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Shadow on the Plant: A Strategy to Exit

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The light spectrum perceived by plants is affected by crowding and results in the shade avoidance syndrome (SAS). Findings presented in this issue of *Cell* bring cryptochromes to the forefront of SAS and elucidate a fascinating molecular crosstalk between photoreceptors operating in red/far-red and blue light, respectively.

Plants convert light into chemical energy through photosynthesis. This process is fundamental for the existence of life on our planet. The two extreme conditions, full sunlight and low light, are harmful to plants. High light intensity causes photo-damage through formation of reactive oxygen species (ROS), which are formed by misguided transfer of energy or electrons in the photosynthetic apparatus, or by direct damage of DNA and other cellular compounds through UV-B absorption. These types of damage can be prevented, at least in part, by formation of sunscreen pigments, movement of leaves and chloroplasts reducing the light exposed area, inactivation of ROS, or repair of DNA-lesions. In contrast, low light reduces the capacity for photosynthesis, which may ultimately lead to plant starvation. Such low light conditions are particularly harmful under foliar shade where photosynthesis-driving wavebands (red and blue light) are preferentially filtered out compared to green and far-red light. Under a canopy the red/far-red ratio (R:FR) is about 0.15 or lower, in open stands 1.15 or higher. Sun loving plants respond to such conditions by the so-called shade avoidance syndrome (SAS). SAS includes several morphological alterations to escape low light such as enhanced growth of the stem, upward direction of leaves, etc.. Pioneering work by Harry Smith and coworkers revealed that phytochrome photoreceptors (phy) are essential for the SAS (Smith and Whitelam, 1997). These photoreceptors are well suited to detect R:FR because the tetrapyrrole chromophore in phytochrome exists is two interconvertible forms. Upon light absorption the inactive red-light absorbing form (Pr, λmax = 665 nm) is converted to the physiologically active far-red absorbing form (Pfr, λmax = 730 nm). Thus, the fraction of the active Pfr-form is much lower under low R:FR (Figure 1C). *Arabidopsis thaliana*, the model plant used in this study, encodes five phytochromes (phyA-phyD), and phyB is the main phytochrome involved in SAS (Franklin et

al., 2003). Under a canopy not only the R:FR is decreased but likewise the radiance of blue light. In this issue of *Cell* Pedmale et al. (2016) show that the cryptochrome blue light photoreceptors (cry) contribute to SAS under low blue and provide fascinating insight into the molecular mechanism of cryptochrome function under these conditions. One of the major observations of this study is that the two Arabidopsis cryptochromes, cry1 and cry2, directly interact with the bHLH PHYTOCHROME INTERACTING FACTORS PIF4 and PIF5. Moreover, cry2 and PIF4/PIF5 localize to the same promoter regions under low blue light conditions suggesting that the PIF4/PIF5/cry2 complex directly regulates genes involved in SAS (Figure 1).

PIF transcription factors are known to be required for phytochrome-mediated SAS. In *Arabidopsis thaliana* the PIF clade has 15 members. Active phyB (PfrB) was shown to bind PIF1, 2, 3, 4, 5 and 7 (Leivar and Quail, 2011). Among these interactions, the phyB/PIF7 complex has the dominant role in low R:FR SAS (Li et al., 2012), but PIF4 and PIF5 are likewise involved in low R:FR- (Lorrain et al., 2008) as in the low blue light response (Keller et al., 2011; Pedmale et al., 2016). Intriguingly, phy and cry bind different sites of the PIFs (Pedmale et al., 2016) suggesting that different PIF-photoreceptor complexes form depending on the light regime resulting in the appropriate transcriptional output.

As outlined above, phytochromes are optimized to detect R:FR and thus are perfectly suited for SAS. Why then do plants use additional photoreceptors to regulate this response? One reason could be that a canopy is a very noisy environment since wind force moves leaves causing changing light intensities and spectral distribution on the ground. In addition, plants reflect far-red leading to a reduced R:FR ratio due to plant proximity prior to shading. Thus, canopy detection is much more precise by using different photoreceptors systems measuring spectral distribution and light intensity, respectively. Finally, this study suggests another reason for the use of different light inputs, which is kinetics of the growth response (Pedmale et al., 2016). The response to low R:FR occurs faster than the one to low blue. Thus, both responses together may contribute to a sustainable program to escape from shade.

Another intriguing result presented by Pedmale et al. (2016) is the fact that phytochrome and cryptochrome-mediated SAS result in similar morphological changes but through different mechanisms. Enhanced stem growth is induced by the phytohormone auxin, which is to large extent produced in cotyledons and young leaves from the precursor L-tryptophan. Auxin is then transported to the stem and root via the PIN auxin efflux carriers. Phytochrome- and PIF7-mediated SAS is caused by upregulation of auxin biosynthesis and redistribution of auxin (Li et al., 2012; Casal, 2013). In contrast, SAS-induced by cry and PIF4/PIF5 seems to be largely regulated by cell wall modification with auxin still playing a role here (Keuskamp et al., 2011; Pedmale et al., 2016). Thus, phy and cry use different strategies to achieve the same goal namely extension growth of the stem to escape from unfavorable light conditions.

There is some debate about the lit-state of cryptochromes. Its chromophore is FAD, which can exist in different redox states. The absorbance of fully oxidized FAD with peaks in UV-A and blue fits perfectly well with a model proposing that the ground state of cry contains fully oxidized FAD. The FAD neutral radical is formed by uptake of one electron and one proton, and this redox state has an altered absorption spectrum extending into the green and red region. Assuming that the lit state of plant cryptochromes contains the neutral flavin radical it is tempting to speculate that these photoreceptors may be responsive to green light. Indeed, a decrease in the blue/green ratio causes stem elongation similar to a decrease in R:FR (Sellaro et al., 2010). Thus, plant crys may be photoreversible pigments.

Future work should address the question how different blue/green ratios affect formation of the cry/PIF complex. The effect of light on interaction of cry1 and cry2 with PIF5 is not the same and low blue light has an inductive effect only on PIF5 but not on PIF4 levels. Therefore, the question whether cry1 and cry2 regulate PIFs by the same mechanism remains unanswered. Finally, future studies are needed to figure out in which organs, cell types and at which time points low blue and R:FR are monitored to extend the knowledge of circuits underlying the SAS.

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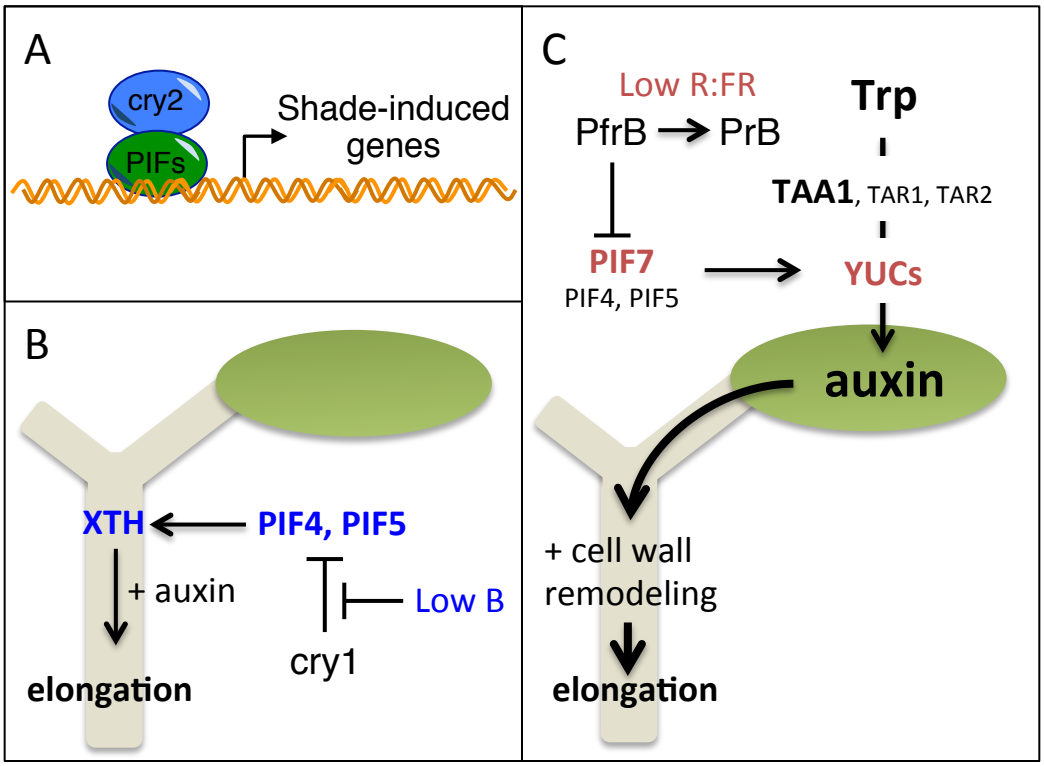
Figure 1. Model of the shade avoidance syndrome allowing plants to escape from competition

Plants use different photoreceptor systems to detect unfavorable low light conditions caused by shading. (A) The cryptochrome 2 (cry2) blue light photoreceptor binds to phytochrome interacting factors 4 and 5 (PIFs) on the promoter regions of shade-induced genes leading to their expression. (B) The inhibitory role of cry1 on PIF4 and PIF5 is suppressed under low blue light. PIF-induced genes encode cell wall-remodeling enzymes (such as expansins, XTH) allowing extension growth of the stem in a process that also requires auxin. (C) Phytochromes, in particular phyB, measure the red:far-red (R:FR) ratio, which is strongly lowered under foliar shade. Under such conditions most of the phyB is converted to its inactive red-light absorbing form (PrB), releasing the inhibitory effect of phyB as Pfr (PfrB) on the activity of PIF7 and other PIFs. PIF7 induces genes (YUCCAs) required for the biosynthesis of the phytohormone auxin from the precursor tryptophan (Trp) in the leaves. Auxin is then transported to the stem through efflux carriers (PINs) where it promotes elongation growth.


A
cry2
PIFs
Shade-induced genes
B
XTH
PIF4, PIF5
+ auxin
Low B
cry1
elongation
C
Low R:FR
PfrB
PrB
Trp
TAA1, TAR1, TAR2
PIF7
PIF4, PIF5
YUCs
auxin
+ cell wall remodeling
elongation