specialized epidermal chloroplasts or iridoplasts whose physical properties enhance light harvesting and photosynthetic yield under low light conditions, especially in the green range of the spectrum [14]. Moreover, recent comparison of two closely related Geranium species highlight the contrasted growth and gene expression patterns as well as the opposite regulation of defense genes between shade tolerant versus avoiding species [15].

Natural canopies are however not homogeneous environments. Foliar cover is often uneven providing some plants with transient access to unfiltered sunlight depending on the position of the sun or the time of day. These sunflecks inhibit the shade avoidance response (e.g. stem growth), especially when occurring in the afternoon [16]. Gaps in canopies also provide potential access to unfiltered sunlight and represent a good opportunity for plants to get higher amounts of light for photosynthesis. In such conditions, plants tend to reorientate their growth towards the more favorable light environment [17]. This is particularly visible at the edge of a canopy where plants are submitted to a stable lateral light gradient (Figure 1B-C), triggering directional growth or phototropism, with bending of stem-like structures favoring the repositioning of photosynthetic organs for optimized light absorption [17-19].

In this review, we aim at describing how light perception modulates the extent and direction of plant growth leading to enhanced light harvesting for photosynthesis. In particular, we will describe the current understanding of the shade avoidance and phototropism responses, with an emphasis on the integration of information coming from various photoreceptors. We will primarily focus on *Arabidopsis thaliana*, a shade-avoiding plant, because most of the molecular mechanisms underlying these responses have been identified in this species.

Photoreceptors regulating the extent and direction of growth depending on plant density.

Plants use light parameters such as spectral composition, light intensity, direction and duration as a source of information from the environment to modulate growth and control developmental transitions. Different classes of photoreceptors perceive specific ranges of the light spectrum: cryptochromes, phototropins and Zeitlupes absorb blue/UV-A, phytochromes maximally absorb red and FR but also absorb blue light, and UVR8 absorbs UV-B (λ=280-315 nm) [20]. With the notable exception of UVR8, photoreceptors are chromoproteins composed of an apoprotein associated with a light-absorbing chromophore. UVR8 uses a triad of photosensitive tryptophane residues to absorb light [21]. Three classes of photoreceptors primarily control elongation-growth responses depending on the prevalent light environment: phytochromes, cryptochromes and UVR8 [22]. Phototropism is primarily induced by directional UV-A/blue light perceived by the phototropin family, but plants can also bend towards UV-B [23]. The crosstalk between these different photosensory systems will be described below. In contrast, we will not discuss members of the Zeitlupe family, which are primarily involved in the control of floral transition and entrainment of the circadian clock, (for more information about Zeitlupes, see [20, 24]).

Although phototropism is not typically regarded as a component of plant responses to a crowded environment, directional growth contributes to phenotypic plasticity in such environments [19, 25, 26]. We will thus start by a brief description of signaling events associated with phototropism. Angiosperms possess two phototropin photoreceptors, phot1 and phot2, with partially overlapping roles in several physiological responses to blue light like phototropism, stomatal opening or leaf flattening finally leading to optimized

photosynthetic activity. Phot1 functions over a broad range of intensities whereas phot2 is only active at high blue light intensities [27].

Phototropins belong to the AGC kinase family and are located at the plasma membrane. They are composed of two blue light-sensing LOV (Light Oxygen Voltage) domains and a C-terminal serine/threonine kinase domain. Upon blue light perception, a conformational change releases the kinase activity repressed by LOV2, leading to the subsequent autophosphorylation of phototropins [24, 28]. This is followed by a cascade of signaling events finally resulting in the establishment of an auxin gradient driving directional growth towards the light (See box 1). Early signaling components have been identified but the link between activation of phototropins and the auxin gradient is still not entirely elucidated (Figure 2A). For example, NPH3 and RPT2, two proteins from the same family, are essential for a proper phototropism response [29]. They are both located at the plasma membrane and interact with phot1 [24, 28]. NPH3 is rapidly dephosphorylated in blue light in a phot1-dependent manner [24, 28], a phenomenon which is modulated by RPT2 [30]. NPH3 associates with Cullin3 in a CUL3-based E3 ligase complex, which regulates phot1 ubiquitination [31]. However, the functional consequences of this post-translational modification of phot1 remain poorly understood. The PKS family of proteins are also considered as early signal transducers required for phototropism, among which PKS4 is a direct target of phot1 phosphorylation [32]. PKS proteins were proposed to act upstream of auxin gradient formation but their biochemical mode of action remains unknown [33]. For further details on phototropin signaling we recommend the following publications [24, 28, 29, 34].

Photoreceptors and early signaling events regulating elongation

In contrast to the phototropins, phytochromes, cryptochromes and UVR8 are not anchored to the plasma membrane but mainly function in the nucleus. Interestingly, despite having different action spectra, they show similar features in terms of signaling mechanisms which converge to the modulation of gene expression through regulation of transcription factors (Figure 2B). Herein, we provide a synthetic overview of early signaling events associated with

light regulation of elongation, more comprehensive reviews on the function and signaling mechanisms elicited by these photosensory receptors can be found here [21, 24, 35-37].

Plants possess several phytochrome photoreceptors with partially overlapping roles (5 in *Arabidopsis thaliana*, phyA-E) and functioning as homo- or heterodimers. Phytochromes exist in two forms: a FR-absorbing form (Pfr) and its more stable red-absorbing conformer (Pr). Upon perception of red light, the inactive Pr is converted into the active Pfr which translocates into the nucleus. Conversion from Pfr to Pr is facilitated by FR light perception, however this also occurs slowly in the dark. This so-called dark reversion is temperature-dependent and participates in plant perception and response to temperature variations, suggesting that phytochromes also function as thermosensors [38-40]. Cryptochromes are related to the family of DNA repair-involved photolyases and are found in many eukaryotic clades, including fungi and metazoans, as well as in some bacterial species [41]. Two cryptochrome photoreceptors, cry1 and cry2, are present in Arabidopsis and are activated by blue light through conformational changes [36]. UVR8 is the most recently identified plant photoreceptor and is involved in physiological and developmental responses to UV-B [21, 42]. UV-B perception allows the conversion of UVR8 homodimers to active monomers.

In all cases, light activation of these photoreceptors enables controlled interactions with downstream signaling components, which finally leads to regulation of gene expression via two main mechanisms. Phytochromes and cryptochromes have a direct impact on transcription factors from the basic Helix-Loop-Helix (bHLH) family, especially on Phytochrome Interacting Factors (PIFs) (Figure 2B). PIFs are central integrators of internal and external cues regulating plant growth and development [43-45]. They are conserved in land plants, pointing to an early establishment of this signaling module during evolution [46, 47]. Arabidopsis has eight PIF/PIF-like proteins which can interact with phyB but only play partially overlapping roles at different stages of development: PIF1, PIF3-8 and PIL1/PIF2 [44]. It is noteworthy that while most PIFs have a growth-promoting function, PIF6 and PIL1/PIF2 tend to have opposite effects on growth [44]. PIFs regulate expression of target genes by binding preferentially in promoter regions enriched in G-box and PBE-box (PIF binding E-box) motifs [43]. Active phyB interacts with PIFs in the nucleus and inhibits their activity [43]. In many cases this interaction leads to phosphorylation and further

proteasome-dependent degradation of PIFs. Interestingly, PIF7 is not degraded upon interaction with phyB but accumulates in a phosphorylated form [48]. Additionally, phytochromes may have a direct action at the chromatin level on the promoters of PIF target genes. PhyB is detected on chromatin [39] and active phyB inhibits the binding of PIF1 and PIF3 to the *PIL1* promoter independently of the degradation processes [49]. Recently both crys have also been shown to physically interact with PIF4 and PIF5 *in vitro* and *in vivo* [50, 51]. However how these interactions affect PIF activity is still not fully understood. One possibility is that crys repress PIFs transcriptional activity by interacting directly with PIFs at their target genes loci [51]. Cry2 also interacts with CIB bHLH transcription factors, in a blue light-dependent manner, but this rather stimulates CIB-induced expression of target genes to initiate flowering [52]. Cryptochrome-dependent regulation of gene expression may thus vary depending on the type of bHLH factor involved [36].

On the other hand, all three photoreceptors suppress the activity of the COP1/SPA ubiquitin E3 ligase through different mechanisms ultimately leading to the stabilization of transcription factors like HY5 (Figure 2B) [53]. HY5 regulates many target genes to promote photomorphogenesis and inhibit hypocotyl elongation [54]. In the dark, COP1 together with SPAs act as substrate receptor in a CUL4-DDB1 E3 ligase to recruit HY5 for poly-ubiquitination and further degradation by the proteasome. Light-activated cryptochromes and phytochromes interact with SPA which disrupts or inactivates COP1/SPA complexes, thereby inhibiting their ubiquitin E3 ligase activity [55-58]. HY5 is also stabilized under UV-B, and initial models considered COP1 as a positive regulator of UV-B-dependent photomorphogenesis [21]. However monomeric light-activated UVR8 sequesters COP1, which limits COP1 association to the CUL4-DDB1 E3 ligase and thus promotes HY5 stabilization [21, 42, 59], indicating that UVR8 has a negative effect on COP1 activity. Photoreceptor-mediated control of COP1/SPA activity also affects the abundance of other negative modulators of shade-regulated growth such as the bHLH proteins HFR1 and PAR1 [53, 60-62] as well as some members of the BBX family of transcriptional regulators [63].

Collectively these mechanisms tend to activate transcription factors promoting elongation in shaded environments (e.g. PIFs) but also lead to the production of inhibitors of the process

(e.g. HY5, HFR1) which are implicated in negative feedback loops required for controlled growth regulation [3, 61, 62, 64, 65].

Molecular mechanisms associated with neighbor detection and outgrowth

Neighbor detection is probably the simplest situation of light quality regulating plant growth because perception of the characteristic low R/FR ratio is primarily controlled by one photoreceptor, phyB. Most of our current knowledge on related signaling mechanisms have been obtained on hypocotyl elongation in lab conditions, where the low R/FR ratio is easily mimicked by adding supplemental FR light to the control white light source. Under such conditions, conversion of phyB from the active FR-absorbing Pfr to its inactive red-absorbing Pr form leads to stabilization of PIFs which are responsible for the rapid reprogramming of gene expression upon shade perception [48, 66, 67]. Although PIF4, PIF5 and PIF7 have partially overlapping roles, PIF7 plays a predominant function in neighbor detection in seedlings [48, 68]. The same PIFs also control adult responses to low R/FR such as petiole elongation, however which PIF dominates those responses is less clear [69, 70]. PIFs regulate expression of numerous genes, including other transcription factors and negative regulators, resulting in a complex signaling network [3, 71].

A major mechanism whereby PIFs modulate growth is by controlling auxin biosynthesis and signaling [66]. In seedlings a low R/FR ratio is primarily sensed in cotyledons where it leads to PIF-mediated auxin production followed by transport to the hypocotyl [72] (Figure 3A). Increased auxin synthesis requires enzymes of the TAA1-YUC pathway (see box 1) [73, 74]. Four of the eleven *YUCs* (*YUC2*, *YUC5*, *YUC8* and *YUC9*) are induced upon low R/FR treatment in a PIF-dependent manner [48, 66, 67]. The importance of this regulatory step is highlighted by the absence of a low R/FR response in a *yuc2yuc5yuc8yuc9* mutant [67, 75]. Comparable mechanisms are likely involved in adult plants, where both PIFs and auxin synthesis are required for neighbor proximity-induced petiole elongation [70, 76, 77]. Blocking auxin transport with chemical inhibitors also abolishes low R/FR-induced elongation, underlining the importance of a proper auxin distribution for this response [70, 73, 78, 79]. Auxin is directed to the hypocotyl through PIN-dependent polar auxin transport and distributed to the different cell layers [78] where it induces cell elongation. Three PIN-coding genes are

induced upon low R/FR treatment and the corresponding *pin3pin4pin7* mutant does not elongate under shade-mimicking conditions [67, 78]. Regulation of apolar ABCB efflux carriers is also involved in auxin basipetal transport in the hypocotyl in shade, which may facilitate PIN function [80].

However, cotyledon-produced auxin does not fully explain hypocotyl elongation in neighbor detection, and organ-specific analyses have been a key asset to understand the role of local responses [67, 72, 81, 82]. Shade-marker genes like *PIL1*, *HFR1* or *ATHB2* are still induced in the hypocotyl of decapitated *Brassica rapa* seedlings [72]. Because homologous genes in Arabidopsis are direct PIF targets [62, 66], this observation suggests that PIFs play specific roles in the hypocotyl. Accordingly, comparison of transcriptomics analysis of cotyledons versus hypocotyl in low R/FR with ChIP-seq data reveals that many early low R/FR-induced genes in both organs are indeed direct PIF targets [67]. A large proportion of auxin-regulated genes are induced simultaneously in cotyledons and hypocotyl, and some are even expressed first in the hypocotyl. Furthermore, some auxin-responsive genes like *SAUR22* are still induced in the hypocotyl of mutants deficient in auxin biosynthesis or transport [67]. Finally, local auxin inactivation in the hypocotyl also participates in the regulation of elongation, independently of cotyledon-derived auxin [83]. Altogether, these observations illustrate that the neighbor detection response also depends on local hypocotyl signals (Figure 3A).

Once in the hypocotyl, lateral distribution of auxin to the different cell layers is mediated at least by PIN3 [78]. However how each hypocotyl tissue responds to auxin is poorly understood. Interestingly, blocking auxin signaling by expressing a dominant negative form of the transcriptional repressor IAA17/AXR3 (see box 1) in a tissue-specific manner leads to defects in hypocotyl elongation in all tested lines with particularly strong effects upon epidermal expression [84]. Auxin signaling is thus needed in all hypocotyl cell layers, and the prominent role of the epidermis favors the idea that external cell layers drive stem elongation [85].

Among other growth-related hormones, brassinosteroids (BR) are required for hypocotyl and petiole elongation in low R/FR and other shade-mimicking conditions [76, 84, 86] and

BR-related GO terms are significantly detected among shade up-regulated genes [65, 67, 76, 77, 81]. Nevertheless, no significant increase in BR levels is observed in seedlings upon low R/FR treatment [87]. Interestingly BZR1, the main transcription factor regulating gene expression downstream of BR perception, interacts with PIF4 and the auxin-responsive ARF6 to regulate common target genes [88]. A high proportion of low R/FR-induced genes identified as PIF4 or PIF5 targets are also bound by ARF6 and BZR1, which suggest that transcription factors of different hormonal pathways work together in the control of gene expression in neighbor proximity-mimicking conditions [67]. Accordingly auxin-mediated hypocotyl growth in neighbor detection occurs partially through the control of the BR pathway [84] (Figure 3A). Gibberellic acid (GA) is also required for low R/FR-induced elongation, but contrary to BR, slightly higher GA levels have been measured at late time-points in response to plant proximity [87]. DELLA transcriptional repressors are degraded in a GA-dependent manner under low R/FR [89], which releases PIFs from DELLA inhibition [90, 91]. An additional level of regulation involves BBX24, a positive regulator of shade responses, whose interaction with DELLAs favors PIF4 activity [92]. Finally recent analysis of an ethylene-insensitive mutant suggests that this hormone is not essential for shade-induced hypocotyl elongation [81], and may be important specifically for petiole elongation where increased ethylene levels were measured upon low R/FR treatment [79].

Integrating complex light information to modulate growth

In natural environments, light signals are complex and activate several photoperception pathways at the same time. More and more studies focus on these photosensory crosstalks to understand how plants integrate multifaceted information from their environment and what the final growth output is.

Shade avoidance responses are modulated by PIF-dependent negative feedback loops but also by other photosensory mechanisms. When not yet filtered by a canopy, strong UV-B signals inhibit neighbor proximity-induced hypocotyl and petiole elongation but also leaf hyponasty through UVR8 activity [93, 94]. As other UVR8-dependent mechanisms, this repression relies partially on HY5-driven gene induction through inhibition of COP1 activity [21, 93]. The COP1/SPA complex is indeed required for shade avoidance responses, as shown

by the weak low R/FR-induced elongation phenotypes of *cop1* and *spa* mutants [95, 96]. Besides combined low R/FR + UV-B treatment triggers the degradation of PIF4 and PIF5 proteins but how UVR8 controls PIFs stability remains unknown [93]. Phytochrome A also negatively controls hypocotyl elongation under prolonged low R/FR conditions through late-induced expression of *HY5* [65]. The impact of phyA is particularly strong when the low R/FR ratio is perceived early in development, right after germination [97, 98]. In such a case, shade avoidance occurs at the same time as de-etiolation, a developmental process enabling plants to become photoautotrophic. De-etiolation comprises inhibition of hypocotyl elongation and promotion of cotyledon expansion, processes which are reversed to some extent during shade avoidance [99]. PhyA is the sole photoreceptor triggering de-etiolation under FR light and is thus essential for seedling establishment and survival in deep canopy shade, on the other hand it antagonizes phyB-controlled shade avoidance.

Under dense vegetation, depletion of blue and red wavelengths is added to increased FR transmission, which affects both photosynthetic activity and light signaling. Although there is no evidence for a natural situation in which only blue light would be reduced, studies using blue-depleted light have allowed disentangling the confounding effects of low blue and low R/FR in true shade conditions. A drastic reduction in blue light intensity as experienced by plants under a canopy induces typical shade avoidance phenotypes in both seedlings [50, 79, 86] and adult plants [69, 79, 100]. Although low blue and low R/FR show distinct transcriptional patterns and induce different hypocotyl growth kinetics the long-term phenotypic responses are quite comparable [50, 69]. Phenotypic analyses of cryptochrome-deficient mutants indicate that these photoreceptors function as negative regulators of low blue-dependent shade responses and prevent excessive elongation [69, 79, 100]. Genetic and biochemical evidence suggest that cry1 and cry2 act at least partially upstream of PIF transcription factors in the regulation of low blue-induced hypocotyl elongation [50]. However, how the interaction between crys and PIFs is differentially regulated under low blue and in canopy shade conditions and how this affects PIF activity remains poorly understood. Interestingly, low blue enhances the effect of low R/FR, leading to growth and transcriptional responses that are very similar to plants grown under true canopy shade [69]. One mechanism underlying this combined photoreceptor action is the reduction of low R/FR-induced negative feedback loops by low blue [69]. This represents a good example of

how complex natural light environments can be simulated in laboratory conditions and how this leads to mechanistic insights into photoreceptor crosstalk.

A similar approach comparing natural and artificial light combinations was recently used to study the crosstalk between phytochromes and phototropins during the control of phototropism in green seedlings [19]. In neighbor detection conditions, phototropic bending is enhanced gradually with the decrease of the R/FR ratio. The response is negatively regulated by phyB and the cryptochromes while the PIF-YUC regulon is also required for this asymmetric growth response [19]. Importantly, increase in hypocotyl curvature under low R/FR does not simply correlate with the growth potential. This suggests that plants in a shaded environment can reorient their growth more efficiently towards a more favorable light and that co-action between phytochrome inhibition and phototropin signaling helps plants to optimize light capture (Figure 3B). Cryptochromes also participate in the modulation of phototropism by shade and might be especially important under canopy shade where blue light is greatly reduced [19]. Phytochrome-phototropin cooperation is also essential in cryptogams like mosses and ferns to regulate bending towards unidirectional red light. This phenomenon depends on direct interaction of phytochromes and phototropins at the plasma membrane in *Physcomitrella patens* [101] or on a phytochrome-phototropin chimeric photoreceptor, or neochrome, in some polypodiaceous fern species [102-104]. Neochromes may favor sensitivity for light perception, a crucial asset for plants, growing in dim light environments.

Blue light-dependent phototropism has been mostly studied in seedlings seeing light for the first time. Interestingly as observed in green seedlings, phototropism in de-etiolating seedlings is also controlled by a phytochrome-phototropin coaction. Nevertheless the mechanisms are distinct as in de-etiolating seedlings phyA promotes phototropism while as described before phyB inhibits the process in green seedlings [29]. However, as outlined below in both cases phytochromes regulate the process by controlling the expression of distinct elements in phototropin signaling. Constitutive expression of a nuclear phyA leads to a faster phototropic response, suggesting that nuclear localization of phyA is required for its action on phototropism [105]. Light-induced translocation of phyA into the nucleus (by red light) prior to directional blue light illumination likely favors phyA-dependent induction of

phototropism signaling components like *PKS1* and *RPT2* [29, 105]. The other phytochromes do not seem to be much involved in the regulation of phototropism in de-etiolating seedlings, as shown by the normal blue light-induced bending of Arabidopsis mutant seedlings lacking phyB-phyE [106]. Cryptochromes are also important for a proper phototropic bending response in etiolated seedlings and might act together with both phototropins and phytochromes [19, 29, 107-109]. Cry1 and cry2 redundantly enhance phototropism at low fluence, perhaps by modulating blue light-regulated growth [107, 108]. As for phyA-mediated phototropic enhancement this has been linked to the control of *RPT2* expression [109]. Finally, etiolated hypocotyls also bend towards UV-B light, a response which depends on both phototropins and UVR8 [23]. Indeed a *phot1phot2* double mutant is able to bend towards monochromatic UV-B, yet at a slower rate than wild type seedlings, suggesting that phot1 and phot2 are important for the early phase of directional growth towards UV-B [23, 110]. Interestingly, UVR8-dependent bending requires HY5, which accumulates at the lit side of the hypocotyl upon directional UV-B perception [111]. The underlying mechanism may involve a gradient of HY5 activity negatively regulating cell elongation from the illuminated to the shaded side of the organ. How UV-B modulates phototropism in green seedlings and how this pertains to growth modulation in a complex canopy remains an interesting question for the future.

Conclusions/outlook

Over the past decades much has been learned about individual signaling pathways by using simplified light environments that are primarily sensed by a single photoreceptor (e.g. the control of neighbor perception by phyB). Much remains to be understood about shade responses at the tissue and cellular levels. However, the current information now enables the community to study more realistic light conditions to investigate the mechanisms underlying the integration of signals emanating from several light sensors [19, 69, 93]. The next challenge will be to test hypotheses generated in controlled environments in much more variable natural conditions. Interestingly, outdoors experiments aimed at determining the influence of various pathways controlling the timing of reproduction in Arabidopsis yielded quite some surprises [112]. It is likely that novel discoveries will also result from using such approaches to study shade avoidance and phototropism. For example soil

412 resources and pathogen load both have an influence on plant competition and canopy
413 formation and hence it will be interesting to study the integration of light cues with other
414 important variables [113, 114]. Such studies will likely provide mechanistic insight into
415 complex signaling integration that is of interest to understand plant growth at the individual
416 level but also how these factors influence community composition [113-115]. In order to
417 reach this level of understanding it will be important to compare and contrast ecotypes and
418 species with different responses to shade cues.

Text Boxes

Box 1: Auxin, the growth hormone.

Auxin is the main hormonal regulator of cell elongation in shade avoidance and phototropism responses. In young seedlings, it is mostly produced in the cotyledons and channeled down to the hypocotyl and root [73]. Indole-3-acetic acid (IAA), the main auxin form, is primarily synthetized from tryptophan through the TAA1-YUC pathway. TAA1 converts tryptophan into indole-3-pyruvate (IPA) and enzymes of the YUCCA (YUC) family are responsible for converting IPA into free IAA in a rate-limiting step [74]. Auxin is then transported from cell to cell in a directional manner through controlled transport routes. The fast and long-range basipetal stream of auxin corresponds to the polar auxin transport (PAT) whereas a slower local distribution of auxin to the different tissues has recently been identified as the connective auxin transport (CAT) [116]. Auxin freely enters the cell in its protonated form, the most abundant one at the acidic pH of the apoplast. Once in the cytoplasm, auxin is deprotonated and is thus “trapped” inside the cell. Its transport is also regulated by three families of transporters: AUX1/LAX auxin influx carriers enable auxin to enter into the cell whereas auxin efflux is mediated by both the apolar ABCBs and the polar PIN transporters [117]. ABCB and PIN activities are regulated by phosphorylation by AGC VIII kinases [118]. Auxin is perceived in the cytoplasm by specific receptors from the TIR/AFB family and favors the interaction of $SCF^{TIR/AFB}$ E3 ligase complexes with Aux/IAA proteins, which are targeted to the proteasome. Degradation of Aux/IAA transcriptional repressors releases the activity of ARF transcription factors which then drive expression of specific auxin-responsive genes, among which cell wall remodeling factors involved in cell elongation [119].

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Figure legends

Figure 1. Features of the light environment and consequences on plant growth.

A. Leaf spectral properties as the main determinant for light composition in plant communities. Upon absorption of sunlight (top spectrum) by photosynthetic pigments, a leaf filters most of the blue and red wavelengths and the resulting transmitted light is relatively enriched in green and FR (bottom spectrum). Besides, green tissues also reflects FR, which lowers the R/FR ratio perceived by neighboring plants. Spectra were adapted from [120].

B. Plant growth responses in different light environments. (1) Full sunlight. An isolated plant under full sunlight receives high amounts of UV-B, blue and red light and relatively low amount of FR (top spectrum figure 1A). (2) Neighbor detection. In crowded environments, high reflection of FR light from neighboring plants is a signal for strong competition and indicates a forming canopy. The decrease in R/FR ratio perceived by plant photoreceptors induces a suite of morphological changes helping to overtop encroaching neighbors and get a better access to sunlight: elongation of stem, internodes and petioles; leaf elevation (hyponasty); reduced branching; acceleration of flowering. (3) True shade. Under a canopy, light is strongly filtered by high tree leaves and the understory receives a much lower light intensity, characterized by low UV-B, low PAR and low R/FR (bottom spectrum figure 1A). This leads to a similar but more pronounced phenotypic response than described in (2) in shade-avoiding species. Conversely shade-tolerant plants display various adaptations to life under dim light conditions (not represented here). Finally plants located at the edge of a canopy gap face a horizontal light gradient, which induces a reorientation of growth towards the more favorable environment or phototropism.

C. Example of ivy plants (*Hedera helix*) in the shade of higher trees showing phototropism towards a canopy gap (Lausanne, University campus, fall 2016).

Figure 2. Overview of signaling mechanisms controlling the direction and extent of plant growth.

A. Simplified view of early signaling events involved in blue light-induced phototropism. Activation of membrane-localized phototropins by a directional light signal induces a suite of phosphorylation/dephosphorylation events which are essential for the establishment of an auxin gradient across the hypocotyl. Auxin accumulates in cells located on the shaded side,

484 which elongate more than the one on the lit side, leading to hypocotyl bending. More details
485 in the text. Phot: phototropins.
486
487 B. Simplified view of photosensory mechanisms involved in light regulation of growth. Light-
488 activated photoreceptors (phytochromes, cryptochromes and UVR8) negatively regulate
489 seedling elongation by acting in the nucleus via two main mechanisms: inactivation of PIFs
490 and activation of HY5 through inhibition of COP1/SPA activity. More details in the text. Phy:
491 phytochromes; Cry: cryptochromes.
492
493 **Figure 3. Current models of neighbor proximity-induced hypocotyl elongation and**
494 **promotion of phototropism dependent on the PIF-auxin regulon.**
495 A. Neighbor proximity-induced hypocotyl elongation results from a combination of signaling
496 mechanisms in both cotyledons and hypocotyl. In the cotyledons, stabilization of PIFs in low
497 R/FR leads to specific responses, which include the induction of auxin biosynthetic genes
498 from the *YUCCA* family. Auxin is transported to the hypocotyl via polar auxin transport and
499 distributed laterally to the different cell layers, where it has specific functions. Cotyledon-
500 derived auxin drives cell elongation in the hypocotyl, partly through activation of the
501 brassinosteroid pathway. In parallel, PIFs activate local responses in the hypocotyl which are
502 necessary for low R/FR-induced elongation. Local metabolism also regulate auxin availability
503 to prevent excessive growth.
504 B. Low R/FR conditions enhance phototropic bending towards directional blue light.
505 Activation of phototropins by a directional blue light induces an auxin gradient in the
506 hypocotyl which leads to hypocotyl bending. Parallel inactivation of phytochromes (phyB)
507 and subsequent activation of PIFs triggers a boost of auxin which further promotes the
508 phototropic response.
509 More details in the text. Trp: tryptophan; IPA: indole-3-pyruvate; IAA: indole-3-acetic acid;
510 PAT: polar auxin transport; BR: brassinosteroids.
511

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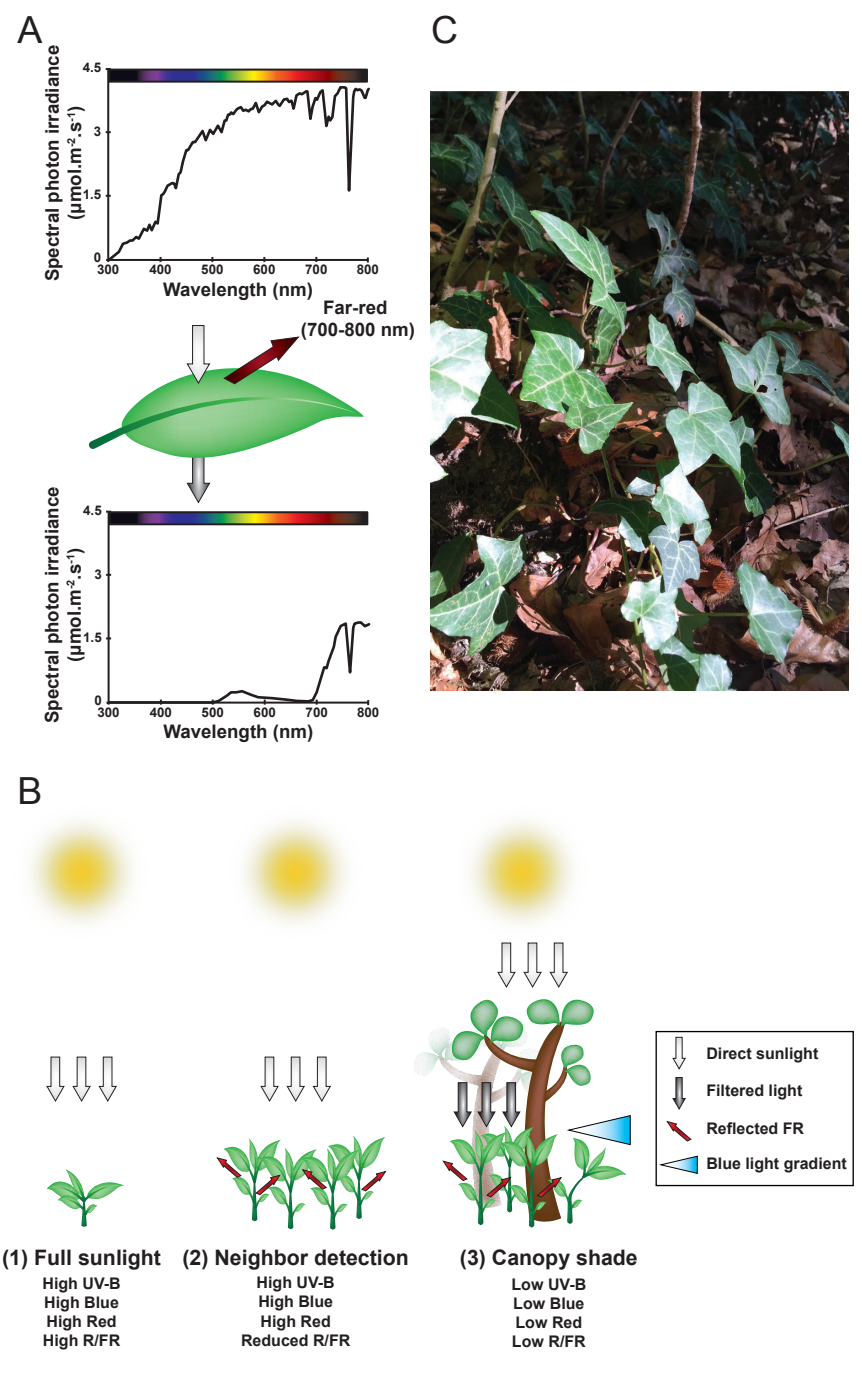
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Spectral photon irradiance (µmol.m-2.s-1)
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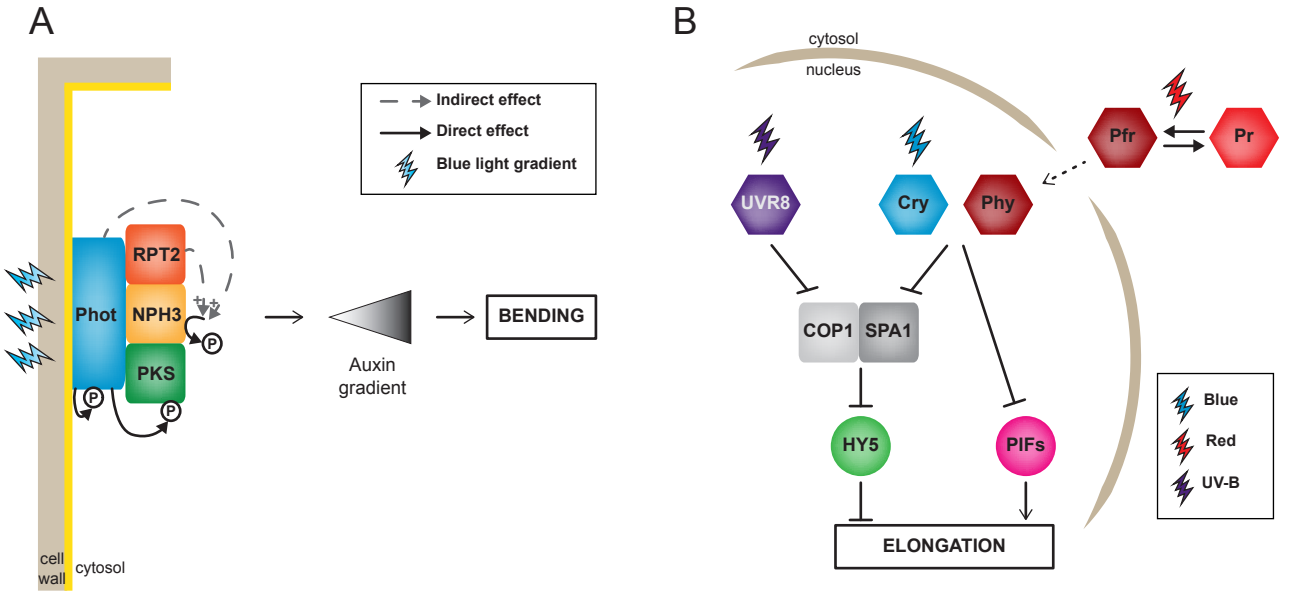
C
B
Direct sunlight
Filtered light
Reflected FR
Blue light gradient
(1) Full sunlight
High UV-B
High Blue
High Red
High R/FR
(2) Neighbor detection
High UV-B
High Blue
High Red
Reduced R/FR
(3) Canopy shade
Low UV-B
Low Blue
Low Red
Low R/FR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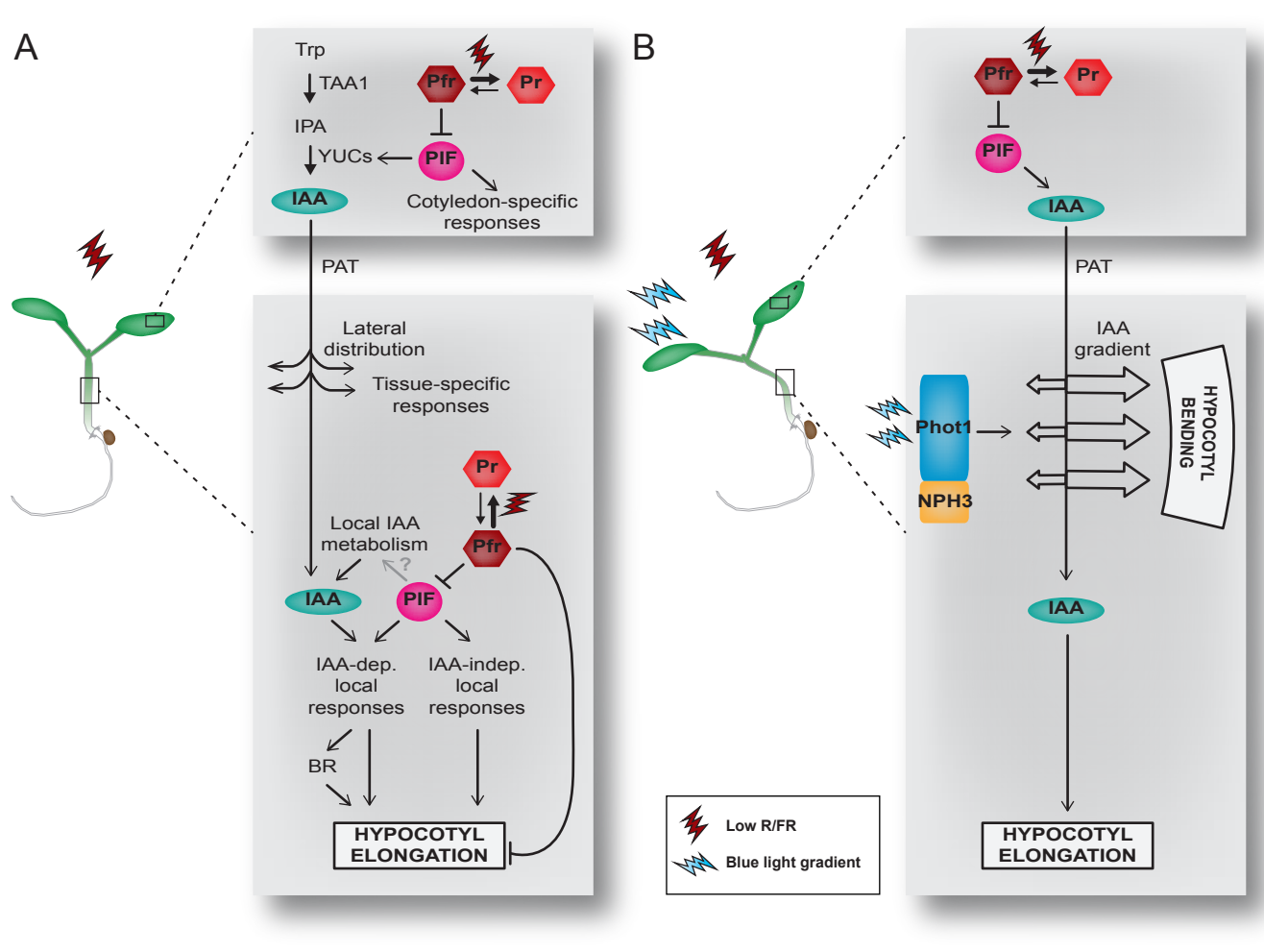
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Cotyledon-specific responses
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IAA-indep. local responses
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IAA gradient
HYPOCOTYL BENDING
Low R/FR
Blue light gradient