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Photomorphogenesis: Plants feel blue in the shade

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Plants integrate multiple environmental signals to detect and avoid shading from neighbouring vegetation. Two new studies highlight the importance of blue light in the regulation of stem elongation and bending during shade escape.

Shading within canopies is major threat to the survival of plants in natural environments. Many species have therefore evolved escape responses, termed shade avoidance. These include the rapid elongation of stems, in an attempt to overtop neighbours, and elevation of leaves towards canopy gaps [1]. Plants detect the presence and density of competing vegetation primarily through alterations in light quality. Green tissue absorbs red and blue wavelengths for photosynthesis while reflecting green and far-red wavelengths [1]. Plants growing within dense canopies therefore perceive reductions in the ratio of both red to far red light (R:FR) and blue to green light (B:G). In addition to light signals, plants can detect neighbours through the physical touching of leaf tips [2] and accumulation of volatiles, such as the gaseous hormone, ethylene [3]. Plants perceive light signals using specialised photoreceptors, which include the red and far-red light-absorbing phytochromes and the blue light-absorbing cryptochromes and phototropins. The role of phytochromes in regulating shade avoidance in response to low R:FR is well established [1]. Although low blue light signals, mediated by cryptochromes, are known to contribute to shade avoidance responses, they have previously been studied in isolation and not in conjunction with low R:FR [4]. In addition to elongation growth, shaded plant stems display enhanced bending towards sunlight. Termed phototropism, this process is mediated by the blue light-absorbing phototropin photoreceptors [5]. The molecular mechanisms controlling shade/phototropism interaction have, until now, remained elusive. Two studies published in this issue of *Current Biology* highlight the importance of blue light signals in plant shade escape. de Wit *et al*. show that reduced blue light potentiates low R:FR-mediated stem elongation [6], while Goyal et al. explain why shaded plant stems display enhanced phototropic curvature [7].

Shade avoidance is characterised in the model species, *Arabidopsis thaliana*, by elongation of embryonic stems (hypocotyls) and leaf stems (petioles) [1]. These responses are primarily driven by biosynthesis of the plant growth hormone auxin, via a tryptophan –dependent pathway requiring TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS1 (TAA1) and YUCCA enzymes [8-9]. This process requires three key transcription factors, PHYTOCHROME INTERACTING FACTOR 4 (PIF4), PIF5 and PIF7 [10-11]. In sunlight, phytochrome photoreceptors are converted to an active form which binds to PIFs, reducing their abundance and activity. This reduces auxin synthesis. Plant stems remain short and resources are directed towards leaf growth for photosynthesis. Plants growing near neighbouring vegetation perceive reflected FR light (and therefore a reduction in R:FR) prior to canopy closure. This acts as an early warning signal, promoting escape responses before shading occurs [12]. Low R:FR inactivates phytochromes, stabilising and activating PIFs. PIF4, PIF5 and PIF7 act collectively to promote auxin biosynthesis and stem elongation [10-11]. In true shade, plants additionally experience reduced levels of blue light. Although low R:FR and low blue light-mediated effects on plants have been investigated independently, few studies have examined the effect of both concomitantly, as would be found in vegetational shade.

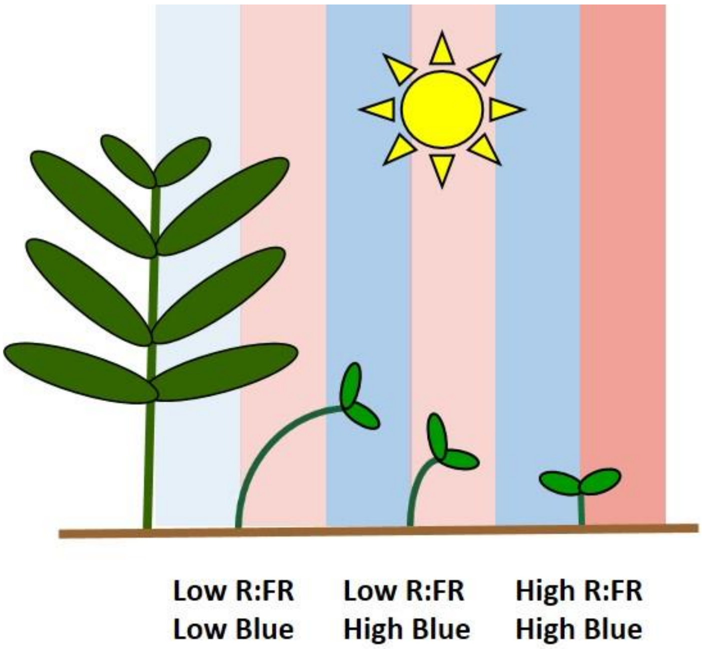
de Wit *et al.* show that a low blue light stimulus exaggerates low R:FR-mediated shade avoidance in both hypocotyls and petioles. Low blue light enhances PIF5 abundance and reduces levels of the transcription factor, LONG HYPOCOTYL IN FAR-RED 1 (HFR1). HFR1 can bind to PIFs, forming non-functional heterodimers [13]. In low R:FR, HFR1 levels increase and inhibit PIF function [13]. This negative feedback loop prevents excessive stem elongation which could reduce plant stability and compromise survival. HFR1 is degraded following binding to the protein complex, CONSTITUTIVELY PHOTOMORPHOGENIC1-SUPPRESSOR OF PHYA-105 (COP1-SPA) [14]. In sunlight, COP1 activity is inhibited by activated phytochrome and cryptochromes [15]. The combination of low R:FR and low B in vegetational shade inactivates these photoreceptors, resulting in enhanced COP-SPA-mediated degradation of HFR1. Reduced HFR1 levels enhance PIF function, auxin synthesis and hypocotyl elongation. In this way, low blue light signals enable plants to distinguish between true shade (low blue and low R:FR) and the threat of shade (low R:FR). True shade represents a serious threat to plant survival and therefore elicits the strongest escape response. Importantly plant responses to a combined treatment of low R:FR and low blue light mimicked those observed under a green filter, suggesting that these two signals are the dominant signalling components of vegetatational shade [6].

In a parallel study, Goyal *et al.* demonstrate that blue light-mediated phototropism is directly influenced by R:FR [7]. Put more simply, the greater the degree of vegetational shading plants experience, the more they bend towards the light. Phototropism is an asymmetric growth response requiring auxin. Lateral blue light promotes auxin accumulation on the shaded side of plant stems. Cells on this side then elongate more than cells on the illuminated side, resulting in stem curvature [16]. Although phototropism of green seedlings has been observed in patchy canopies [5], the mechanistic basis of this response has not been identified. Goyal *et al.* show that PIF-mediated auxin production in low R:FR enhances phototropic curvature. R:FR was inversely correlated with the transcript abundance of auxin biosynthesis enzymes and the magnitude of stem curvature. Phytochrome B was shown to inhibit phototropism in high R:FR. Laboratory experiments are supported by field studies, providing environmental context to the study. Here, seedlings displayed enhanced phototropism in response to unilateral shading from tall grasses. Intriguingly, mutants deficient in phytochrome B (and therefore largely insensitive to changes in R:FR) displayed a residual enhancement of phototropism to true shade in the field. The authors show that cryptochrome photoreceptors work with phytochromes to supress phototropism in sunlight. Collectively, these data suggest that plants in natural canopies would bend more strongly away from true shade than from the threat of shade.

Together, these elegant studies provide compelling evidence that blue light photoreceptors are key components of a core signalling hub controlling plant shade escape in dense canopies. Moreover, phototropism can now been added to the suite of developmental responses comprising the plant ‘shade avoidance syndrome’ [1]. An important take home message from both papers is that plant photoreceptors do not operate in isolation. A major future objective for plant photobiologists will be to understand how different photoreceptors communicate not only with each other, but with other abiotic and biotic signalling pathways in the plant.

Figure 1. Blue light signals regulate plant shade escape responses.

Plants grown in dense vegetation perceive a reduction in the ratio of red to far-red light (low R:FR) and low levels of blue light (low Blue). Together, these factors strongly promote hypocotyl elongation and phototropic curvature to facilitate shade escape. Plants growing in close proximity to neighbouring vegetation experience low R:FR before canopy closure. The combination of low R:FR and high blue light levels signals the threat of shade. This results in some elongation and phototropic curvature of hypocotyls. Plants grown in sunlight experience high R:FR and high blue light levels. These plants remain short with vertically-orientated hypocotyls and promote leaf expansion for photosynthesis.



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