

# Chapter 6

## Photomorphogenesis and Photoreceptors

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### Summary

Plants use light as their main source of energy and to gather information about their surroundings. The light environment is monitored through an extensive set of photoreceptors and largely dictates plant development through induction of processes such as germination and flowering, entrainment of the circadian clock and photomorphogenic responses. Plants display remarkable phenotypic plasticity upon perception of changes in the light, ranging from seedling de-etiolation to shade avoidance and phototropic responses in competition for light. Here, we describe photomorphogenic responses and their underlying mechanisms such as they occur in a leaf canopy. This shade avoidance review will largely focus on the model plant species *Arabidopsis thaliana* as the underlying mechanisms controlling shade avoidance are particularly well elucidated in this species.

**Keywords** Shade avoidance • Plant architecture • Photoreceptor • Light • Photomorphogenesis

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## I. Competition for Light: Shade Tolerance and Shade Avoidance

Plants growing at high density are at risk of becoming shaded and have to compete for light to prevent losing access to their main source of energy. The consequence of becoming overgrown is clearly demonstrated by the life style of several (sub)tropical species of *Ficus*. These “strangler” figs can avoid germination at the dark forest floor by starting their life as an epiphyte, which then grows its roots downward and envelops the host tree’s stem (Athreya 1999). When these plants reach the light at the top of the canopy they establish a large crown shading the host tree, which eventually dies from lack of light. When plants are growing in dense canopies, size inequalities between individual plants increase with increasing density (Weiner 1985). This shows that a small initial difference in size can have a huge competitive advantage leading to suppression of smaller individuals, whose light capture will be diminished as their taller neighbours start to grow. To conserve energy and enhance fitness in adverse conditions, plants can employ different types of stress responses. Stresses that cannot be outgrown might require a quiescent response, while other stresses can be overcome by an escape strategy (Voesenek and Pierik 2008). In competition for light, both strategies can be found.

Plants that are adapted to completing their life cycle under shade conditions are considered to be shade tolerant. For example, plants living in the forest understory will not be able to outgrow the tall neighbouring trees and a shade tolerance strategy is therefore more adaptive. A photosynthetically optimal strategy in low light environments is to form

leaves with a high specific leaf area (SLA: leaf area / leaf dry weight). A high SLA indicates leaves with a relatively large surface area per unit invested dry weight and usually represents relatively thin leaves. This is highly suitable under low light conditions since these leaves will be able to intercept the majority of photons available and have low respiration per unit leaf area due to fewer cell layers. Such acclimated leaves, therefore, have a low light compensation of photosynthesis. These leaf morphological acclimations, combined with photosynthetic adjustments such as reduced chlorophyll a/b ratio’s and increased photosystem (PS)II:I ratio’s (Meils and Harvey 1981) constitute the so-called carbon gain hypothesis of shade tolerance (reviewed in Givnish 1988; Valladares and Niinemets 2008). Although these leaf traits optimize carbon acquisition in low light, leaves with a high SLA tend to be more prone to mechanical damage and herbivory. In low light conditions, however, plants cannot always afford to lose biomass quite so easily. Therefore, it is observed that very shade tolerant species in deep forest shade produce well-protected, tough and relatively thick leaves rather than the photosynthetically optimal thin leaves (Kitajima and Poorter 2010; Poorter and Bongers 2006). This constrained SLA development is typical of true shade tolerant species. Many shade avoiding species show an even stronger increase of SLA in response to shade to optimize light harvesting but would not be shade tolerant because of a relatively short leaf longevity. It has been proposed that shade tolerant species are therefore less plastic for various morphological traits than are shade avoiding species and invest more in leaf longevity. This hypothesis has been coined the stress tolerance hypothesis of shade tolerance (Kitajima 1994); reviewed in (Valladares and Niinemets 2008).

Another category of plants displays an array of escape responses that serve to ensure light capture in a competitive light environment and collectively are called the shade avoidance syndrome (SAS) (Casal 2012; Franklin 2008; Vandenbussche et al. 2005).

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*Abbreviations:* ABA – Abscisic acid; B – Blue light; BR – Brassinosteroid; Cry – Cryptochrome; ET – Ethylene; FR – Far-red light; GA – Gibberellin; PAR – Photosynthetically Active Radiation; Phot – Phototropin; Phy – Phytochrome; PIF – Phytochrome-interacting Factor; R – Red light; R:FR – Red: Far-red light ratio; UV – Ultraviolet light; VOC – Volatile Organic Compound



Fig. 6.1. Shade avoidance in low R:FR-exposed (right) sunflower (*Helianthus annuus*) versus control light conditions (left). Three weeks old plants that have been exposed to high (1.8) or low (0.2) R:FR light conditions from 4 day after sowing onwards. Plants were grown at  $180 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR (16 h light, 8 h dark), 21 °C and 70 % RH

These include changes in morphology to position the leaves in a more competitive position through increased leaf angles (hyponasty), elongation of hypocotyls, internodes, petioles and stems (Fig. 6.1), reduced shoot branching due to reduced bud outgrowth (Finlayson et al. 2010; Kebrom et al. 2006), and adjustment of the photosynthetic apparatus. The effect of shade signals on leaf surface area varies between species and both growth stimulation and inhibition have been reported (Bittebiere et al. 2012; Carabelli et al. 2007; Chitwood et al. 2012; Liu et al. 2012). As an ultimate escape response, shade also induces accelerated flowering. Shade avoidance responses are influenced by environmental conditions. Shade-induced flowering and changes in leaf architecture are highly temperature-dependent (Franklin 2009; Halliday et al. 2003) and the effect of light quality on branching is dependent on the light intensity (Su et al. 2011).

Shade avoidance responses have great impact on patterns and species distribution of natural plant communities and plant biodiversity (Goldberg and Barton 1992; Hautier et al. 2009) and can have a major impact on agricultural yield. In homogeneous crop fields shade avoidance negatively affects yield because resources are invested in non-harvestable organs such as stems at the expense of crops. Furthermore, the reduced branching (tillering) in cereals, strongly affects the yield potential, while stem elongation and apical dominance may lead to crop lodging. Expression of shade avoidance responses reduces plant fitness in the absence of competition, but has great adaptive value when plants have to compete for light (Ballaré et al. 1988; Casal and Smith 1989; Casal et al. 1994; Pierik et al. 2003; Schmitt et al. 1995). Thus, to avoid unnecessary fitness costs on one hand and small size differences that may cause great competitive imbalance on the other, it is essential that plants adjust their growth to neighbours exactly at the right time.

## II. Perception of Neighbour-Derived Signals

To perceive the presence of proximate neighbours plants make use of the qualitative changes in the spectral composition of the light that occur in the transmitted and reflected light in a canopy (see Chap. 1, Goudriaan 2016). Red (R) and blue (B) light are absorbed for photosynthesis and thus depleted from the transmitted light, whereas far-red (FR) wavelengths are reflected by green tissues. The different light components are signalled through a variety of photoreceptors, notably phytochromes, cryptochromes and phototropins (Fig. 6.2). Besides these plant-specific light signals plants may also perceive nearby competitors through touching neighbouring leaves, accumulation of the plant hormone ethylene and possibly other volatile components.

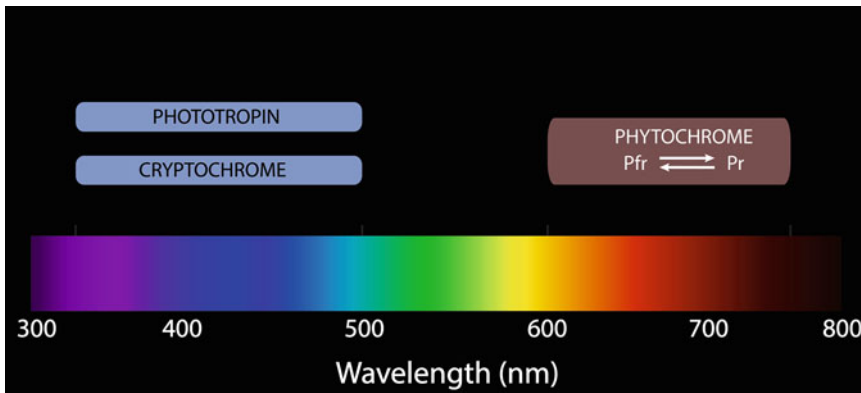


Fig. 6.2. Solar spectrum and the wavebands at which the three major plant photoreceptor classes (phytochromes, cryptochromes and phototropins) display their activities

### A. Low R:FR Perception and Signal Transduction

As R light (wavelength 600–700 nm) is absorbed by plant tissues while FR (700–800 nm) light is mostly reflected, the ratio between R and FR (R:FR) decreases in the vertically incoming light inside a canopy (Ballaré et al. 1987b). Since it is reflected by plants, a FR signal can lower the R:FR even before actual shading takes place and thus play an important role as an early neighbour detection signal. A low R:FR in high PAR background was indeed shown to induce shade avoidance responses in plants grown without neighbours (Morgan and Smith 1978; Morgan et al. 1980). Final proof that plants can detect remote vegetation through reflected FR radiation came from plants that failed to respond to neighbours with increased stem elongation at an early stage of competition when they were blinded to FR by a  $\text{CuSO}_4$  filter around individual internodes (Ballaré et al. 1990).

The R:FR is perceived by the phytochrome photoreceptors, which exist in two photo-convertible conformation states. Photoconversion of phytochromes is brought about by cis-trans isomerisation of the associated tetrapyrrole bilin chromophore called the phytychromobilin (Rockwell et al. 2006). The inactive Pr form absorbs R light and has an absorption peak at 665 nm,

whereas the active Pfr form absorbs FR light with an absorption peak at 730 nm (Smith 2000; Fig. 6.2). *PhyB* mutants in various plant species show a constitutive shade avoidance phenotype (Devlin et al. 1992; Reed et al. 1993; Somers et al. 1991), indicating that this is the main regulating photoreceptor in low R:FR signalling. The phytochrome B photoequilibrium thus reflects the R:FR and acts as a sensor for qualitative changes in the red spectrum of the light environment (Holmes and Smith 1975; Smith and Holmes 1977). The Pfr form of phytochrome A is rapidly degraded (Clough et al. 1997; Hennig et al. 1999), making it mostly active in FR. In low R:FR, phyA can inhibit shade-induced elongation growth (Fairchild et al. 2000; Johnson et al. 1994; Reed et al. 1994; Rousseaux et al. 1997).

Upon activation of phytochrome by R light the Pfr form translocates from the cytosol, where it resides in its inactive Pr form, to the nucleus (Kircher et al. 1999; Sakamoto and Nagatani 1996; Yamaguchi et al. 1999), where it is required for regulation of growth inhibition (Huq et al. 2003). In the nucleus, Pfr interacts with several members of the BASIC HELIX-LOOP-HELIX (bHLH) family of transcription factors called PIF or PIL for phytochrome interacting factor (–like) (Duek and Fankhauser 2005). Of these, the positive regulators of elongation

growth PIF4, PIF5 and PIF7 play an important role in shade avoidance signalling, as shown by attenuated hypocotyl elongation of *pif* mutants in low R:FR (Li et al. 2012; Lorrain et al. 2008). PIF4 and PIF5 are targeted for proteasome-mediated degradation in red light, which is dependent on their active phytochrome binding (APB) domain (Lorrain et al. 2008). This suggests that in low R:FR conditions inactivation of phytochrome releases phytochrome-mediated degradation of these PIFs, allowing for their interaction with downstream components of growth regulation. PIF7 action on the other hand seems to involve its de-phosphorylation upon detection of shade (Li et al. 2012).

Perception of low R:FR leads to rapid induction of gene expression (Salter et al. 2003; Sessa et al. 2005). Among the first identified genes regulated by changes in R:FR was the homeobox transcription factor *ATHB2* (Carabelli et al. 1993, 1996), which was later confirmed to be important for expression of a shade avoidance phenotype (Steindler et al. 1999). Another well-characterised shade avoidance marker gene is the bHLH transcription factor *PIL1*, whose expression is upregulated within minutes of exposure to low R:FR (Salter et al. 2003). The expression of negative regulators of growth such as the bHLH transcription factors *PHY RAPILY REGULATED (PAR)1* and 2, and *LONG HYPOCOTYL IN FR (HFR)1* are also induced by a low R:FR signal (Roig-Villanova et al. 2007; Sessa et al. 2005). *HFR1* was shown to form heterodimers with PIF4 and PIF5, thereby preventing their DNA-binding capacity and limiting the PIF-modulated growth response (Hornitschek et al. 2009). Further downstream, low R:FR-induced elongation growth through cell expansion is enabled by regulation of cell wall modifying proteins, which involve several members of the xyloglucan endotransglucosylase/hydrolase (XTH) family in Arabidopsis (Sasidharan et al. 2010).

### B. Blue Light Perception and Signalling

Like R light, B light (length 400–500 nm) is absorbed for photosynthesis and thus reduced in the light environment inside a canopy. Although reduction of B fluence rates cannot be detected as early as an increase in reflected FR it can induce shade avoidance responses, suggesting that low B serves as a light signal at later stages of competition. Depletion of B light was first shown to affect growth responses in *Datura ferox* monocultures, which showed enhanced internode elongation when blue light was filtered out of the light spectrum (Ballaré et al. 1991). Internode elongation in response to attenuated B has furthermore been shown in the herbaceous perennial *Stellaria longipes* (Sasidharan et al. 2008). Cultivated tobacco (*Nicotiana tabacum*) displays enhanced elongation as well as hyponasty in response to a reduced B environment obtained through low pressure sodium light (Pierik et al. 2004). In Arabidopsis seedlings, low B induces strong hypocotyl elongation (Djakovic-Petrovic et al. 2007; Keuskamp et al. 2011; Pierik et al. 2009). In adult Arabidopsis plants, low B can induce hyponasty and enhanced petiole elongation (Keller et al. 2011), although the latter response is not always apparent (Djakovic-Petrovic et al. 2007; Pierik et al. 2009) and may be dependent on total PAR and duration of treatment.

UV-A/blue light (320–500 nm) is perceived through distinct types of photoreceptors involved in the regulation of different responses; the cryptochromes, the phototropins and the zeatlupe family of photoreceptors. Low B-induced shade avoidance responses in adult Arabidopsis plants have been reported to be dependent on the blue light photoreceptor cryptochrome (cry) 1 (Keller et al. 2011) and hypocotyl elongation in response to reduced B light was shown to be regulated by both cry1 and cry2 (Ahmad et al. 1995; Lin et al. 1998; Pierik et al. 2009). The phototropic response, which is especially important for growth

towards canopy-gaps and thus optimisation of light capture in high density (Ballaré et al. 1987a), is regulated through the phototropins.

Cryptochrome (cry)1 and 2, like the phytochromes, play a role in photoperiodic flowering, entrainment of the circadian clock and in photomorphogenesis through regulation of stem elongation and leaf expansion (Lin and Shalitin 2003; Losi and Gartner 2012). *Cry1* mutants have elongated hypocotyls in both high and low fluence rates of B light. *Cry2* mutants only show this phenotype under low B fluence rates due to rapid blue-light induced degradation of cry2, which is therefore thought to act only in low B conditions (Lin et al. 1998). The cryptochromes are localised in the nucleus, where they are best known to directly interact with the E3 ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENIC (COP)1 in the regulation of light-induced inhibition of hypocotyl growth called photomorphogenesis (Wang et al. 2001; Yang et al. 2001). In darkness, COP1 interacts with the positive regulator of photomorphogenesis HY5 (long hypocotyl 5), thereby targeting this basic leucine zipper (bZIP) transcription factor for proteasome-mediated degradation (Ang et al. 1998; Osterlund et al. 2000). In light, COP1 translocates to the cytosol, thereby rescuing HY5 from degradation and allowing it to inhibit growth (Osterlund et al. 2000). The light-induced nuclear depletion of COP1 is believed to be established through its interaction with cry, which undergoes structural changes upon light perception (Chen et al. 2004). Although phyA and phyB have also been found to directly bind to COP1 (Seo et al. 2004; Yang et al. 2001), it is not known how this affects COP1 binding activity to HY5. COP1 interaction may however be a point of convergence between the phytochrome and cryptochrome signalling pathways. A second point of convergence might be the earlier mentioned PIF proteins since PIFs are also required for low blue-mediated petiole elongation (Keller et al. 2011). It remains to be studied if interaction between cryptochromes and PIFs indeed occur.

Another type of blue light receptors are the phototropins (phot)1 and 2. Phototropins are involved in phototropism (directional growth towards a unilateral light source), stomatal opening and chloroplast movement; responses that serve to optimise photosynthesis upon changes in light intensity (Christie 2007). *Phot1* mutants do not show phototropism in low B fluence rates and both *phot1* and *phot2* show a normal phototropic response in higher light intensities (Liscum and Briggs 1995; Sakai et al. 2000, 2001). Phototropism however is completely abolished in the *phot1phot2* double mutant (Sakai et al. 2001), which implies that phot1 is important for low fluence rates while both phototropins act redundantly at high fluence rates. The phototropins are localised at the plasmamembrane (Kong et al. 2006; Sakamoto and Briggs 2002), where they might regulate the distribution of auxin efflux carriers. Phot1 was found to interact with NONPHOTOTROPIC HYPOCOTYL (NPH)3, by which a lateral auxin gradient is established to allow for growth on the shaded side of the stem (Haga et al. 2005; Motchoulski and Liscum 1999). NPH3-like proteins were shown to regulate directional auxin transport through PIN-FORMED (PIN) auxin efflux carriers (Furutani et al. 2011). In relation to this, the auxin efflux carriers PIN1 and PIN3 have been shown to be required for a proper phototropic response (Blakeslee et al. 2004; Ding et al. 2011; Friml et al. 2002). Upon illumination, PIN3 trafficking to all cell sides by the PINOID (PID) kinase is repressed and unidirectional trafficking is brought about by the GNOM ARF GTPase GUANINE NUCLEOTIDE EXCHANGE FACTOR (GEF) (Ding et al. 2011). This directional targeting of PIN3 is likely to induce the differential auxin concentration between the illuminated and shaded side, leading to bending of hypocotyls and stems. Furthermore, the auxin-regulated transcription factors NPH4/ARF7 and MASSUGU (MSG)2/IAA19 have been involved in phototropism (Stowe-Evans et al. 1998; Tatematsu et al. 2004), emphasizing the importance of auxin

signalling in this response. Other signalling components implemented in the regulation of phototropic responses are PHYTOCHROME KINASE SUBSTRATE (PKS)1 and 2 (Boccalandro et al. 2008; de Carbonnel et al. 2010; Lariguet et al. 2006). PKS1 was found to bind both phot1 and NPH3 (Lariguet et al. 2006), and might thus play an essential role in phototropin signal transduction. As PKSs also interact with phytochromes and since phyA and phyB have been shown to be required for red-light-induced enhancement of phototropism (Janoudi et al. 1997; Parks et al. 1996; Whippo and Hangarter 2004), they might cross-talk between the two different photoreceptor pathways.

More recently, a novel class of blue light photoreceptors has been described. The zeitelupe family of photoreceptors consists of three members (ZTL, FKF1, and LKP2) with a photosensory domain similar to that of the phototropins (Christie 2007; Demarsy and Fankhauser 2009). So far, this type of photoreceptor has been described to play a role in regulation of photoperiodic flowering and the circadian clock, although ZTL might also be involved in photomorphogenesis (Kiba et al. 2007).

### C. Other Light Signals: Low PAR and Enriched Green Light

In a closing canopy total light intensity at the lower levels of the vegetation will decrease, even when the leaves might still be in full sunlight (Ballaré et al. 1991). Perception of drastically reduced light intensity induces a hyponastic response and petiole elongation in *Arabidopsis* even when the spectral composition of the light is similar to sunlight, which is dependent on both phyA and phyB, cry1 and cry2 and photosynthesis-derived signals (Kozuka et al. 2005; Millenaar et al. 2009). Although spectral-neutral reduction of photosynthetically active radiation (PAR) also enhanced stem elongation in tobacco (Pierik et al. 2004) it does not affect internode lengths in *Datura ferox* monocultures (Ballaré et al. 1991), indicating that the role for reduced PAR may be species-specific.

Like FR, green light is reflected by plant tissues containing chlorophyll, making them appear green to the human eye. In a canopy, this results in enrichment of green wavelengths in the light environment. Green light irradiation indeed increased hypocotyl elongation in *Arabidopsis* seedlings, and addition of green light to constant red and blue light induced the shade avoidance phenotype of increased leaf angles and enhanced petiole elongation in adult *Arabidopsis* plants (Folta 2004; Zhang et al. 2011). Cryptochromes have been shown to have a green-sensing state with biological activity (Banerjee et al. 2007; Bouly et al. 2007), but other modes of green light perception may exist.

### D. Light-Independent Signals

Various plant species are known to have increased emissions of the volatile plant hormone ethylene (ET) upon perception of low R:FR (Finlayson et al. 1999; reviewed in Kegge and Pierik 2010). ET is known to be the main regulator of hyponasty and subsequent petiole elongation in the semi-aquatic species *Rumex palustris* upon submergence stress (Peeters et al. 2002; Voeselek et al. 2003), a response that much resembles the growth adjustments that occur upon shading (Pierik et al. 2011). Indeed, ET has been found to accumulate inside the atmosphere of tobacco canopies to a level in which it induces shade avoidance-like growth responses in single-grown plants (Pierik et al. 2004). ET can induce elevated leaf angles even at very low concentrations (Polko et al. 2012) and it was mainly due to a retarded hyponastic response that ET-insensitive tobacco plants were outcompeted by wild-type plants when grown in high density (Pierik et al. 2003, 2004). These results show that ET can be an important player in neighbour detection.

In *Arabidopsis*, ethylene is perceived through a family of five redundant receptors (ETR1-2, ERS1-2 and EIN4) divided into two subfamilies based on structural similarities (Bleecker 1999; Chang and

Stadler 2001). All five receptors interact with the Raf-like kinase CONSTITUTIVE TRIPLE RESPONSE (CTR)1 upon binding of ethylene, thereby releasing its inhibition of EIN2 and other downstream signalling components in the ethylene pathway (Hall et al. 2007). Recent progress in the field of plant volatile signalling has shown that emissions of plant-produced volatile organic compounds (VOCs) are light-dependent and are affected by competition (reviewed in Kegge and Pierik 2010). Recently, it was shown that the composition of the VOC blend emitted by Arabidopsis plants is affected by R:FR signalling, leading to altered multitrophic interactions (Kegge et al. 2013). Although not much is known about the perception of the different biogenic volatile organic compounds, it is possible that they are used as a neighbour detection signal in competition for light.

The earliest response to neighbours in Arabidopsis, hyponasty, was found to be induced through touching leaf tips (de Wit et al. 2012). This touch-induced hyponasty is driven by an unidentified touch mechanism and occurs prior to a reduction in the R:FR. In fact, hyponasty was shown to be required to create a low R:FR in an Arabidopsis canopy (de Wit et al. 2012). Touch thus appears to be an especially important detection signal in rosette species, but may also play a role at later stages of competition for light in stem-forming species.

### III. Hormonal Regulation of Shade Avoidance

Besides ethylene, several other hormones play a role in the shade avoidance response. Gibberellin (GA) is a key regulator of many growth processes in plants and was shown to be essential for low R:FR-induced elongation. Auxin is involved in phototropism as described previously, but also plays an important role in phytochrome-mediated shade avoidance responses. More recently brassinosteroids (BR), which have partly overlapping functions with auxin, have been

implicated in low R:FR signalling as well. Besides their linear pathways these hormones are known to interact, which adds another level of complexity to understanding their actions. Here, it is described how these hormones are involved in regulation of the shade avoidance response.

#### A. Gibberellin

In the 1990s, it was shown that the constitutively elongated phenotype of *phyB* mutants was related to increased sensitivity to GA (Lopez-Juez et al. 1995; Reed et al. 1996) and could be suppressed by GA deficiency and insensitivity (Peng and Harberd 1997). GA deficient and insensitive mutants have indeed been found to show reduced low R:FR-induced responses (Djakovic-Petrovic et al. 2007; Pigliucci and Schmitt 2004). In an unbiased microarray approach, GA-related genes were found to be upregulated in response to low R:FR and in the *cry1* mutant (Devlin et al. 2003; Folta et al. 2003). Furthermore, *GA20ox2* expression is increased by an end-of-day (EOD) pulse of FR light while mutants with impaired *GA20ox2* expression showed a reduced elongation response to EOD-FR (Hisamatsu et al. 2005), suggesting that the shade avoidance response requires de-novo synthesis of GA.

Binding of GA to its receptor GID1 (GA insensitive dwarf 1; a-c in Arabidopsis) leads to interaction between the receptor and the nuclear growth-inhibiting DELLA proteins, which are subsequently targeted for proteasome-mediated degradation through the SCF<sup>Sly1</sup> complex (Dill et al. 2004; Fu et al. 2004; Nakajima et al. 2006; Ueguchi-Tanaka et al. 2005). Degradation of DELLAs relieves their suppression of genes sensitive to GA, thereby allowing for GA-induced growth responses. The discovery of DELLAs allowed for further understanding of the role GA has in shade avoidance. Abundance of the DELLA protein RGA, which has been implicated in GA-induced vegetative growth (Fleet and Sun 2005), was shown to be strongly reduced in petioles in response to



neighbours, low R:FR and low B (Djakovic-Petrovic et al. 2007). RGA was found to interact with PIF3 and PIF4, thereby preventing their transcriptional activity (De Lucas et al. 2008; Feng et al. 2008). Besides nuclear depletion of active phytochrome upon perception of low R:FR, GA-regulated degradation of DELLAs thus contributes to the release of PIF suppression to allow for growth during the shade avoidance response.

### B. Auxin and BR

Many auxin-regulated genes were found to be regulated during shade avoidance-inducing conditions (Devlin et al. 2003; Folta et al. 2003; Roig-Villanova et al. 2007), suggesting the importance of this hormone for the response. Expression of auxin-inducible genes is, like for the GA pathway, dependent on relieved suppression of transcriptional inhibitors (Aux/IAAs) that are targeted for 26S proteasome-mediated degradation when auxin binds to its receptor (the F-box protein TRANSPORT INHIBITOR RESPONSE (TIR)1). Auxin binding to the SCF<sup>TIR1</sup> complex thus stimulates the removal of Aux/IAAs from the ARF (auxin response family) transcription factors that are already bound to the promoter of auxin-responsive genes, allowing for their expression (Benjamins and Scheres 2008; Teale et al. 2006).

Auxin biosynthesis was shown to be rapidly induced by low R:FR through the TRYPTOPHAN AMINOTRANSFERASE OF ARABIDOPSIS (TAA)1 and YUCCA-dependent auxin biosynthetic pathway (Li et al. 2012; Stepanova et al. 2008; Tao et al. 2008; Won et al. 2011). This increase of auxin production proved to be essential for full induction of a shade avoidance response, as was shown by two allelic mutants for the *TAA1* gene; *sav3-1* and *wei8-1* (Keuskamp et al. 2010; Moreno et al. 2009; Tao et al. 2008). Apart from enhanced auxin biosynthesis, lateral redistribution of auxin was proposed to be important for a shade avoidance phenotype (Morelli and Ruberti 2000). Indeed, the auxin efflux carriers *PIN3* and

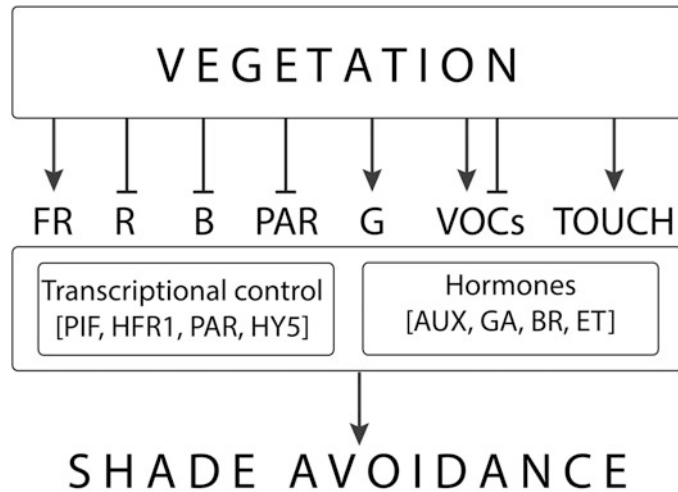
*PIN7* were found to be upregulated in low R:FR (Devlin et al. 2003). Besides its previously described role in phototropism (Friml et al. 2002), auxin redistribution through *PIN3* was reported to be required for shade avoidance responses to both neighbours and low R:FR (Keuskamp et al. 2010).

A microarray study on leaves of EOD-FR-treated plants revealed a strong overrepresentation of both auxin and BR-related genes (Kozuka et al. 2010). BR-regulated gene expression is brought about when active BR (brassinolide) binds to the leucine-rich repeat receptor-like kinase BRASSINOSTEROID INSENSITIVE (BRI)1, followed by a number of (de)phosphorylation events leading to accumulation and DNA-binding of the transcription factors BES1 (BRI1 EMS SUPPRESSOR1) and BZR1 (BRASSINAZOLE RESISTANT1) (Clouse 2011; Kim and Wang 2010). The same study on EOD-FR reported a reduced petiole elongation response in the auxin-deficient mutant *doc1* and the BR-deficient mutant *rot3* (Kozuka et al. 2010). Another study on low B-induced hypocotyl elongation showed that this response requires both auxin and BR action (Keuskamp et al. 2011), further confirming a role for BR in shade avoidance.

### C. Hormone Physiological Control of Shoot Branching

The above described modes of molecular regulation have been researched for low R:FR-mediated shoot elongation responses. Very little research has been devoted to low R:FR-induced inhibition of shoot branching and tillering. Therefore, it remains mostly unknown if the above-mentioned regulatory network also controls signalling toward branching control. A few recent studies have identified Abscisic acid (ABA), auxin and strigolactones as candidate regulators of phytochrome control of shoot branching (Finlayson et al. 2010; Reddy et al. 2013). The latter two hormones are also implied in phytochrome control of shoot elongation,

*Fig. 6.3.* Simplified schematic of regulation of shade avoidance responses to different neighbour detection cues. For more detailed schematic representations of signal transduction component interactions we suggest the following recent reviews: Casal (2012) and Pierik and Testerink (2014)



which may imply that branching and elongation are phytochrome-controlled through at least some shared regulators.

#### IV. Future Perspective

The majority of studies on shade avoidance have focussed on internode, petiole or hypocotyl elongation in *Arabidopsis*. These studies have provided breakthrough insights into molecular and physiological regulation of light signalling and signal transduction towards these responses (summarized in Fig. 6.3). Nevertheless, several aspects of how shade avoidance signals alter plant architecture are less intensively studied. For example, the phytochrome-mediated signalling mechanisms that drive changes in leaf blade morphology and shoot branching, important traits for crop yield, remain largely unknown. Phytochrome control of shoot branching is known to involve two TCP domain proteins, called BRANCHED (BRC)1 and BRC2 (Finlayson et al. 2010), but much more in-depth knowledge is needed on this trait. Although *Arabidopsis* flowering stems do show branching and this is controlled by phytochromes (Finlayson et al. 2010; Reddy et al. 2013), inclusion of other species might facilitate such research. Current technological developments such as

high-throughput phenotyping and next generation RNA sequencing enable the characterization of shade avoidance responses with unprecedented resolution and facilitate the use of non-model species. This furthermore opens up possibilities to study the molecular mechanisms behind the alternative strategy of shade tolerance (Gommers et al. 2013). Filling in such gaps will provide a more complete understanding of plant responses to competition for light in both natural and agricultural environments.

#### References

- Ahmad M, Lin C, Cashmore AR (1995) Mutations throughout an *Arabidopsis* blue-light photoreceptor impair blue-light-responsive anthocyanin accumulation and inhibition of hypocotyl elongation. *Plant J* 8:653–658
- Ang LM, Chattopadhyay S, Wei N, Oyama T, Okada K, Batschauer A, Deng XW (1998) Molecular interaction between COP1 and HY5 defines a regulatory switch for light control of *Arabidopsis* development. *Mol Cell* 1:213–222
- Athreya VR (1999) Light or presence of host trees: which is more important for the strangler fig? *J Trop Ecol* 15:589–602
- Ballaré CL, Scopel AL, Sánchez RA (1987a) Plant photomorphogenesis in canopies, crop growth and yield. *HortScience* 30:1172–1181
- Ballaré CL, Sánchez RA, Scopel AL, Casal JJ, Ghera CM (1987b) Early detection of neighbour plants by

- phytochrome perception of spectral changes in reflected sunlight. *Plant Cell Environ* 10:551–557
- Ballaré CL, Sanchez RA, Scopel AL, Ghersa CM (1988) Morphological responses of *Datura ferox* L. seedlings to the presence of neighbors – their relationships with canopy microclimate. *Oecologia* 76:288–293
- Ballaré CL, Scopel AL, Sánchez RA (1990) Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* 247:329–332
- Ballaré CL, Scopel AL, Sánchez RA (1991) Photocontrol of stem elongation in plant neighbourhoods: effects of photon fluence rate under natural conditions of radiation. *Plant Cell Environ* 14:57–65
- Banerjee R, Schleicher E, Meier S, Viana RM, Pokorný R, Ahmad M, Bittl R, Batschauer A (2007) The signaling state of arabidopsis cryptochrome 2 contains flavin semiquinone. *J Biol Chem* 282:14916–14922
- Benjamins R, Scheres B (2008) Auxin: the looping star in plant development. *Annu Rev Plant Biol* 59:443–465
- Bittebiere A, Renaud N, Clement B, Mony C (2012) Morphological response to competition for light in the clonal *Trifolium repens* (fabaceae). *Am J Bot* 99:646–654
- Blakeslee JJ, Bandyopadhyay A, Peer WA, Makam S, Murphy AS (2004) Relocalization of the PIN1 auxin efflux facilitator plays a role in phototropic responses. *Plant Physiol* 134:28–31
- Bleecker AB (1999) Ethylene perception and signaling: an evolutionary perspective. *Trends Plant Sci* 4:269–274
- Boccalandro HE, De Simone SN, Bergmann-Honsberger A, Schepens I, Fankhauser C, Casal JJ (2008) Phytochrome kinase substrate1 regulates root phototropism and gravitropism. *Plant Physiol* 146:108–115
- Bouly JP, Schleicher E, Dionisio-Sese M, Vandebussche F, Van Der Straeten D, Bakrim N, Meier S, . . . , Ahmad M (2007) Cryptochrome blue light photoreceptors are activated through interconversion of flavin redox states. *J Biol Chem* 282:9383–9391
- Carabelli M, Sessa G, Baima S, Morelli G, Ruberti I (1993) The arabidopsis *athb-2* and *-4* genes are strongly induced by far-red-rich light. *Plant J* 4:469–479
- Carabelli M, Morelli G, Whitelam G, Ruberti I (1996) Twilight-zone and canopy shade induction of the *athb-2* homeobox gene in green plants. *Proc Natl Acad Sci U S A* 93:3530–3535
- Carabelli M, Possenti M, Sessa G, Ciolfi A, Sassi M, Morelli G, Ruberti I (2007) Canopy shade causes a rapid and transient arrest in leaf development through auxin-induced cytokinin oxidase activity. *Genes Dev* 21:1863–1868
- Casal JJ (2012) Shade avoidance. *Arabidopsis Book* 10:e0157
- Casal JJ, Smith H (1989) The function, action and adaptive significance of phytochrome in light-grown plants. *Plant Cell Environ* 12:855–862
- Casal JJ, Ballaré CL, Tourn M, Sánchez RA (1994) Anatomy, growth and survival of a long-hypocotyl mutant of *cucumis sativus* deficient in phytochrome B. *Ann Bot* 73:569–575
- Chang C, Stadler R (2001) Ethylene hormone receptor action in arabidopsis. *Bioessays* 23:619–627
- Chen M, Chory J, Fankhauser C (2004) Light signal transduction in higher plants. *Annu Rev Genet* 38:87–117
- Chitwood DH, Headland LR, Filiault DL, Kumar R, Jimenez-Gomez JM, Schragar AV, Park DS, . . . , Maloof JN (2012) Native environment modulates leaf size and response to simulated foliar shade across wild tomato species. *PLoS One* 7:e29570
- Christie JM (2007) Phototropin blue-light receptors. *Annu Rev Plant Biol* 58:21–45
- Clough RC, Lohman KN, Vierstra RD (1997) Sequences within both the N- and C-terminal domains of phytochrome are required for Pfr-specific degradation. *Plant Physiol* 114:1476
- Clouse SD (2011) Brassinosteroid signal transduction: from receptor kinase activation to transcriptional networks regulating plant development. *Plant Cell* 23:1219–1230
- de Carbonnel M, Davis P, Roelfsema MRG, Inoue S, Schepens I, Lariguet P, Geisler M, . . . , Fankhauser C (2010) The Arabidopsis PHYTOCHROME KINASE SUBSTRATE2 protein is a phototropin signaling element that regulates leaf flattening and leaf positioning. *Plant Physiol* 152:1391–1405
- De Lucas M, Davière JM, Rodríguez-Falcón M, Pontin M, Iglesias-Pedraz JM, Lorrain S, Fankhauser C, . . . , Prat S (2008) A molecular framework for light and gibberellin control of cell elongation. *Nature* 451:480–484
- de Wit M, Kegge W, Evers JB, Vergeer-van Eijk MH, Gankema P, Voeselek LACJ, Pierik R (2012) Plant neighbor detection through touching leaf tips precedes phytochrome signals. *Proc Natl Acad Sci U S A* 109:14705–14710
- Demarsy E, Fankhauser C (2009) Higher plants use LOV to perceive blue light. *Curr Opin Plant Biol* 12:69–74

- Devlin PF, Rood SB, Somers DE, Quail PH, Whitelam GC (1992) Photophysiology of the elongated internode (ein) mutant of *Brassica rapa*: ein mutant lacks a detectable phytochrome B-like polypeptide. *Plant Physiol* 100:1442–1447
- Devlin PF, Yanovsky MJ, Kay SA (2003) A genomic analysis of the shade avoidance response in arabidopsis. *Plant Physiol* 133:1617–1629
- Dill A, Thomas SG, Hu J, Steber CM, Sun T (2004) The arabidopsis F-box protein SLEEPY1 targets gibberellin signaling repressors for gibberellin-induced degradation. *Plant Cell* 16:1392–1405
- Ding Z, Galvan-Ampudia CS, Demarsy E, Langowski L, Kleine-Vehn J, Fan Y, Morita MT, . . . , Friml (2011) Light-mediated polarization of the PIN3 auxin transporter for the phototropic response in Arabidopsis. *Nat Cell Biol* 13:447–453
- Djakovic-Petrovic T, de Wit M, Voesenek LACJ, Pierik R (2007) DELLA protein function in growth responses to canopy signals. *Plant J* 51:117–126
- Duek PD, Fankhauser C (2005) bHLH class transcription factors take centre stage in phytochrome signaling. *Trends Plant Sci* 10:51–54
- Fairchild CD, Schumaker MA, Quail PH (2000) HFR1 encodes an atypical bHLH protein that acts in phytochrome A signal transduction. *Genes Dev* 14:2377–2391
- Feng S, Martinez C, Gusmaroli G, Wang Y, Zhou J, Wang F, Chen L, . . . , Deng XW (2008) Coordinated regulation of *Arabidopsis thaliana* development by light and gibberellins. *Nature* 451:475479
- Finlayson SA, Lee IJ, Mullet JE, Morgan PW (1999) The mechanism of rhythmic ethylene production in sorghum. The role of phytochrome B and simulated shading. *Plant Physiol* 119:1083–1089
- Finlayson SA, Krishnareddy SR, Kebrom TH, Casal JJ (2010) Phytochrome regulation of branching in arabidopsis. *Plant Physiol* 152:1914–1927
- Fleet CM, Sun TP (2005) A DELLAcate balance: the role of gibberellin in plant morphogenesis. *Curr Opin Plant Biol* 8:77–85
- Folta KM (2004) Green light stimulates early stem elongation, antagonizing light-mediated growth inhibition. *Plant Physiol* 135:1407–1416
- Folta KM, Pontin MA, Karlin-Neumann G, Bottini R, Spalding EP (2003) 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* 36:203–214
- Franklin KA (2008) Shade avoidance. *New Phytol* 179:930–944
- Franklin KA (2009) Light and temperature signal crosstalk in plant development. *Curr Opin Plant Biol* 12:63–68
- Friml J, Wiśniewska J, Benková E, Mendgen K, Palme K (2002) Lateral relocation of auxin efflux regulator PIN3 mediates tropism in arabidopsis. *Nature* 415:806–809
- Fu X, Richards DE, Fleck B, Xie D, Burton N, Harberd NP (2004) The Arabidopsis mutant sleepy1gar2-1 protein promotes plant growth by increasing the affinity of the SCFSLY1 E3 ubiquitin ligase for DELLA protein substrates. *Plant Cell* 16:1406–1418
- Furutani M, Sakamoto N, Yoshida S, Kajiwarra T, Robert HS, Friml J, Tasaka M (2011) Polar-localized NPH3-like proteins regulate polarity and endocytosis of PIN-FORMED auxin efflux carriers. *Development* 138:2069–2078
- Givnish TJ (1988) Adaptation to sun and shade – a whole-plant perspective. *Aust J Plant Physiol* 15:63–92
- Goldberg DE, Barton AM (1992) Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am Nat* 139:771–801
- Gommers CMM, Visser EJW, St. Onge KR, Voesenek LACJ, Pierik R (2013) Shade tolerance: when growing tall is not an option. *Trends Plant Sci* 18:65–71
- Goudriaan J (2016) Light distribution. In: Hikosaka K, Niinemets Ü, Anten N (eds) *Canopy photosynthesis: from basics to applications*. Springer, Berlin, pp 3–22
- Haga K, Takano M, Neumann R, Iino M (2005) The rice coleoptile phototropism1 gene encoding an ortholog of Arabidopsis NPH3 is required for phototropism of coleoptiles and lateral translocation of auxin. *Plant Cell* 17:103–115
- Hall BP, Shakeel SN, Schaller GE (2007) Ethylene receptors: ethylene perception and signal transduction. *J Plant Growth Regul* 26:118–130
- Halliday K, Salter M, Thingnaes E, Whitelam G (2003) Phytochrome control of flowering is temperature sensitive and correlates with expression of the floral integrator FT. *Plant J* 33:875–885
- Hautier Y, Niklaus PA, Hector A (2009) Competition for light causes plant biodiversity loss after eutrophication. *Science* 324:636–638
- Hennig L, Buche C, Eichenberg K, Schafer E (1999) Dynamic properties of endogenous phytochrome A in Arabidopsis seedlings. *Plant Physiol* 121:571–577
- Hisamatsu T, King RW, Helliwell CA, Koshioka M (2005) The involvement of gibberellin 20-oxidase genes in phytochrome-regulated petiole elongation of Arabidopsis. *Plant Physiol* 138:1106–1116
- Holmes MG, Smith H (1975) The function of phytochrome in plants growing in the natural environment. *Nature* 254:512–514
- Hornitschek P, Lorrain S, Zoete V, Michielin O, Fankhauser C (2009) Inhibition of the shade avoidance response by formation of non-DNA binding bHLH heterodimers. *EMBO J* 28:3893–3902

- Huq E, Al-Sady B, Quail PH (2003) Nuclear translocation of the photoreceptor phytochrome B is necessary for its biological function in seedling photomorphogenesis. *Plant J* 35:660–664
- Janoudi A, Konjević R, Whitelam G, Gordon W, Poff KL (1997) Both phytochrome A and phytochrome B are required for the normal expression of phototropism in *Arabidopsis thaliana* seedlings. *Physiol Plant* 101:278–282
- Johnson E, Bradley M, Harberd NP, Whitelam GC (1994) Photoresponses of light-grown phy mutants of *Arabidopsis* – phytochrome-a is required for the perception of daylength extensions. *Plant Physiol* 105:141–149
- Keibrom TH, Burson BL, Finlayson SA (2006) Phytochrome B represses teosinte Branched1 expression and induces sorghum axillary bud outgrowth in response to light signals. *Plant Physiol* 140:1109–1117
- Kegge W, Pierik R (2010) Biogenic volatile organic compounds and plant competition. *Trends Plant Sci* 15:126–132
- Kegge W, Weldegergis BT, Soler R, Vergeer – van Eijk M, Dicke M, Voeselek LACJ, Pierik R (2013) Canopy light cues affect emission of constitutive and methyl jasmonate-induced volatile organic compounds in *Arabidopsis thaliana*. *New Phytol* 200:861–874
- Keller MM, Jaillais Y, Pedmale UV, Moreno JE, Chory J, Ballaré CL (2011) Cryptochrome 1 and phytochrome B control shade-avoidance responses in *Arabidopsis* via partially independent hormonal cascades. *Plant J* 67:195–207
- Keuskamp DH, Pollmann S, Voeselek LACJ, Peeters AJM, Pierik R (2010) Auxin transport through PIN-FORMED 3 (PIN3) controls shade avoidance and fitness during competition. *Proc Natl Acad Sci U S A* 107:22740–22744
- Keuskamp DH, Sasidharan R, Vos I, Peeters AJM, Voeselek LACJ, Pierik R (2011) Blue-light-mediated shade avoidance requires combined auxin and brassinosteroid action in *Arabidopsis* seedlings. *Plant J* 67:208–217
- Kiba T, Henriques R, Sakakibara H, Chua NH (2007) Targeted degradation of PSEUDO-RESPONSE REGULATOR5 by an SCFZTL complex regulates clock function and photomorphogenesis in *Arabidopsis thaliana*. *Plant Cell* 19:2516–2530
- Kim TW, Wang ZY (2010) Brassinosteroid signal transduction from receptor kinases to transcription factors. *Annu Rev Plant Biol* 61:681–704
- Kircher S, Kozma-Bognar L, Kim L, Adam E, Harter K, Schäfer E, Nagy F (1999) Light quality-dependent nuclear import of the plant photoreceptors phytochrome A and B. *Plant Cell* 11:1445–1456
- Kitajima K (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* 98:419–428
- Kitajima K, Poorter L (2010) Tissue-level leaf toughness, but not lamina thickness, predicts sapling leaf lifespan and shade tolerance of tropical tree species. *New Phytol* 186:708–721
- Kong SG, Suzuki T, Tamura K, Mochizuki N, Hara-Nishimura I, Nagatani A (2006) Blue light-induced association of phototropin 2 with the golgi apparatus. *Plant J* 45:994–1005
- Kozuka T, Horiguchi G, Kim GT, Ohgishi M, Sakai T, Tsukaya H (2005) The different growth responses of the *Arabidopsis thaliana* leaf blade and the petiole during shade avoidance are regulated by photoreceptors and sugar. *Plant Cell Physiol* 46:213–223
- Kozuka T, Kobayashi J, Horiguchi G, Demura T, Sakakibara H, Tsukaya H, Nagatani A (2010) Involvement of auxin and brassinosteroid in the regulation of petiole elongation under the shade. *Plant Physiol* 153:1608–1618
- Lariguet P, Schepens I, Hodgson D, Pedmale UV, Trevisan M, Kami C, De Carbonnel M, ..., Fankhauser C (2006) Phytochrome kinase substrate 1 is a phototropin 1 binding protein required for phototropism. *Proc Natl Acad Sci USA* 103:10134–10139
- Li L, Ljung K, Breton G, Schmitz RJ, Pruneda-Paz J, Cowing-Zitron C, Cole BJ, ..., Chory J (2012) Linking photoreceptor excitation to changes in plant architecture. *Genes Dev* 26:785790
- Lin C, Shalitin D (2003) Cryptochrome structure and signal transduction. *Annu Rev Plant Biol* 54:469–496
- Lin C, Yang H, Guo H, Mockler T, Chen J, Cashmore AR (1998) Enhancement of blue-light sensitivity of *Arabidopsis* seedlings by a blue light receptor cryptochrome 2. *Proc Natl Acad Sci U S A* 95:2686–2690
- Liscum E, Briggs WR (1995) Mutations in the NPH1 locus of *Arabidopsis* disrupt the perception of phototropic stimuli. *Plant Cell* 7:473–485
- Liu J, Zhang F, Zhou J, Chen F, Wang B, Xie X (2012) Phytochrome B control of total leaf area and stomatal density affects drought tolerance in rice. *Plant Mol Biol* 78:289–300
- Lopez-Juez E, Kobayashi M, Sakurai A, Kamiya Y, Kendrick RE (1995) Phytochrome, gibberellins, and hypocotyl growth. A study using the cucumber (*Cucumis sativus* L.) long hypocotyl mutant. *Plant Physiol* 107:131–140

- Lorrain S, Allen T, Duek PD, Whitelam GC, Fankhauser C (2008) Phytochrome-mediated inhibition of shade avoidance involves degradation of growth-promoting bHLH transcription factors. *Plant J* 53:312–323
- Losi A, Gartner W (2012) The evolution of flavin-binding photoreceptors: an ancient chromophore serving trendy blue-light sensors. *Annu Rev Plant Biol* 63:49–72
- Meils A, Harvey G (1981) Regulation of photosystem stoichiometry, chlorophyll a and chlorophyll b content and relation to chloroplast ultrastructure. *Biochim Biophys Acta* 637:138–145
- Millenaar FF, Van Zanten M, Cox MCH, Pierik R, Voeselek LACJ, Peeters AJM (2009) Differential petiole growth in *Arabidopsis thaliana*: photocontrol and hormonal regulation. *New Phytol* 184:141–152
- Morelli G, Ruberti I (2000) Shade avoidance responses. Driving auxin along lateral routes. *Plant Physiol* 122:621–626
- Moreno JE, Tao Y, Chory J, Ballaré CL (2009) Ecological modulation of plant defense via phytochrome control of jasmonate sensitivity. *Proc Natl Acad Sci U S A* 106:4935–4940
- Morgan DC, Smith H (1978) The relationship between phytochrome-photoequilibrium and development in light grown *Chenopodium album* L. *Planta* 142:187–193
- Morgan DC, O'Brien T, Smith H (1980) Rapid photomodulation of stem extension in light-grown *Sinapis alba* L. – studies on kinetics, site of perception and photoreceptor. *Planta* 150:95–101
- Motchoulski A, Liscum E (1999) Arabidopsis NPH3: a NPH1 photoreceptor-interacting protein essential for phototropism. *Science* 286:961–964
- Nakajima M, Shimada A, Takashi Y, Kim YC, Park SH, Ueguchi-Tanaka M, Suzuki H, . . . , Yamaguchi I (2006) Identification and characterization of arabidopsis gibberellin receptors. *Plant J* 46:880–889
- Osterlund MT, Hardtke CS, Ning W, Deng XW (2000) Targeted destabilization of HY5 during light-regulated development of *Arabidopsis*. *Nature* 405:462–466
- Parks BM, Quail PH, Hangarter RP (1996) Phytochrome A regulates red-light induction of phototropic enhancement in *Arabidopsis*. *Plant Physiol* 110:155–162
- Peeters AJM, Cox MCH, Benschop JJ, Vreeburg RAM, Bou J, Voeselek LACJ (2002) Submergence research using *Rumex palustris* as a model; looking back and going forward. *J Exp Bot* 53:391–398
- Peng J, Harberd NP (1997) Gibberellin deficiency and response mutations suppress the stem elongation phenotype of phytochrome-deficient mutants of *Arabidopsis*. *Plant Physiol* 113:1051–1058
- Pierik R, Testerink C (2014) The art of being flexible: how to escape from shade, salt and drought. *Plant Physiol* 166:5–22
- Pierik R, Visser EJW, De Kroon H, Voeselek LACJ (2003) Ethylene is required in tobacco to successfully compete with proximate neighbours. *Plant Cell Environ* 26:1229–1234
- Pierik R, Whitelam GC, Voeselek LACJ, De Kroon H, Visser EJW (2004) Canopy studies on ethylene-insensitive tobacco identify ethylene as a novel element in blue light and plant-plant signalling. *Plant J* 38:310–319
- Pierik R, Djakovic-Petrovic T, Keuskamp DH, de Wit M, Voeselek LACJ (2009) Auxin and ethylene regulate elongation responses to neighbor proximity signals independent of gibberellin and DELLA proteins in *Arabidopsis*. *Plant Physiol* 149:1701–1712
- Pierik R, de Wit M, Voeselek LACJ (2011) Growth-mediated stress escape: convergence of signal transduction pathways activated upon exposure to two different environmental stresses. *New Phytol* 189:122–134
- Pigliucci M, Schmitt J (2004) Phenotypic plasticity in response to foliar and neutral shade in gibberellin mutants of *Arabidopsis thaliana*. *Evol Ecol Res* 6:243–259
- Polko JK, van Zanten M, van Rooij JA, Maree AFM, Voeselek LACJ, Peeters AJM, Pierik R (2012) Ethylene-induced differential petiole growth in *Arabidopsis thaliana* involves local microtubule reorientation and cell expansion. *New Phytol* 193:339–348
- Poorter L, Bongers F (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology* 87:1733–1743
- Reddy SK, Holalu SV, Casal JJ, Finlayson S (2013) Abscisic acid regulates axillary bud outgrowth responses to the ratio of red to far-red light. *Plant Physiol* 163:1047–1058
- Reed JW, Nagpal P, Poole DS, Furuya M, Chory J (1993) Mutations in the gene for the red/far-red light receptor phytochrome B alter cell elongation and physiological responses throughout *Arabidopsis* development. *Plant Cell* 5:147–157
- Reed JW, Nagatani A, Elich TD, Fagan M, Chory J (1994) Phytochrome-a and phytochrome-B have overlapping but distinct functions in *Arabidopsis* development. *Plant Physiol* 104:1139–1149
- Reed JW, Foster KR, Morgan PW, Chory J (1996) Phytochrome B affects responsiveness to gibberellins in *Arabidopsis*. *Plant Physiol* 112:337–342

- Rockwell NC, Su Y, Lagarias JC (2006) Phytochrome structure and signaling mechanisms. *Annu Rev Plant Biol* 57:837–858
- Roig-Villanova I, Bou-Torrent J, Galstyan A, Carretero-Paulet L, Portolés S, Rodríguez-Concepción M, Martínez-García JF (2007) Interaction of shade avoidance and auxin responses: a role for two novel atypical bHLH proteins. *EMBO J* 26:4756–4767
- Rousseaux MC, Ballaré CL, Jordan ET, Vierstra RD (1997) Directed overexpression of PHYA locally suppresses stem elongation and leaf senescence responses to far-red radiation. *Plant Cell Environ* 20:1551–1558
- Sakai T, Wada T, Ishiguro S, Okada K (2000) RPT2: a signal transducer of the phototropic response in *Arabidopsis*. *Plant Cell* 12:225–236
- Sakai T, Kagawa T, Kasahara M, Swartz TE, Christie JM, Briggs WR, Wada M, Okada K (2001) *Arabidopsis* nph1 and npl1: blue light receptors that mediate both phototropism and chloroplast relocation. *Proc Natl Acad Sci U S A* 98:6969–6974
- Sakamoto K, Briggs WR (2002) Cellular and subcellular localization of phototropin 1. *Plant Cell* 14:1723–1735
- Sakamoto K, Nagatani A (1996) Nuclear localization activity of phytochrome B. *Plant J* 10:859–868
- Salter MG, Franklin KA, Whitlam GC (2003) Gating of the rapid shade-avoidance response by the circadian clock in plants. *Nature* 426:680–683
- Sasidharan R, Chinnappa CC, Voesenek LACJ, Pierik R (2008) The regulation of cell wall extensibility during shade avoidance: a study using two contrasting ecotypes of *Stellaria longipes*. *Plant Physiol* 148:1557–1569
- Sasidharan R, Chinnappa CC, Staal M, Elzenga JTM, Yokoyama R, Nishitani K, Voesenek LACJ, Pierik R (2010) Light quality-mediated petiole elongation in *Arabidopsis* during shade avoidance involves cell wall modification by xyloglucan endotransglucosylase/hydrolases. *Plant Physiol* 154:978–990
- Schmitt J, McCormac AC, Smith H (1995) A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbors. *Am Nat* 146:937–953
- Seo HS, Watanabe E, Tokutomi S, Nagatani A, Chua NH (2004) Photoreceptor ubiquitination by COP1 E3 ligase desensitizes phytochrome A signaling. *Genes Dev* 18:617–622
- Sessa G, Carabelli M, Sassi M, Ciolfi A, Possenti M, Mitterpergher F, Becker J, . . . , Ruberti I (2005) A dynamic balance between gene activation and repression regulates the shade avoidance response in *Arabidopsis*. *Genes Dev* 19:2811–2815
- Smith H (2000) Phytochromes and light signal perception by plants – an emerging synthesis. *Nature* 407:585–591
- Smith H, Holmes MG (1977) The function of phytochrome in the natural environment? III. Measurement and calculation of phytochrome photoequilibria. *Photochem Photobiol* 25:547–550
- Somers DE, Sharrock RA, Tepperman JM, Quail PH (1991) The hy3 long hypocotyl mutant of *Arabidopsis* is deficient in phytochrome B. *Plant Cell* 3:1263–1274
- Steindler C, Matteucci A, Sessa G, Weimar T, Ohgishi M, Aoyama T, Morelli G, Ruberti I (1999) Shade avoidance responses are mediated by the ATHB-2 HD-zip protein, a negative regulator of gene expression. *Development* 126:4235–4245
- Stepanova AN, Robertson-Hoyt J, Yun J, Benavente LM, Xie DY, Doležal K, Schlereth A, . . . , Alonso JM (2008) TAA1-mediated auxin biosynthesis is essential for hormone crosstalk and plant development. *Cell* 133:177–191
- Stowe-Evans EL, Harper RM, Motchoulski AV, Liscum E (1998) NPH4, a conditional modulator of auxin-dependent differential growth responses in *Arabidopsis*. *Plant Physiol* 118:1265–1275
- Su H, Abernathy SD, White RH, Finlayson SA (2011) Photosynthetic photon flux density and phytochrome B interact to regulate branching in *Arabidopsis*. *Plant Cell Environ* 34:1986–1998
- Tao Y, Ferrer JL, Ljung K, Pojer F, Hong F, Long JA, Li L, . . . , Chory J (2008) Rapid synthesis of auxin via a new tryptophan-dependent pathway is required for shade avoidance in plants. *Cell* 133:164–176
- Tatematsu K, Kumagai S, Muto H, Sato A, Watahiki MK, Harper RM, Liscum E, Yamamoto KT (2004) 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* 16:379–393
- Teale WD, Paponov IA, Palme K (2006) Auxin in action: signalling, transport and the control of plant growth and development. *Nat Rev Mol Cell Bio* 7:847–859
- Ueguchi-Tanaka M, Ashikari M, Nakajima M, Itoh H, Katoh E, Kobayashi M, Chow TY, . . . , Matsuoka M (2005) GIBBERELLIN INSENSITIVE DWARF1 encodes a soluble receptor for gibberellin. *Nature* 437:693–698
- Valladares F, Niinemets Ü (2008) Shade tolerance, a key plant feature of complex nature and consequences. *Annu Rev Ecol Evol Syst* 39:237–257
- Vandenbussche F, Pierik R, Millenaar FF, Voesenek LACJ, Van Der Straeten D (2005) Reaching out of the shade. *Curr Opin Plant Biol* 8:462–468

- Voeselek LACJ, Pierik R (2008) Plant science: plant stress profiles. *Science* 320:880–881
- Voeselek LACJ, Jackson MB, Toebes AHW, Huibers W, Vriezen WH, Colmer TD (2003) De-submergence-induced ethylene production in *Rumex palustris*: regulation and ecophysiological significance. *Plant J* 33:341–352
- Wang H, Ma LG, Li JM, Zhao HY, Deng XW (2001) Direct interaction of *Arabidopsis* cryptochromes with COP1 in light control development. *Science* 294:154–158
- Weiner J (1985) Size hierarchies in experimental populations of annual plants. *Ecology* 66:743–752
- Whippo CW, Hangarter RP (2004) Phytochrome modulation of blue-light-induced phototropism. *Plant Cell Environ* 27:1223–1228
- Won C, Shen X, Mashiguchi K, Zheng Z, Dai X, Cheng Y, Kasahara H, . . . , Zhao Y (2011) Conversion of tryptophan to indole-3-acetic acid by TRYPTOPHAN AMINOTRANSFERASES OF *ARABIDOPSIS* and *YUCCAs* in *Arabidopsis*. *Proc Natl Acad Sci USA* 108:18518–18523
- Yamaguchi R, Nakamura M, Mochizuki N, Kay SA, Nagatani A (1999) Light-dependent translocation of a phytochrome B-GFP fusion protein to the nucleus in transgenic *Arabidopsis*. *J Cell Biol* 145:437–445
- Yang HQ, Tang RH, Cashmore AR (2001) The signaling mechanism of *Arabidopsis* CRY1 involves direct interaction with COP1. *Plant Cell* 13:2573–2587
- Zhang T, Maruhnich SA, Folta KM (2011) Green light induces shade avoidance symptoms. *Plant Physiol* 157:1528–1536