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Reaching out of the shade

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Competition for light determines the success of individual plants in dense vegetation. Much depends on the capacity of plants to detect neighbours quickly and on their ability to respond to these signals. Recent findings indicate that although red:far-red ratios, and thus phytochromes, are of major importance in shade-avoidance responses, they do not act alone. Differences in light intensity also provoke shade-avoidance phenotypes, with blue light playing an important role in dense stands. Moreover, links between shade-avoidance signalling and auxins, gibberellins and ethylene have emerged. Additional breakthroughs are based on transcriptome studies that have unveiled new components in the response to shading. Amongst these, the phytochrome interacting factor 3-like proteins PIL1 and PIL2 underline the importance of circadian gating in shade avoidance.

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Introduction

Plants acquire their energy from light; hence, an optimal positioning of leaves for photon harvest is desired. When plants are shaded by neighbours, two types of reactions can occur. Shade-acclimation responses maximize light harvesting in shade conditions through increases in specific leaf area and reduced chlorophyll a:b ratio [1], whereas shade-avoidance responses maximize light capture by positioning the leaves out of the shade [2].

Light that has passed through a canopy is rich in far-red (FR) but poor in red (R) and blue (B) light (Figure 1a). R and B are depleted by chlorophyll whereas FR is predominantly reflected and transmitted. Shade-avoiding plants

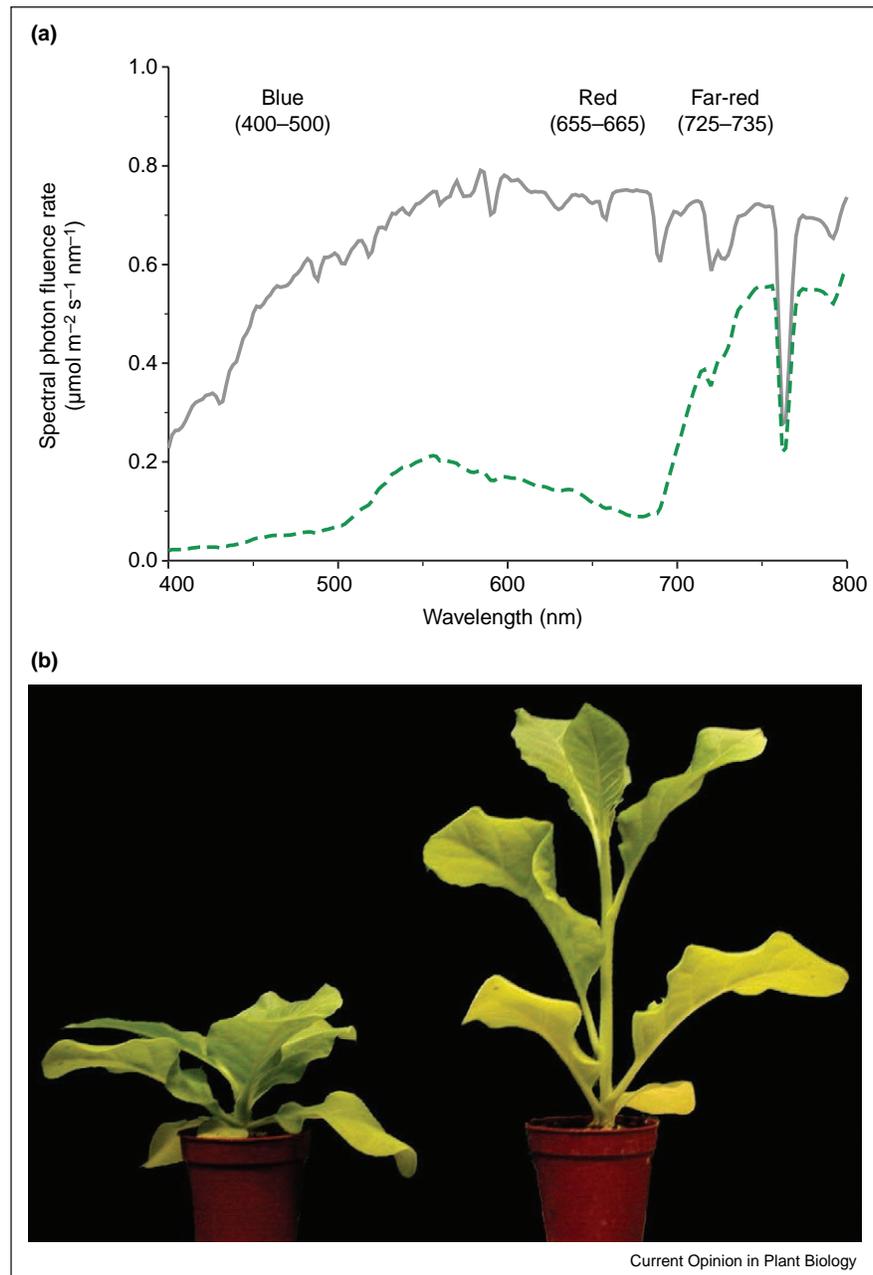
have machinery that reacts quickly to changes in R:FR ratio that are sensed by the phytochrome family of photoreceptors [3,4]. The provoked phenotype (Figure 1b) mainly consists of the elongation of stem-like organs (including hypocotyls and petioles), the upward orientation of leaves (hyponasty) and reduced branching. In the long term, low R:FR exposure leads to early flowering [5] and seed set, which is considered to be an escape mechanism because it shortens generation time. These responses constitute the adaptive plasticity of plants to shading [6].

Until recently, shade-avoidance responses were considered predominantly as a function of R:FR ratio. Evidence is accumulating, however, that plants also adjust growth to diminishing light intensities, including that of blue light [7–9]. Light intensity affects chloroplast positioning, allowing optimal light harvesting [10]. Thus, photoreceptors serve not only as quality detectors but also as photon counters [2]. Recent advances in understanding the molecular mechanisms of shade-avoidance responses have unveiled interactions between light signalling and the circadian clock, and have revealed a more profound view of the hormonal pathways that are involved.

Light signalling

The R:FR ratio decreases from approximately 1.2 in full sunlight to 0.05 in closed canopies, with a significant decrease occurring before canopy closure (reviewed in [2,4]). R:FR is sensed by the phytochrome family of photoreceptors, which consists of five members (PHYA–PHYE) in *Arabidopsis*. Of these, the light-stable PHYB, PHYD, and PHYE operate redundantly and in a R:FR-reversible fashion in allowing plants to detect neighbours [11]. Phytochromes act as dimers and exist in two photoconvertible forms: ‘Pr’ (the R absorbing, inactive form) and ‘Pfr’ (the FR absorbing, active form) [3], with the Pfr:Pr ratio reflecting the R:FR ratio of the environment. Upon photoconversion into active Pfr, part of the cytoplasmic phytochrome pool travels into the nucleus, where it regulates gene expression by interacting with several basic helix–loop–helix (bHLH) transcription factors [12], including phytochrome interacting factor (PIF) and PIF-like (PIL) proteins [13]. PHYB signalling involves not only PIF3 [14] but also PIF1/PIL5, PIF4, and PIF5/PIL6 [13]. To date, however, only PIL1 is known to be involved in low R:FR-mediated shade avoidance. Phytochromes regulate the transcription of light-responsive G-box-containing genes through their direct interaction with PIF/PIL proteins [15,16]. Phytochrome-regulated genes that are involved in shade avoidance include the *Arabidopsis thaliana* homeobox HD-ZIP

Figure 1

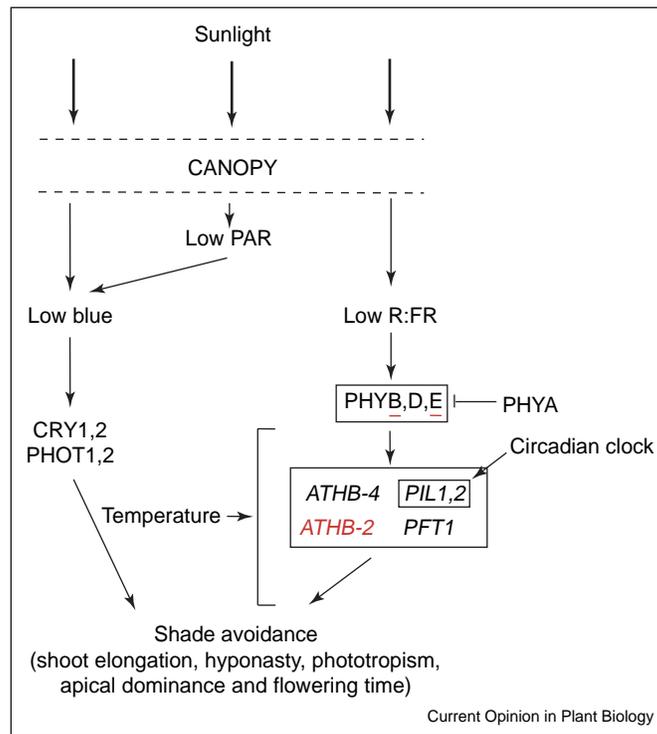


(a) Light spectral changes of normal daylight (grey solid line) and daylight filtered through a tobacco canopy (green dashed line) measured in a greenhouse. (b) Individual tobacco plants in a high (left) or a low (right) R:FR ratio. Low R:FR induces shade-avoidance responses, including enhanced stem elongation and hyponastic leaf growth.

transcription factor genes *ATHB-2* and *ATHB-4* (reviewed in [4[•],17]). The expression of *ATHB-2* is specifically controlled by PHYB and PHYE [11[•]]. Furthermore, *ATHB-2* stimulates shade avoidance: transgenic plants that overexpress *ATHB-2* display a phenotype that is reminiscent of the low R:FR-induced wildtype phenotype, whereas reduced expression of this gene has the opposite effect [18].

Besides R:FR, reduced blue-light photon fluence rates in canopies also induce shade-avoidance responses ([2,9[•]]; Figure 2). The UV-A/blue-light-perceiving cryptochromes regulate blue-light-mediated changes in growth and development [12^{••}]. Two cryptochromes (CRY1 and CRY2) and their functions have been identified in *Arabidopsis*. CRY1 is light-stable and acts at high blue-light intensities, whereas CRY2 is light-labile and is considered

Figure 2



Schematic representation of light signals that act in a canopy, including downstream components that are known to be involved in shade avoidance. R:FR is signalled through a subset of phytochromes to regulate shade avoidance. These PHYB,D,E-mediated responses are counteracted by PHYA [33] and gated by the circadian clock through modulation of *PIL1* and *PIL2* expression [29**]. FR-induced early flowering involves transcriptional regulation of *PFT1* [5*]. Furthermore, phytochrome-mediated growth responses are temperature-dependent and involve transcriptional regulation of the *ATHB-2* and *ATHB-4* homeobox genes (reviewed in [4*]). Blue-light responses are mediated by cryptochromes and phototropins.

to be important at low blue-light intensities [19]. Still, CRY2 does affect petiole elongation in *Arabidopsis* in high-blue light [20*], and it therefore remains uncertain which cryptochrome(s) regulate(s) growth responses to reduced blue light in canopies [9*]. Cryptochromes show structural similarities to DNA photolyases, and accumulate in the nucleus in the dark. In the light, CRY1 predominantly occurs in the cytosol, whereas CRY2 remains nuclear [19]. Cryptochromes interact with the E3 ubiquitin ligase CONSTITUTIVELY PHOTOMORPHOGENIC1 (COP1), which targets the growth-inhibiting transcription factor HY5 for degradation [21]. COP1-mediated HY5 breakdown is prevented by light-activated cryptochrome, allowing HY5 accumulation and the inhibition of elongation growth [19]. Interestingly, phytochromes transcriptionally control HY5, providing a point of convergence for CRY and PHY signalling [15,16].

The second class of UV-A/blue-light receptors are the phototropins (PHOT1 and PHOT2), which might regulate phototropic growth [22] towards gaps in canopies [2]. PHOT1 and PHOT2 have redundant functions in phototropism and the optimization of photosynthesis-

related traits, including chloroplast positioning and stomatal opening [12**]. This optimization of photosynthesis was recently shown to dramatically increase the growth of *Arabidopsis* in shaded conditions [10**]. PHOT2 operates predominantly in high light, whereas PHOT1 is more important for responses at low blue-light intensities [23]. Upon light activation, part of the plasma-membrane-associated PHOT1 is released into the cytoplasm [12**]. The NON-PHOTOTROPIC HYPOCOTYL 3 (NPH3) and ROOT PHOTOTROPISM 2 (RPT2) proteins act downstream of PHOT1 [12**,22]. The exact function of these proteins in PHOT1 signalling is unknown, but it has been suggested that NPH3 and RPT2 function as substrate adapters for CULLIN3 (CUL3)-based ubiquitin ligases, and thus target specific proteins for degradation [22]. Tentatively, these target proteins might include MASSUGU2 (MSG2)/INDOLE-3-ACETIC ACID-REGULATED19 (IAA19), which was recently shown to suppress the action of NPH4/ARF7, an auxin response factor that regulates phototropism [24].

Interestingly, PHOT-mediated phototropism towards unilateral blue light is modulated by cryptochromes

[25] and phytochromes [26^{*}]. In addition, interactions between CRY1 and PHYA [27] and between CRY2 and PHYB [28] have been reported in *Arabidopsis*. We can conclude, therefore, that interactions between all photoreceptors determine shade-avoidance responses.

Circadian clock control

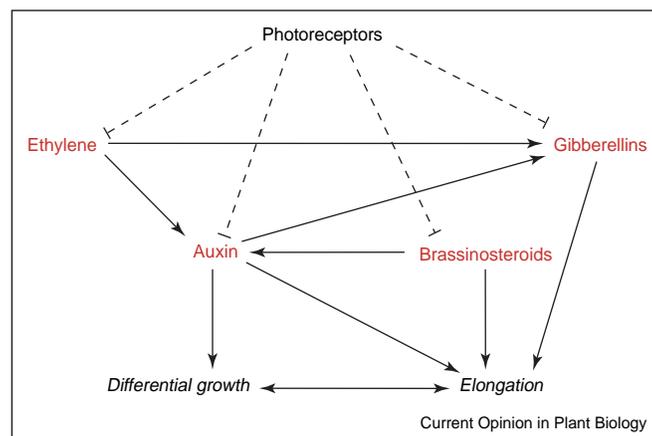
Enhanced hypocotyl elongation caused by reduced R:FR in *Arabidopsis* is day-time-dependent, and is most effectively induced around (subjective) dusk [29^{**}]. Under these conditions, several growth-related genes, including some that include auxin efflux regulators and cell wall modifying enzymes, are highly expressed [30,31]. The maximal growth increase at dusk, when sunlight in natural conditions is enriched in longer (FR) wavelengths, is thus anticipated by the plant. Hence, the circadian clock controls shade-avoidance responses. The clock in *Arabidopsis* is essentially an oscillator that contains MYB factors (e.g. CIRCADIAN CLOCK ASSOCIATED1 [CCA1] and LATE ELONGATED HYPOCOTYL [LHY]) and a quintet of pseudo response regulators (APRRs), including APRR1/TIMING OF CAB1 (TOC1). PIL1 is among the proteins that interact with TOC1 [32], and the *pil1* knockout has an attenuated elongation response to a transient reduction in R:FR. *PIL1* is also rapidly and strongly induced upon low R:FR exposure, and its expression shows circadian regulation, with highest expression at dawn [29^{**},33]. This evidence paved the way for the discovery of a molecular link between shade avoidance and clock-regulation (Figure 2), although the exact role of *PIL1* in regulating circadian-clock-gated shade avoidance remains to be elucidated because *PIL1* transcription and low-R:FR-induced elongation are out of phase.

Hormonal interactions in shade avoidance

All of the plant hormones that are involved in elongation growth are potential actors in shade-avoidance responses (Figure 3). Auxin has been implicated in whole-plant plasticity and more specifically in phototropic bending. Phototropism is known to involve both differential auxin transport through auxin efflux carriers [34,35^{*}] and auxin signalling: the *nph4-1 Arabidopsis* mutant is defective in the auxin-response factor ARF7 [24]. Furthermore, the elongation response to low R:FR is auxin dependent [18]. It has been suggested that the mechanism for elongation relies on the lateral distribution (from the vascular tissue) of auxin in the shoot (i.e. hypocotyl or stem) and a consequent reduction in auxin transport towards the roots, which remain shorter than in high R:FR [17]. Auxin involvement is confirmed by the low R:FR-mediated induction of *IAA2*, *IAA7* and *IAA19*, and by the increased expression of several auxin-inducible genes in cryptochrome and phytochrome mutants [17,33,36]. Furthermore, low-light-induced shade avoidance also requires intact auxin signalling [7^{*}].

Low light intensity and low R:FR also increase ethylene production [7^{*},37,38]. Hence, ethylene can accumulate in canopies [9^{*}]. The *Arabidopsis* ethylene overproducing mutant *eto2* has an exaggerated response to decreased light intensities [7^{*}], and ethylene treatment can cause rapid (within 2h) upward movement of leaves in *Arabidopsis*, as can low-light treatment [8^{*}]. The importance of ethylene for shading responses has been convincingly shown in tobacco. Ethylene-insensitive transgenic lines have reduced stem-elongation and leaf-elevation responses to low R:FR or in plant canopies [9^{*},39]. These

Figure 3



Working model for hormonal crosstalk in the effect of shade on plants. Shading diminishes the negative action (dotted lines) of photoreceptors on the biosynthesis of ethylene, on (active) brassinosteroids and on the biosynthesis and signalling of (active) gibberellins. In addition, shading plays a part in the regulation of auxin transport, implying that shading affects the differential distribution of this hormone. The hormones themselves also interact (arrows), which makes it likely that several signals from the photoreceptors pass through various hormonal pathways. This results in differential growth (towards light patches) and stem and petiole elongation. Positive regulation is represented by arrows and solid lines, and negative regulation by blocked arrows and dotted lines. The double-headed arrow indicates possible overlap in the downstream components of light-mediated changes in differential growth and shoot elongation.

R:FR and ethylene-induced elongation responses are gibberellic acid (GA)-dependent [38]. Furthermore, the shade-avoidance phenotype of *Arabidopsis phyB* mutants is suppressed by the inactivation of *GAI*, a gene that encodes ent-copalyl diphosphate synthase (CPS), which catalyses the first step in GA biosynthesis [40]. Depending on the species, PHYB negatively controls GA sensitivity and/or biosynthesis [41]. Evidently, the action of blue light through cryptochromes might repress GA biosynthesis, as GA biosynthesis genes are upregulated in *cry1* mutant seedlings [36]. Recent breakthroughs in GA signalling have provided a handle for our understanding of the interactions between GA and other signalling routes. Not only is the breakdown of the growth-inhibiting DELLA proteins enhanced by GA signalling, but also auxin and ethylene determine DELLA protein stability [42,43], thus integrating several hormone signals.

The brassinosteroid (BR) pathway that stimulates elongation is yet another factor implicated in the already complex regulation of shade avoidance. The *Arabidopsis* BR-biosynthesis mutant *dwarf1-101* (*dwf1-101*) lacks elongated hypocotyls in canopy shade [44]. Enhanced expression of the BR-inactivating enzyme BAS1 suppresses the phenotype of *phyB-4* mutants [45]. The observation that BRs control the lateral distribution of auxins or auxin signals in hypocotyls [46] tempts speculation about a link with the above-mentioned model for the low R:FR response [17]. In shading, higher levels of BRs could enhance lateral auxin transport out of the vascular tissue, leading to increased auxin signalling. Alternatively, auxin and BRs might directly stimulate common target genes [46,47].

Ecological implications: adaptive exploitation of shade avoidance

Shade avoidance confers a fitness advantage by enhancing light capture in dense stands, and plants whose shade-avoidance properties are inhibited are therefore out-competed by wildtype neighbours [6,39]. However, the elongated phenotype is a disadvantage in stands of low density [6,48]. This disadvantage implies costs, such as the reduced investment in roots and photosynthesizing leaves and mechanical problems such as lodging [6]. These costs can even have consequences in dense stands; for example, low water availability negatively affects selection for shade avoidance traits, probably because of the reduced investment in roots [49]. Thus, shade avoidance is advantageous only when displayed under specific environmental conditions and disadvantageous under other conditions. As a result, variation for shade-avoidance properties exists between [50] and within [51] species, which might be related to each species' or genotype's habitat of origin. For example, the alpine *Stellaria longipes* ecotype occurs in open, non-competitive fields and shows no low R:FR-induced internode elongation, whereas this response is shown by the prairie

ecotype from dense, competitive vegetation [52]. Furthermore, woodland populations of *Impatiens capensis* cannot outgrow the shading trees, and hence show no shade avoidance to low R:FR, whereas open field populations do show this response because, in this environment, the ability to respond to low R:FR provides a competitive advantage over neighbours [53].

Conclusions

New perspectives on plant neighbour detection and the paradigm of PHYB-mediated shade avoidance through R:FR signalling have now been merged into a complex model that involves numerous signals and photoreceptors. Besides PHYB, PHYD and PHYE also contribute redundantly to R:FR signalling. Recent studies have identified important roles for blue and total light intensity as cues for the detection of neighbours, and there are even indications that neighbours could be detected through the perception of volatile chemicals such as ethylene [9]. However, it remains to be determined which UV-A/blue-light receptors are actually involved in neighbour detection, and the use of combined photoreceptor mutants in canopy studies could shed new light on this emerging topic.

At the level of hormone interactions, major progress has been made recently. It has been shown that not only gibberellins but also auxins, brassinosteroids and ethylene regulate shade-avoidance responses. The involvement of these hormones is best described in R:FR-mediated responses, but data on blue light-regulated traits are accumulating. Interestingly, light and hormone signal transduction have a fundamental process in common: the breakdown of proteins that are targeted by ubiquitination [54]. This has recently inspired several authors to postulate light-hormone interactions in the protein-degradation process, and this research area will undoubtedly yield interesting insights in the near future.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Evans JR, Poorter H: **Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain.** *Plant Cell Environ* 2001, **24**:755-767.
 2. Ballaré CL: **Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms.** *Trends Plant Sci* 1999, **4**:97-102.
 3. Smith H: **Phytochromes and light signal perception by plants – an emerging synthesis.** *Nature* 2000, **407**:585-591.

4. Franklin KA, Whitelam GC: **Phytochromes and shade avoidance responses in plants.** *Ann Bot* 2005, in press.
An excellent update on how multiple phytochrome mutants have been exploited to identify the relative contribution of each phytochrome family member to low R:FR-induced shade avoidance.
5. Cerdán PD, Chory J: **Regulation of flowering time by light quality.** *Nature* 2003, **423**:881-885.
The authors show the existence of a light-quality pathway that regulates flowering time in plants. This explains the flowering time-regulation by R:FR ratios through a PHYB-dependent pathway that involves the PFT1 (PHYTOCHROME AND FLOWERING TIME1) protein.
6. Schmitt J, McCormac AC, Smith H: **A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbors.** *Am Nat* 1995, **146**:937-953.
7. Vandenbussche F, Vriezen WH, Smalle J, Laarhoven LJ, Harren FJ, Van Der Straeten D: **Ethylene and auxin control the *Arabidopsis* response to decreased light intensity.** *Plant Physiol* 2003, **133**:517-527.
This work stresses the effect of light intensity on shading responses in *Arabidopsis*. The authors demonstrate the involvement of auxin and ethylene in the establishment of the shade-avoidance phenotype found in low R:FR ratios.
8. Millenaar FF, Cox MC, van Berkel YE, Welschen RA, Pierik R, Voeselek LA, Peeters AJ: **Ethylene-induced differential growth of petioles in *Arabidopsis*. Analyzing natural variation, response kinetics, and regulation.** *Plant Physiol* 2005, **137**:998-1008.
In this paper, plants responses to several treatments that induce hyponastic growth (or leaf elevation) in *Arabidopsis* are compared. Hyponasty is stimulated by submergence, shading and ethylene and differs between ecotypes. Ethylene has an effect similar to that of neutral shade on hyponastic growth.
9. Pierik R, Whitelam GC, Voeselek LACJ, de Kroon H, Visser EJV: **Canopy studies on ethylene-insensitive tobacco identify ethylene as a novel element in blue light and plant-plant signalling.** *Plant J* 2004, **38**:310-319.
The authors describe the role of ethylene in plant neighbour detection and competitive success. Furthermore, they show the important role played by blue light in responses that allow plants to avoid shade from neighbours. These responses are entirely ethylene-dependent, suggesting the potential for chemical detection of neighbours.
10. Takemiya A, Inoue S, Doi M, Kinoshita T, Shimazaki K: **Phototropins promote plant growth in response to blue light in low light environments.** *Plant Cell* 2005, **17**:1120-1127.
The authors of this paper describe elegant experiments that show dramatic phototropin-dependent effects on overall plant growth, proving that PHOT-mediated optimization of photosynthesis parameters is of paramount importance for plant growth in shaded conditions.
11. Franklin KA, Prækel U, Stoddart WM, Billingham OE, Halliday KJ, Whitelam GC: **Phytochromes B, D and E act redundantly to control multiple physiological responses in *Arabidopsis*.** *Plant Physiol* 2003, **131**:1340-1346.
The authors exploit single, double, triple and quadruple phytochrome mutants to functionally interpret the action of the individual phytochromes. This was previously impossible because of redundancy between the different members of this family of photoreceptors.
12. Chen M, Chory J, Fankhauser C: **Light signal transduction in higher plants.** *Annu Rev Genet* 2004, **38**:87-117.
This excellent review provides an accessible, in-depth insight into the action and signalling of all photoreceptors known in plants to date.
13. Duek PD, Fankhauser C: **bHLH class transcription factors take centre stage in phytochrome signalling.** *Trends Plant Sci* 2005, **10**:51-54.
14. Quail PH: **Phytochrome photosensory signalling networks.** *Nat Rev Mol Cell Biol* 2002, **3**:85-93.
15. Gyula N, Schafer E, Nagy F: **Light perception and signalling in higher plants.** *Curr Opin Plant Biol* 2003, **6**:446-452.
16. Quail PH: **Photosensory perception and signalling in plant cells: new paradigms?** *Curr Opin Cell Biol* 2002, **14**:180-188.
17. Morelli G, Ruberti I: **Light and shade in the photocontrol of *Arabidopsis* growth.** *Trends Plant Sci* 2002, **7**:399-404.
18. Steindler C, Matteucci A, Sessa G, Weimar T, Ohgishi M, Aoyama T, Morelli G, Ruberti I: **Shade avoidance responses are mediated by the ATHB-2 HD-zip protein, a negative regulator of gene expression.** *Development* 1999, **126**:4235-4245.
19. Lin C, Shalitin D: **Cryptochrome structure and signal transduction.** *Annu Rev Plant Biol* 2003, **54**:469-496.
20. Kozuka T, Horiguchi G, Kim G-T, Ohgishi M, Sakai T, Tsukaya H: **The different growth responses of the *Arabidopsis thaliana* leaf blade and the petiole during shade avoidance are regulated by photoreceptors and sugars.** *Plant Cell Physiol* 2005, **46**:213-223.
The authors show that light of FR, R and B wavelengths enhances leaf blade expansion. They not only demonstrate the involvement of stable phytochromes as negative regulators of petiole length in red light, but also show that cryptochromes are responsible for the same process in both blue and red light. This stresses the importance of cryptochromes for plant adaptation to shading.
21. Osterlund MT, Hardtke CS, Wei N, Deng XW: **Targeted destabilization of HY5 during light-regulated development of *Arabidopsis*.** *Nature* 2000, **405**:462-466.
22. Celaya RB, Liscum E: **Phototropins and associated signaling: providing the power of movement in higher plants.** *Photochem Photobiol* 2005, **81**:73-80.
23. Briggs WR, Christie JM: **Phototropins 1 and 2: versatile plant blue-light receptors.** *Trends Plant Sci* 2002, **7**:204-210.
24. Tatematsu K, Kumagai S, Muto H, Sato A, Watahiki MK, Harper RM, Liscum E, Yamamoto KT: **MASSUGU2 encodes Aux/IAA19, an auxin-regulated protein that functions together with the transcriptional activator NPH4/ARF7 to regulate differential growth responses of hypocotyl and formation of lateral roots in *Arabidopsis thaliana*.** *Plant Cell* 2004, **16**:379-393.
25. Whippe CW, Hangarter RP: **Second positive phototropism results from coordinated co-action of the phototropins and the cryptochromes.** *Plant Physiol* 2003, **132**:1499-1507.
26. Whippe CW, Hangarter RP: **Phytochrome modulation of blue-light-induced phototropism.** *Plant Cell Environ* 2004, **27**:1223-1228.
The authors show that phytochromes modulate phototropism to unilateral blue light in a fluence-rate-dependent manner. At low fluence rates, phytochromes facilitate a robust phototropic response, whereas at high fluence rates, PHYA suppresses phototropism.
27. Ahmad M, Jarillo JA, Smirnova O, Cashmore AR: **The CRY1 blue light photoreceptor of *Arabidopsis* interacts with phytochrome A *in vitro*.** *Mol Cell* 1998, **1**:939-948.
28. Más P, Devlin PF, Panda S, Kay SA: **Functional interaction of phytochrome B and cryptochrome 2.** *Nature* 2000, **408**:207-211.
29. Salter MG, Franklin KA, Whitelam GC: **Gating of the rapid shade-avoidance response by the circadian clock in plants.** *Nature* 2003, **426**:680-683.
This breakthrough paper clearly demonstrates that shade-avoidance signalling in plants is a target for circadian clock control. The authors present evidence that the induction of PIL1 and PIL2 (PIF3-like genes) is gated through the circadian clock.
30. Dowson-Day MJ, Millar AJ: **Circadian dysfunction causes aberrant hypocotyl elongation patterns in *Arabidopsis*.** *Plant J* 1999, **17**:63-71.
31. Harmer SL, Hogenesch JB, Straume M, Chang HS, Han B, Zhu T, Wang X, Kreps JA, Kay SA: **Orchestrated transcription of key pathways in *Arabidopsis* by the circadian clock.** *Science* 2000, **290**:2110-2113.
32. Makino S, Matsushika A, Kojima M, Yamashino T, Mizuno T: **The APRR1/TOC1 quintet implicated in circadian rhythms of *Arabidopsis thaliana*: I. Characterization with APRR1-overexpressing plants.** *Plant Cell Physiol* 2002, **43**:58-69.
33. Devlin PF, Yanovsky MJ, Kay SA: **A genomic analysis of the shade avoidance response in *Arabidopsis*.** *Plant Physiol* 2003, **133**:1617-1629.

34. Friml J, Wisniewska J, Benkova E, Mendgen K, Palme K: **Lateral relocation of auxin efflux regulator PIN3 mediates tropism in *Arabidopsis***. *Nature* 2002, **415**:806-809.
35. Blakeslee JJ, Bandyopadhyay A, Peer WA, Makam SN,
 • Murphy AS: **Relocalization of the PIN1 auxin efflux facilitator plays a role in phototropic responses**. *Plant Physiol* 2004, **134**:28-31.
- Localization studies on the PIN1 auxin-efflux facilitator protein show its involvement in phototropic redistribution of auxin in *Arabidopsis* hypocotyls.
36. Folta KM, Pontin MA, Karlin-Neumann G, Bottini R, Spalding EP: **Genomic and physiological studies of early cryptochrome 1 action demonstrate roles for auxin and gibberellin in the control of hypocotyl growth by blue light**. *Plant J* 2003, **36**:203-214.
37. Finlayson SA, Lee I-J, Morgan PW: **Phytochrome B and the regulation of circadian ethylene production in sorghum**. *Plant Physiol* 1998, **116**:17-25.
38. Pierik R, Cuppens MLC, Voeselek LACJ, Visser EJW: **Interactions between ethylene and gibberellins in phytochrome-mediated shade avoidance responses in tobacco**. *Plant Physiol* 2004, **136**:2928-2936.
39. Pierik R, Visser EJW, de Kroon H, Voeselek LACJ: **Ethylene is required in tobacco to successfully compete with proximate neighbours**. *Plant Cell Environ* 2003, **26**:1229-1234.
40. Peng J, Harberd NP: **Gibberellin deficiency and response mutations suppress the stem elongation phenotype of phytochrome-deficient mutants of *Arabidopsis***. *Plant Physiol* 1997, **113**:1051-1058.
41. Kamiya Y, Garcia-Martinez JL: **Regulation of gibberellin biosynthesis by light**. *Curr Opin Plant Biol* 1999, **2**:398-403.
42. Achard P, Vriezen WH, Van Der Straeten D, Harberd NP: **Ethylene regulates *Arabidopsis* development via the modulation of DELLA protein growth repressor function**. *Plant Cell* 2003, **15**:2816-2825.
43. Vriezen WH, Achard P, Harberd N, Van Der Straeten D: **Ethylene-mediated enhancement of apical hook formation in etiolated *Arabidopsis thaliana* seedlings is gibberellin dependent**. *Plant J* 2004, **37**:505-516.
44. Luccioni LG, Oliverio KA, Yanovsky MJ, Boccalandro HE, Casal JJ: **Brassinosteroid mutants uncover fine tuning of phytochrome signaling**. *Plant Physiol* 2002, **128**:173-181.
45. Neff MM, Nguyen SM, Malancharuvil EJ, Fujioka S, Noguchi T, Seto H, Tsubuki M, Honda T, Takatsuto S, Yoshida S, Chory J:
 • ***BAS1*: a gene regulating brassinosteroid levels and light responsiveness in *Arabidopsis***. *Proc Natl Acad Sci USA* 1999, **96**:15316-15323.
46. De Grauwe L, Vandenbussche F, Tietz O, Palme K, Van Der Straeten D: **Auxin, ethylene and brassinosteroids: tripartite control of growth in the *Arabidopsis* hypocotyl**. *Plant Cell Physiol* 2005, **46**:827-836.
47. Nakamura A, Higuchi K, Goda H, Fujiwara MT, Sawa S, Koshiba T, Shimada Y, Yoshida S: **Brassinolide induces IAA5, IAA19, and DR5, a synthetic auxin response element in *Arabidopsis*, implying a cross talk point of brassinosteroid and auxin signaling**. *Plant Physiol* 2003, **133**:1843-1853.
48. Donohue K, Messiqua D, Pyle EH, Heschel MS, Schmitt J: **Evidence of adaptive divergence in plasticity: density- and site-dependent selection on shade avoidance responses in *Impatiens capensis***. *Evolution* 2000, **54**:1956-1968.
49. Huber H, Kane NC, Heschel MS, von Wettberg EJ, Banta J,
 • Leuck A-M, Schmitt J: **Frequency and microenvironmental pattern of selection on plastic shade-avoidance traits in a natural population of *Impatiens capensis***. *Am Nat* 2004, **163**:548-563.
- This paper challenges the idea that shade-avoidance responses are always beneficial to shade-avoiding plants grown in natural dense stands. The authors show that other environmental factors, such as low water availability, can strongly affect these benefits.
50. Gilbert IR, Jarvis PG, Smith H: **Proximity signal and shade avoidance differences between early and late successional trees**. *Nature* 2001, **411**:792-795.
51. Botto JF, Smith H: **Differential genetic variation in adaptive strategies to a common environmental signal in *Arabidopsis* accessions: phytochrome-mediated shade avoidance**. *Plant Cell Environ* 2002, **25**:53-63.
52. Alokam S, Chinnappa CC, Reid DM: **Red/far-red light mediated stem elongation and anthocyanin accumulation in *Stellaria longipes*: differential response of alpine and prairie ecotypes**. *Can J Bot* 2002, **80**:72-81.
53. von Wettberg EJ, Schmitt J: **Physiological mechanisms of population differentiation in shade-avoidance responses between woodland and clearing genotypes of *Impatiens capensis***. *Am J Bot* 2005, **95**:868-874.
54. Vandenbussche F, Van Der Straeten D: **Shaping the shoot: a circuitry that integrates multiple signals**. *Trends Plant Sci* 2004, **9**:499-506.