

REVIEW PAPER

# Shade avoidance: phytochrome signalling and other aboveground neighbour detection cues

Ronald Pierik<sup>1,\*</sup> and Mieke de Wit<sup>2</sup>

<sup>1</sup> Plant Ecophysiology, Institute of Environmental Biology, Utrecht University, Padualaan 8, 3584 CH Utrecht, The Netherlands

<sup>2</sup> Centre for Integrative Genomics, University of Lausanne, CH-1015 Lausanne, Switzerland

\* To whom correspondence should be addressed. E-mail: [r.pierik@uu.nl](mailto:r.pierik@uu.nl)

Received 30 August 2013; Revised 23 October 2013; Accepted 24 October 2013

## Abstract

**Plants compete with neighbouring vegetation for limited resources. In competition for light, plants adjust their architecture to bring the leaves higher in the vegetation where more light is available than in the lower strata. These architectural responses include accelerated elongation of the hypocotyl, internodes and petioles, upward leaf movement (hyponasty), and reduced shoot branching and are collectively referred to as the shade avoidance syndrome. This review discusses various cues that plants use to detect the presence and proximity of neighbouring competitors and respond to with the shade avoidance syndrome. These cues include light quality and quantity signals, mechanical stimulation, and plant-emitted volatile chemicals. We will outline current knowledge about each of these signals individually and discuss their possible interactions. In conclusion, we will make a case for a whole-plant, ecophysiology approach to identify the relative importance of the various neighbour detection cues and their possible interactions in determining plant performance during competition.**

**Key words:** *Arabidopsis*, canopy, competition, cryptochrome, mechanostimulation, phytochrome, shade avoidance.

## Introduction

Plants are photoautotrophic organisms and therefore rely on sunlight to power the process of photosynthesis that generates carbohydrates from atmospheric carbon dioxide and water. In most agricultural and natural ecosystems, plants grow at very high densities where different individuals shade their neighbour plants, thereby impairing each other's light interception and thus photosynthesis. Although species that grow in forest understories have evolved ways to tolerate low light intensities, most plant species cannot tolerate severe shade (Grime and Jeffrey, 1965; reviewed in, for example, Valladares and Niinemets, 2008 and Gommers *et al.*, 2013). Many of these shade-intolerant or sun-loving plant species have evolved a suite of traits, called the shade avoidance syndrome, to escape from shade.

Shade avoidance responses include accelerated elongation of hypocotyls, internodes, and petioles, elevated leaf

angles to the horizontal, reduced branching and early flowering (Fig. 1; reviewed in Franklin, 2008; Keuskamp *et al.*, 2010b; Casal, 2012). These shade avoidance responses are often accompanied by reduced investments in other organs such as roots and leaf blades (e.g. Morelli and Ruberti, 2000; Carabelli *et al.*, 2007), which might reflect a trade-off in carbon and energy investments. The most frequently studied shade avoidance aspects are elongation of hypocotyls, internodes, or petioles; responses that depend partly or entirely on unidirectional cell expansion (e.g. Weijsschede *et al.*, 2008; Keuskamp *et al.*, 2011). These elongation responses have been studied intensively and appear to rely on the combined action of a number of plant hormones, including gibberellin, auxin, brassinosteroids, and ethylene (reviewed in Jaillais and Chory, 2010; Stamm and Kumar, 2010; Gommers *et al.*, 2013). Targets for these signalling compounds to control



**Fig. 1.** *Arabidopsis thaliana* in control light (left, white light HPI lamps,  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR) or simulated canopy shade (right, HPI filtered through Lee Fern Green filter,  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  PAR). In canopy shade (low PAR, low B, and low R:FR), *A. thaliana* shows classic shade avoidance features including elevated leaf angles (hyponasty) and elongated petioles. Plants were grown for 30 d at  $20^\circ\text{C}$  and 70% relative humidity under 9/15 h light/dark cycle under control light conditions until the last week where the plants on the right was moved to canopy shade light (this figure is available in colour at JXB online).

organ elongation include various physiological components and processes that control cell-wall extensibility including expansins, XTHs, and cell-wall acidification (Sasidharan *et al.*, 2008, 2010).

The paradigm for aboveground plant neighbour detection is that nearby neighbours are first detected through horizontal reflection of far-red (FR) light (700–800 nm waveband of the light spectrum) by neighbouring vegetation, thus lowering the red:far-red ratio (R:FR) reaching surrounding plants. The R:FR is signalled by the phytochrome family of photoreceptors. This FR enrichment can occur prior to the onset of actual shading, as was elegantly shown in a seminal paper using *Datura ferox* stands (Ballaré *et al.*, 1990): plants that were prevented from exposure to FR reflection by neighbours showed a delayed internode elongation response. FR reflection by neighbouring plants thus serves as a signal to detect neighbours even before they become a competitive threat and nearby plants perceiving this signal use it to initiate shade avoidance responses. These early responses prepare plants for upcoming competition for light. Using mutant and transgenic genotypes with disabled R:FR signalling, including genotypes that are mutant or transgenic for specific phytochrome genes, it has been shown that these shade avoidance responses improve individual plant performance and fitness (Schmitt *et al.*, 1995, 1997).

In the past 15 years numerous additional neighbour detection mechanisms have been identified, including other light signals, volatile chemicals, and mechanical cues. In addition to these aboveground signals, a variety of plant neighbour detection mechanisms exist below ground, such as allelochemicals, volatiles, and soil nutrient status as affected by uptake patterns of competing neighbours (reviewed in de Kroon *et al.*, 2012; Pierik *et al.*, 2013). This review focuses on aboveground plant–plant interactions and discusses the various modes of plant neighbour detection.

## Phytochrome signalling of R:FR

A developing canopy produces several qualitative changes in the light composition, which form reliable plant-specific cues to detect neighbours. As already mentioned, FR light reflected by proximate neighbours lowers the R:FR and thereby reveals imminent vegetative shade. As the vegetation becomes more dense, the R:FR decreases further through depletion of R from the light spectrum in the process of photosynthesis.

The R:FR is perceived through the phytochrome photoreceptors that interconvert between the active (Pfr) and inactive (Pr) conformer upon absorption of R and FR, respectively. The photoequilibrium between Pfr and Pr thus reflects the R:FR, making the phytochromes receptors of qualitative light changes (Holmes and Smith, 1975; Smith and Holmes, 1977). The model plant *Arabidopsis thaliana* has five phytochromes (phyA–E; Clack *et al.*, 1994). Of these, phyB is the predominant regulator of the shade avoidance response, with additional roles for phyD and phyE (Franklin *et al.*, 2003). PhyB is synthesized in the cytosol in the inactive form and transported into the nucleus upon activation (Yamaguchi *et al.*, 1999). There it mediates the phosphorylation and degradation of a group of growth-promoting basic helix–loop–helix (bHLH) transcription factors known as phytochrome interacting factors (PIFs; Lorrain *et al.*, 2008; Li *et al.*, 2012). Particularly PIF4, PIF5, and PIF7 are important positive regulators of shade avoidance responses, with some redundancy of PIF3 together with PIF1 (Lorrain *et al.*, 2008; Hornitschek *et al.*, 2012; Leivar *et al.*, 2012; Li *et al.*, 2012). The inactivation of phyB in low R:FR relieves its suppression of the PIFs, leading to accumulation of PIF protein and subsequent transcription of genes whose products are involved in growth. In addition to PIFs also other transcriptional regulators are induced, such as the homeodomain-leucine zipper protein-encoding genes *ATHB2* and *ATHB4* and other positive regulators such as *BR-ENHANCED EXPRESSION (BEE)* and *BESI-INTERACTING MYC-LIKE (BIM)* (Steindler *et al.*, 1999; Sorin *et al.*, 2009; Cifuentes-Esquivel *et al.*, 2013). Low R:FR perception also leads to induction of a number of negative regulators of the shade avoidance response, among which bHLH proteins such as *HFR1*, *PAR1*, and *PAR2* (Sessa *et al.*, 2005; Roig-Villanova *et al.*, 2007). A decrease in R:FR thus induces an intricate network of both positive and negative transcriptional regulators. Negative regulators may be employed to moderate the final response that is expressed upon signal perception. This could provide a mechanism to fine-tune shade-induced growth responses in relation to the intensity of the signal, reflecting the severity of impending shade. In accordance with this, *Arabidopsis* plants showed an increasing upward leaf movement with decreasing R:FR ratios that reflect increasing threats of shade (de Wit *et al.*, 2012). Likewise, stem elongation rates in *Chenopodium album*, as well as a number of other species, were shown to increase with decreasing R:FR (Morgan and Smith, 1978, 1979).

## Other light signals

As the canopy closes, availability of photosynthetically active radiation (PAR) decreases at the lower regions. Locally reduced

PAR increased internode length in *Sinapis alba* and *D. ferox* and in tobacco, low PAR induced hyponasty and stem elongation (Ballaré *et al.*, 1991; Pierik *et al.*, 2004b). *Arabidopsis* seedlings grown in low PAR have elongated hypocotyls in comparison with seedlings grown in high light and adult *Arabidopsis* plants show hyponastic leaf growth in response to low light (Mullen *et al.*, 2006; Millenaar *et al.*, 2009; Hornitschek *et al.*, 2012; Table 1). It is not known how exactly reduced PAR is perceived. Photosynthesis is reduced by low PAR and this may generate signals within the plant. A role for photosynthesis-derived signals in the low PAR response in *Arabidopsis* was indicated by a constitutively hyponastic phenotype in plants under control light conditions in which the photosynthetic electron chain was disrupted with 3-(3,4-dichlorophenyl)-1,1-dimethylurea (Millenaar *et al.*, 2009). Furthermore, low PAR may be perceived by specific photoreceptors through a reduction in the light intensity that they detect. The low PAR-induced hyponastic response in *Arabidopsis* was shown to be dependent on phyA and phyB and on the blue light receptors CRY1 and CRY2, as will be discussed further.

Besides a decreased R:FR and a drastically reduced PAR, the light spectrum under a dense canopy shows a relative enrichment of green (G; 500–580 nm) light and a depletion of blue (B; 400–500 nm) light. Green light reflected by or transmitted through surrounding plants may be another cue to detect neighbours, as addition of green light induces hypocotyl elongation in *Arabidopsis* seedlings and hyponasty and petiole elongation in adult *Arabidopsis* plants (Folta, 2004; Zhang *et al.*, 2011). Green light may be perceived through the cryptochromes (Banerjee *et al.*, 2007; Bouly *et al.*, 2007) or through another, unknown, mechanism (Zhang *et al.*, 2011). Finally, similar to most other wavebands, UV-B light

(280–315 nm) is also absorbed by plant tissues and, therefore, gets depleted at high plant densities. UV-B is sensed through the UVR8 photoreceptor (Rizzini *et al.*, 2011), which regulates downstream growth-regulating targets, including ELONGATED HYPOCOTYL 5 (HY5) through interaction with the E3 ubiquitin ligase CONSTITUTIVE PHOTOMORPHOGENIC 1 (COP1; Favory *et al.*, 2009). As a consequence, UV-B perception can suppress elongation growth of *Arabidopsis* seedlings. Tentatively, UV-B depletion through absorption by neighbouring plants could thus derepress elongation growth and promote shade avoidance. Future studies on shade avoidance modulation by UV-B are needed to clarify if this indeed occurs.

Similarly to R, B light is absorbed by chlorophyll and used for photosynthesis and a relative depletion of B in the light spectrum has been suggested to constitute a neighbour- and shade-detection cue. Indeed when blue wavelengths are filtered from the light to create a low B environment, *Arabidopsis* seedlings show enhanced hypocotyl elongation that is even stronger than under low R:FR treatment (Djakovic-Petrovic *et al.*, 2007; Keuskamp *et al.*, 2011). In *D. ferox* and tobacco plants, as well as in the herbaceous perennial *Stellaria longipes*, low B induces enhanced elongation (Ballaré *et al.*, 1991; Pierik *et al.*, 2004b; Sasidharan *et al.*, 2008). In adult *Arabidopsis* plants, long-term low B treatment can induce hyponasty and elongation (Keller *et al.*, 2011).

B is perceived by several classes of photoreceptors, which all seem to have distinct roles. The phototropins are involved in chloroplast movement to optimize light harvesting against light-intensity optimization of photosynthesis upon changing light intensities, but they are best known for their role in the regulation of directional growth towards a unilateral

**Table 1.** Neighbour detection signals and the shade avoidance traits that they elicit

Signal	Seedlings		Adult plants	
	Traits	References	Traits	References
Low R:FR	Elongated hypocotyls	e.g. Casal (2012)	Elongated petioles and internodes	e.g. Franklin (2008); Keuskamp <i>et al.</i> (2010a)
	Elongated cotyledon petiole	Sessa <i>et al.</i> (2005); Roig-Villanova <i>et al.</i> (2007)	Reduced lamina:petiole length	Moreno <i>et al.</i> (2009)
	Reduced cotyledon size	Li <i>et al.</i> (2012)	Reduced primordium outgrowth	Carabelli <i>et al.</i> (2007)
Low B	Elongated hypocotyls	Keuskamp <i>et al.</i> (2011)	Hyponastic leaves	e.g. Franklin (2008); Keuskamp <i>et al.</i> (2010a)
		Pierik <i>et al.</i> (2009)	Short-term treatment (24 h): no effect	Djakovic-Petrovic <i>et al.</i> (2007)
Low PAR	Elongated hypocotyls	Mullen <i>et al.</i> (2006); Hornitschek <i>et al.</i> (2012)	Long-term treatment (several days):	
			Elongated petioles and internodes	Ballaré <i>et al.</i> (1991); Sasidharan <i>et al.</i> (2008);
			Reduced lamina:petiole length	Keller <i>et al.</i> (2011)
Ethylene	Elongated hypocotyls	Smalle <i>et al.</i> (1997); Pierik <i>et al.</i> (2009)	Hyponastic leaves	Keller <i>et al.</i> (2011)
			Hyponastic leaves	Ballaré <i>et al.</i> (1991); Pierik <i>et al.</i> (2004b)
Touching leaf tips	NA		Hyponastic leaves	Millenaar <i>et al.</i> (2009) Millenaar <i>et al.</i> (2005); Polko <i>et al.</i> (2012) de Wit <i>et al.</i> (2012)

A selection of relevant references is shown. B, blue; FR, far-red; NA, not available; PAR, photosynthetically active radiation; R, red.



light source known as phototropism (reviewed in [Christie, 2007](#)). During aboveground competition, phototropins may thus be important for optimization of light capture in a light-limited environment through growth towards canopy gaps. In *Cucumis sativus*, bending away from neighbours was indeed shown to be dependent on a unilateral B gradient, as well as on phytochrome perception of a R:FR gradient ([Ballaré et al., 1992](#)). Another class of B photoreceptors are the three members of the zeitung family ZTL, FKF1, and LKP2 (reviewed in [Demarsy and Fankhauser, 2009](#)). Whether these are involved in neighbour detection is not known, but ZTL may be involved in photomorphogenesis ([Kiba et al., 2007](#)).

The cryptochromes (cry) may be the main photoreceptors in B-dependent neighbour detection, as low B-induced shade avoidance responses depend on CRY1 and CRY2 in *Arabidopsis* ([Ahmad et al., 1995](#); [Lin et al., 1998](#); [Pierik et al., 2009](#); [Keller et al., 2011](#)). CRY1 is light-stable, whereas CRY2 is light labile and acts in low light. The cryptochromes act in the nucleus, where they regulate gene expression upon light activation (reviewed in [Chaves et al., 2011](#)). B-induced conformational changes lead to interaction of CRY1 with SUPPRESSOR OF PHYTOCHROME A 1 (SPA1). SPA proteins bind COP1, thereby contributing to its function as E3 ubiquitin ligase involved in protein degradation (reviewed in [Lau and Deng, 2012](#)). SPA1 binding to CRY1 inhibits SPA1 binding to COP1, resulting in the accumulation of COP1 targets, such as the growth-promoting bZIP transcription factor HY5 ([Lian et al., 2011](#); [Liu et al., 2011](#)). A similar protein interaction with SPA1 has been shown for activated CRY2 in the long-day-induced transition to flowering, which leads to stabilization of the flowering regulator CONSTANS ([Zuo et al., 2011](#)). The light-dependent CRY–SPA protein interaction may affect other COP1-targeted transcription factors such as HFR1 ([Fankhauser and Ulm, 2011](#)) and may thus activate a transcriptional network leading to a shade avoidance phenotype. Finally, low B-induced petiole elongation in *Arabidopsis* has been shown to rely on functional PIF4 and PIF5 ([Keller et al., 2011](#)), regulators that have also been associated with phytochrome signalling towards shade avoidance. Consistent with a role for cry in sensing light intensity through B light-fluence rates, hypocotyl elongation responses to low PAR also rely on PIF4 and PIF5 as the *pif4pif5* double mutant has a severely attenuated low-light-induced hypocotyl elongation response compared to wild-type Col-0 ([Hornitschek et al., 2012](#)). It remains unknown if and how cry regulates PIFs.

## Co-action between light signalling pathways

With an increasing density of the vegetation, the changes in intensity and spectral composition of the light also become more dramatic. A combination of different light signals may therefore provide more specific information about shading intensity than a single signal. There are several indications that co-action of the different light signalling pathways takes place.

The B and G light signals within a dense stand together could provide specific information about shading by neighbours, as

the blue/green ratio (B:G) decreases with increasing density in a fashion that does not correlate with B irradiance ([Sellaro et al., 2010](#)). Absorption of G by the cryptochromes leads to a conformational change that renders them inactive and can thereby counteract blue light effects ([Banerjee et al., 2007](#); [Bouly et al., 2007](#)). The inactivation of CRY1 as a result of decreasing B within a canopy could in this way be accelerated by increased G reflection and add to the shade avoidance response.

There might also be interaction between the red and blue light response. The phytochromes also absorb B light in addition to absorbing R and FR ([Smith, 2000](#)), although it is not known how this may influence shade avoidance responses. *cry2* mutant seedlings showed enhanced hypocotyl elongation in response to low R:FR ([Mas et al., 2000](#)), which suggests that there could indeed be an additive effect of low B and low R:FR signals in severe shading. There are indications that light-activated phyB and *cry2* can physically interact ([Mas et al., 2000](#)), but whether this plays a role in the shade avoidance response in addition to photoreceptor inactivation in shade is not known. One way in which the B and R light signalling pathways may converge is through modulation of COP1 activity. CRY1 interacts with SPA1, which has been shown to inhibit SPA binding to COP1 in the case of CRY1 ([Lian et al., 2011](#); [Liu et al., 2011](#)). Reduced activation of CRY1 in canopy shade may thus enhance interaction of SPA1 with COP1 and thus COP1 activity. This could lead to increased degradation of COP1 targets such as HY5 and HFR1, which are induced by low R:FR and inhibit hypocotyl elongation ([Holm et al., 2002](#); [Sessa et al., 2005](#)). Indeed, COP1 and the SPAs are required for elongation responses to low R:FR ([Rolauuffs et al., 2012](#)). Recently, phyB was also shown to interact with SPA1 ([Zheng et al., 2013](#)), which may further add to increased COP1 activity in shade. These findings are consistent with observations from de-etiolation studies in which dark-grown seedlings are exposed to light, leading to inhibition of hypocotyl elongation. Blue light perception in addition to red light had a synergistic effect on hypocotyl growth inhibition through CRY-enhanced expression of phyB-induced genes, among which *HY5*, *SPA1*, and *SPA4* ([Sellaro et al., 2009](#)).

Another way in which the B and R signalling pathways may interact is at the level of the PIFs, as PIF4 and PIF5 are important for expression of the shade avoidance phenotype both in response to low R:FR and low B ([Lorrain et al., 2008](#); [Keller et al., 2011](#)). Considering this, low B might act especially in combination with low R:FR, as the PIFs are stabilized in this condition. Whether PIF abundance is also regulated in response to low B currently remains to be investigated.

Altogether, light signals and possibly their interactions are very important cues for neighbour detection in a developing canopy.

## Mechanical stimulation (touch)

In order for plants to detect nearby neighbours early through horizontal FR reflection, the surrounding vegetation needs to achieve a vertical stand. Although this occurs in the majority

of vegetations, there are also various plant species that grow mostly horizontally, such as rosette species and various clonal plants. In such predominantly horizontal, flat, stands, the opportunity for horizontal light reflection is minimal and, therefore, the opportunities for FR enrichment of the light inside such a stand is very low. In such cases, it seems unlikely that the R:FR ratio could decrease prior to actual shading between neighbouring plants.

A recent study on early plant–plant signalling in *A. thaliana* stands found that indeed FR-enrichment is not the first means for these plants to detect their neighbours (de Wit *et al.*, 2012). Growing *Arabidopsis* stands have no vertical structure until they move their leaves upward in response to proximate neighbours. The initiation of this leaf movement response, called hyponastic leaf growth, appeared to occur upon touching the leaf tips of neighbouring plants and did not involve a change in light quality or quantity. Once this response was initiated and the plants continued to grow, the stand developed into a vertical structure due to the touch-induced vertical leaf orientation. Only when this vertical orientation was established did the R:FR decrease. Although these experiments were performed under growth chamber light conditions, mathematical modelling exercises combined with physiological experiments indicate that these findings from controlled growth room experiments are also relevant under natural sunlight conditions (de Wit *et al.*, 2012). So far, the molecular and physiological mechanisms underpinning this particular touch response remain to be elucidated, but some of the regulators of established responses to mechanostimulation, including *TCH* genes (Braam and Davis, 1990) and jasmonate signalling (Chehab *et al.*, 2012), do not seem to be involved (de Wit *et al.*, 2012). Nevertheless, putative involvement of several other components associated with mechanical-force-induced morphological responses, including mechanosensitive ion channels (e.g. Kung, 2005; Haswell *et al.*, 2008) and mechanical-force-induced changes of microtubule orientation (e.g. Hamant *et al.*, 2008; Hamant and Traas, 2010) remain to be investigated. Indeed hyponastic leaf movement can involve a very local reorientation of cortical microtubules at the basal abaxial side of the petiole where cell elongation drives hyponasty (Polko *et al.*, 2012).

Thus, mechanical stimulation, at least in some competitive settings, is an early neighbour detection mechanism. However, also in later stages of canopy development and in stands with stem-forming plants, mechanostimulation contributes to plant performance. It could be argued that under outdoor conditions, the reduced wind exposure of plants inside a canopy will, in comparison to often wind-exposed plants grown in isolation, promote an elongated phenotype which is reminiscent of a shade avoidance phenotype (e.g. Braam, 2005). As a consequence, it could be argued that the wind shielding caused by high plant density can serve as an additional factor that promotes a shade-avoidance-like phenotype. It was shown in a study on *Chenopodium album* that stem elongation in dense stands was controlled not only by light quality and quantity but also by mechanical stimuli (Nagashima and Hikosaka, 2012). Stands of plants tend to converge at a particular plant height (e.g. Vermeulen *et al.*,

2008) and this might, in addition to light cues, also be caused by wind exposure. The latter is much higher above than within a canopy (Nagashima and Hikosaka, 2012) and can inhibit stem elongation (e.g. Henry and Thomas, 2002; Anten *et al.*, 2005), thereby preventing a continuation of growth above the top of the canopy.

Summarizing, mechanostimulation can contribute to shade avoidance through (i) early touching of leaf tips and perhaps other organs and (ii) shielding from wind stress by vertically growing neighbour plants.

## Volatile organic compounds

Phytochrome inactivation during low R:FR exposure typically enhances the emission of the volatile plant hormone ethylene (e.g. Finlayson *et al.*, 1999; Foo *et al.*, 2006; Kurepin *et al.*, 2007; Kegge and Pierik, 2010). Based on greenhouse studies using densely cultivated tobacco stands, it has been argued that ethylene might serve as a volatile chemical cue between plants since inside a canopy it was found to accumulate up to 3-fold ambient levels (Pierik *et al.*, 2004b). Although these enhanced emissions are associated with enhanced stem or petiole elongation rates, ethylene is not always a requirement for low R:FR-induced shoot elongation (e.g. Pierik *et al.*, 2004a). Ethylene application can, however, induce responses that are reminiscent of shade avoidance, such as enhanced hypocotyl and internode elongation (Smalle *et al.*, 1997; Pierik *et al.*, 2004b) and hyponasty (Millenaar *et al.*, 2005; Polko *et al.*, 2012).

Although ethylene is produced and emitted by nearly all plants researched so far, many other volatile organic compounds (VOCs) are produced in more species-specific manners. It is tempting to speculate that species-specific emissions of specific combinations of VOCs might hold information not only about the presence but also the identity of a competing neighbour. Indeed, there are some hints that this is possible. In a study on two barley cultivars that used to be intercropped to enhance aphid resistance and attract aphid predators, it was found that exposure of one cultivar to VOC blends from the other altered the plant's allocation of resources between shoots and roots (Ninkovic, 2003). Exposure of one cultivar to VOCs derived from another individual of the same cultivar on the other hand did not affect carbon allocation. Allocation between root and shoot tissues is also typically affected during shade avoidance in response to light signals (e.g. Morelli and Ruberti, 2000; Salisbury *et al.*, 2007). Although the identity of responsible compound(s) has not been established yet, these data indicate that plant–plant signalling can indeed occur through VOCs. Another striking example is on the parasitic plant *Cuscuta pentagona*. It was shown that seedlings of this parasite locate their host (tomato) based on VOCs and discriminate between VOC blends from host (tomato) and non-host (wheat) plants (Runyon *et al.*, 2006). It is suggested that *Cuscuta pentagona* parasitic plants are attracted to the monoterpenes  $\beta$ -phellandrene,  $\beta$ -myrcene, and  $\alpha$ -pinene.

These examples on barley and *Cuscuta* show that there is potential for species-specific detection of nearby neighbour

plants. A question that is not answered, however, is how widespread such interactions are and if these elicit responses that will modulate the competitive interactions between plant individuals. Furthermore, many factors other than nearby plant individuals will also impact on VOC production and emission. It is, for example, well established that attack by herbivores strongly boosts the emission of a variety of VOCs. These emissions are thought to attract predators of the herbivores (reviewed in Dicke, 2009; Dicke and Baldwin, 2010) and signal to distant branches of the same plant individual (Frost *et al.*, 2007; Heil and Silva Bueno, 2007) but they can also be sensed by neighbouring plants (e.g. Karban *et al.*, 2003; reviewed in Baldwin *et al.*, 2006; Dicke and Baldwin, 2010). It remains to be studied whether, and if so how, such inducible VOC signals interact with putative plant neighbour detection through constitutively emitted VOCs.

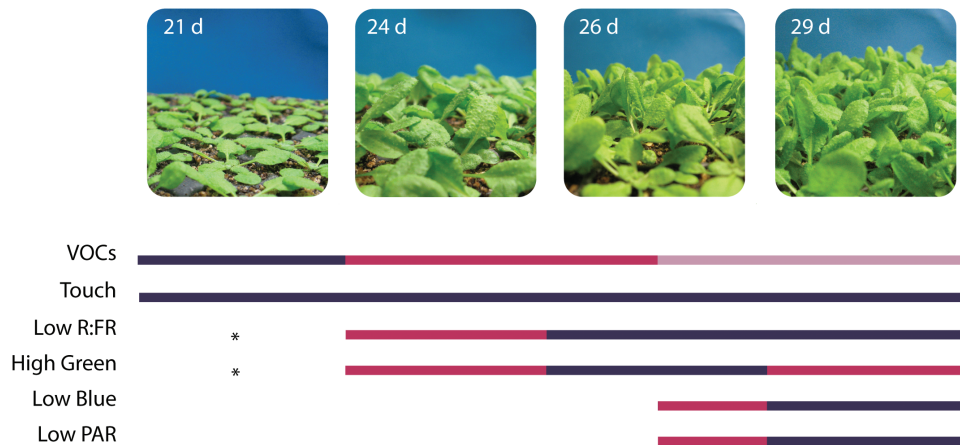
## Multiple signals: timing and signal integration

An interesting question that has not been answered yet is why plants would rely on so many different cues to detect neighbours. As argued previously, a drop in R:FR at relatively high light intensity can be caused by FR reflection from surrounding vegetation and is therefore considered a reliable signal to sense neighbour proximity, although the R:FR is also somewhat reduced at twilight (Smith, 1982). When the canopy closes and competition sets in, additional cues, such as reduced PAR and B (Fig. 2), are generated and can inform plants about the progressing intensity of competitive

threats and induce (subsets of) the shade avoidance syndrome (Table 1). Thus evaluation of different light signals together likely presents a more subtle and intricate picture of the competitive arena, allowing plants to induce different (magnitudes of) responses depending on the severity of competitive threat.

As for non-light cues, touch likely presents a way to detect neighbours early (Fig. 2) in stands where a vertical structure is lacking and horizontal FR reflection towards neighbours consequently is absent. Physical interaction between plants in a vertical stand may increase when neighbours close in and may thus constitute a literal measure of competition pressure in high density. It remains to be studied if touch-induced leaf movements interact with light signals such as low R:FR and low B light that induce similar phenotypic responses. Likewise, volatiles may present a way for plants to detect neighbours at quite an early phase of canopy development (Fig. 2). However, when canopy light signals become abundant, these appear to down regulate the emission of several terpenoid and GLV compounds in *Arabidopsis* (Kegge *et al.*, 2013). This suggests that light signals could be dominant over VOCs, potentially limiting VOC-based neighbour signalling to relatively early phases of canopy development or to relatively low plant densities where the impact on light spectral composition is minimal.

Besides having an additive effect through co-occurrence, multiple simultaneous warning signals may provide more detailed information through their spatial distribution. The different neighbour detection signals associated with above-ground neighbour detection need not all be perceived by the same plant organs. In a regular dense stand, FR light that



**Fig. 2.** Development of *Arabidopsis thaliana* plants at high density (2000 plants  $m^{-2}$ ). Pictures depict different developmental stages given in days after sowing (excluding 3 d stratification that preceded it); the lines underneath identify during which developmental phases specific neighbour detection cues occur (dark is strong signal intensity; light is weak signal intensity). VOC emissions decrease as a result of low R:FR- and low light-mediated suppression of VOC emissions (Kegge *et al.*, 2013). The co-occurrence and interaction of multiple detection cues may form an additional layer of information on competition intensity. \*Although in the example of the rosette plant *A. thaliana*, low R:FR does not occur at the earliest stage of development; in stem-forming species, it will already be present at this stage (Ballaré *et al.*, 1990). Pictures: plants were germinated and grown for 10 d in sowing substrate. Subsequently, seedlings were transferred to high-density competition grids at 2000 plants  $m^{-2}$ . All growth occurred at 20 °C and 70% relative humidity under 9/15 h light/dark cycle with 180  $\mu mol m^{-2} s^{-1}$  PAR. FR, far-red; PAR, photosynthetically active radiation; R, red; VOC, volatile organic compound (this figure is available in colour at JXB online).



is horizontally reflected by neighbours will reach neighbour plants' erect internodes. Indeed, perception of this reflected FR light by internodes is sufficient to induce shade avoidance responses and locally induces a cellular growth response (Ballaré *et al.*, 1987, 1990; Casal and Smith, 1988). Studies on *Arabidopsis*, however, suggest that low R:FR needs to be perceived in the cotyledons/lamina and subsequently induces auxin biosynthesis and transport towards the hypocotyl/petiole epidermis where it induces elongation (Morelli and Ruberti, 2000; Tanaka *et al.*, 2002; Tao *et al.*, 2008; Keuskamp *et al.*, 2010a; Kozuka *et al.*, 2010), thus uncoupling the sites of perception and of growth response. Perception of true shade and B depletion occurring in well-closed canopies can occur at all organs since the entire plant can be shaded and signalling interactions can therefore occur in the shared sites of signal perception and/or response. Touch-induced upward leaf movement as observed in rosette canopies occurs upon touching of the very tips of the leaves. It therefore seems plausible to assume that the leaf tips would be the site of signal occurrence and perception. However, it is also possible that touching the leaves of neighbours changes some of the mechanical forces inside the entire leaf, leading to signalling in compartments other than the leaf tip (e.g. the petiole). Since the molecular mechanisms of this response are unknown, it is difficult to speculate whether these responses would or would not likely interact with other neighbour cues, such as light quality. Taken together, the dispersal of occurrence and possible interaction of multiple signals over time and space could provide plants at high density with a mechanism that allows them to attune their response to severity of competition.

## Future directions

In order to understand the relative contributions of the different neighbour detection cues for plant performance in dense stands, future studies need to be directed towards representative signalling scenarios and plant developmental stages. Young, agar-plate-grown seedlings have been proven to be an extremely suitable study system from a mechanistic viewpoint, but this system has its obvious limitations when trying to understand the progressive complexity of neighbour detection signals in true competition under natural or agricultural conditions. Furthermore, the heterogeneity of the competitive arena is generally not taken into account in high-density-mimicking experiments, while this may be important for the final plant response to its competitive environment. For instance, some leaves may receive direct sunlight, whereas others are shaded and again others receive direct sunlight but also FR-enriched light reflected from nearby plants. Moreover, this condition is not constant, as a shaded leaf may reach full sunlight after enhanced elongation growth or a leaf may receive temporary sunlight through a canopy gap due to solar elevation changes during the day. Some of these leaves may physically touch neighbours, whereas others may not. Furthermore, species-specific VOC blends may determine at an early competitive stage whether a plant will respond to proximate neighbours (Ninkovic 2003; Kegge *et al.*, 2013). In short, there is a

tremendous heterogeneity between and even within organs that may elicit local responses, but it also needs to be integrated at the whole-plant level. Understanding these subtle, local, and systemic interactions calls for combined plant physiology and molecular biology experiments. An integrative approach of ecophysiology and mathematical modelling will subsequently enable these insights to be translated to canopy performance and will increase the understanding of the relative contributions of different signals, signal interactions, and within-plant signalling between organs in heterogeneous conditions.

## Acknowledgements

Research in the Pierik laboratory is funded by grants from the Netherlands Organisation for Scientific Research (VIDI grant no. 864.12.003, open competition grant no. 818.01.003).

## References

- Ahmad M, Lin CT, Cashmore AR. 1995. Mutations throughout an *Arabidopsis* blue-light photoreceptor impair blue-light-responsive anthocyanin accumulation and inhibition of hypocotyl elongation. *The Plant Journal* **8**, 653–658.
- Anten NPR, Casado-Garcia R, Nagashima H. 2005. Effects of mechanical stress and plant density on mechanical characteristics, growth, and lifetime reproduction of tobacco plants. *American Naturalist* **166**, 650–660.
- Baldwin IT, Halitschke R, Paschold A, von Dahl CC, Preston CA. 2006. Volatile signaling in plant–plant interactions: ‘Talking trees’ in the genomics era. *Science* **311**, 812–815.
- Ballaré CL, Sánchez RA, Scopel AL, Casal JJ, Ghersa CM. 1987. Early detection of neighbour plants by phytochrome perception of spectral changes in reflected sunlight. *Plant, Cell and Environment* **10**, 551–557.
- Ballaré CL, Scopel AL, Radosevich SR, Kendrick RE. 1992. Phytochrome-mediated phototropism in de-etiolated seedlings. Occurrence and ecological significance. *Plant Physiology* **100**, 170–177.
- Ballaré CL, Scopel AL, Sánchez RA. 1990. Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* **247**, 329–331.
- 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 and Environment* **14**, 57–65.
- Banerjee R, Schleicher E, Meier S, Viana RM, Pokorny R, Ahmad M, Bittl R, Batschauer A. 2007. The signaling state of *Arabidopsis* cryptochrome 2 contains flavin semiquinone. *Journal of Biological Chemistry* **282**, 14916–14922.
- Bouly J, Schleicher E, Dionisio-Sese M, *et al.* 2007. Cryptochrome blue light photoreceptors are activated through interconversion of flavin redox states. *Journal of Biological Chemistry* **282**, 9383–9391.
- Braam J. 2005. In touch: plant responses to mechanical stimuli. *New Phytologist* **165**, 373–389.

- Braam J, Davis RW.** 1990. Rain-, wind-, and touch-induced expression of calmodulin and calmodulin-related genes in *Arabidopsis*. *Cell* **60**, 357–364.
- 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 and Development* **21**, 1863–1868.
- Casal JJ.** 2012. Shade avoidance. *The Arabidopsis Book* **10**, e0157–e0157.
- Casal JJ, Smith H.** 1988. The loci of perception for phytochrome control of internode growth in lightgrown mustard: promotion by low phytochrome photoequilibria in the internode is enhanced by blue light perceived by the leaves. *Planta* **176**, 277–282.
- Chaves I, Pokorny R, Byrdin M, et al.** 2011. The cryptochromes: blue light photoreceptors in plants and animals. *Annual Review of Plant Biology* **62**, 335–364.
- Chehab EW, Yao C, Henderson Z, Kim S, Braam J.** 2012. *Arabidopsis* touch-induced morphogenesis is jasmonate mediated and protects against pests. *Current Biology* **22**, 701–706.
- Christie JM.** 2007. Phototropin blue-light receptors. *Annual Review of Plant Biology* **58**, 21–45.
- Cifuentes-Esquivel N, Bou-Torrent J, Galstyan A, Gallemí M, Sessa G, Salla Martret M, Roig-Villanova I, Ruberti I, Martínez-García JF.** 2013. The bHLH proteins BEE and BIM positively modulate the shade avoidance syndrome in *Arabidopsis* seedlings. *The Plant Journal* **75**, 989–1002.
- Clack T, Mathews S, Sharrock R.** 1994. The phytochrome apoprotein family in *Arabidopsis* is encoded by 5 genes—the sequences and expression of *PHYD* and *PHYE*. *Plant Molecular Biology* **25**, 413–427.
- de Kroon H, Hendriks M, van Ruijven J, Ravenek J, Padilla FM, Jongejans E, Visser EJW, Mommer L.** 2012. Root responses to nutrients and soil biota: drivers of species coexistence and ecosystem productivity. *Journal of Ecology* **100**, 6–15.
- 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. *Proceedings of the National Academy of Sciences, USA* **109**, 14705–14710.
- Demarsy E, Fankhauser C.** 2009. Higher plants use LOV to perceive blue light. *Current Opinion in Plant Biology* **12**, 69–74.
- Dicke M.** 2009. Behavioural and community ecology of plants that cry for help. *The Plant Cell and Environment* **32**, 654–665.
- Dicke M, Baldwin IT.** 2010. The evolutionary context for herbivore-induced plant volatiles: beyond the ‘cry for help’. *Trends in Plant Science* **15**, 167–175.
- Djakovic-Petrovic T, de Wit M, Voeselek LACJ, Pierik R.** 2007. DELLA protein regulation in growth responses to canopy signals. *The Plant Journal* **51**, 117–126.
- Fankhauser C, Ulm R.** 2011. Light-regulated interactions with SPA proteins underlie cryptochrome-mediated gene expression. *Genes and Development* **25**, 1004–1009.
- Favory J, Stec A, Gruber H, et al.** 2009. Interaction of COP1 and UVR8 regulates UV-B-induced photomorphogenesis and stress acclimation in *Arabidopsis*. *EMBO Journal* **28**, 591–601.
- Finlayson SA, Jung IJ, Mullet JE, Morgan PW.** 1999. The mechanism of rhythmic ethylene production in *Sorghum*. The role of phytochrome B and simulated shading. *Plant Physiology* **119**, 1083–1089.
- Folta KM.** 2004. Green light stimulates early stem elongation, antagonizing light-mediated growth inhibition. *Plant Physiology* **135**, 1407–1416.
- Foo E, Ross JJ, Davies NW, Reid JB, Weller JL.** 2006. A role for ethylene in the phytochrome-mediated control of vegetative development. *The Plant Journal* **46**, 911–921.
- Franklin KA.** 2008. Shade avoidance. *New Phytologist* **179**, 930–944.
- Franklin KA, Davis SJ, Stoddart WM, Vierstra RD, Whitelam GC.** 2003. Mutant analyses define multiple roles for phytochrome C in *Arabidopsis thaliana* photomorphogenesis. *The Plant Cell* **15**, 1981–1989.
- Frost CJ, Appel M, Carlson JE, De Moraes CM, Mescher MC, Schultz JC.** 2007. Within-plant signalling via volatiles overcomes vascular constraints on systemic signalling and primes responses against herbivores. *Ecology Letters* **10**, 490–498.
- Grime JP and Jeffrey DW.** 1965. Seedling establishment in vertical gradients of sunlight. *Journal of Ecology* **53**, 621–642.
- Gommers CMM, Visser EJW, St Onge KR, Voeselek LACJ, Pierik R.** 2013. Shade tolerance: when growing tall is not an option. *Trends in Plant Science* **18**, 65–71.
- Hamant O, Heisler MG, Jonsson H, et al.** 2008. Developmental patterning by mechanical signals in *Arabidopsis*. *Science* **322**, 1650–1655.
- Hamant O, Traas J.** 2010. The mechanics behind plant development. *New Phytologist* **185**, 369–385.
- Haswell ES, Peyronnet R, Barbier-Brygoo H, Meyerowitz EM, Frachisse J.** 2008. Two MscS homologs provide mechanosensitive channel activities in the *Arabidopsis* root. *Current Biology* **18**, 730–734.
- Heil M, Silva Bueno JC.** 2007. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proceedings of the National Academy of Sciences, USA* **104**, 5467–5472.
- Henry H, Thomas S.** 2002. Interactive effects of lateral shade and wind on stem allometry, biomass allocation, and mechanical stability in *Abutilon theophrasti* (Malvaceae). *American Journal of Botany* **89**, 1609–1615.
- Holm M, Ma L, Qu L, Deng X.** 2002. Two interacting bZIP proteins are direct targets of COP1-mediated control of light-dependent gene expression in *Arabidopsis*. *Genes and Development* **16**, 1247–1259.
- Holmes MG, Smith H.** 1975. The function of phytochrome in plants growing in the natural environment. *Nature* **254**, 512–514.
- Hornitschek P, Kohnen MV, Lorrain S, et al.** 2012. Phytochrome interacting factors 4 and 5 control seedling growth in changing light conditions by directly controlling auxin signaling. *The Plant Journal* **71**, 699–711.
- Jailais Y, Chory J.** 2010. Unraveling the paradoxes of plant hormone signaling integration. *Nature Structural and Molecular Biology* **17**, 642–645.



- Karban R, Maron J, Felton GW, Ervin G, Eichenseer H.** 2003. Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. *Oikos* **100**, 325–332.
- Kegge W, Pierik R.** 2010. Biogenic volatile organic compounds and plant competition. *Trends in Plant Science* **15**, 126–132.
- Kegge W, Weldegergis BT, Soler R, Eijk MV, 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 Phytologist* **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. *The Plant Journal* **67**, 195–207.
- Keuskamp DH, Pollmann S, Voeselek LACJ, Peeters AJM, Pierik R.** 2010a. Auxin transport through PIN-FORMED 3 (PIN3) controls shade avoidance and fitness during competition. *Proceedings of the National Academy of Sciences, USA* **107**, 22740–22744.
- Keuskamp DH, Sasidharan R, Pierik R.** 2010b. Physiological regulation and functional significance of shade avoidance responses to neighbors. *Plant Signaling and Behavior* **5**, 655–662.
- 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. *The Plant Journal* **67**, 208–217.
- Kiba T, Henriques R, Sakakibara H, Chua N.** 2007. Targeted degradation of PSEUDO-RESPONSE REGULATOR5 by an SCFZTL complex regulates clock function and photomorphogenesis in *Arabidopsis thaliana*. *The Plant Cell* **19**, 2516–2530.
- 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 Physiology* **153**, 1608–1618.
- Kung C.** 2005. A possible unifying principle for mechanosensation. *Nature* **436**, 647–654.
- Kurepin LV, Shah S, Reid DM.** 2007. Light quality regulation of endogenous levels of auxin, abscisic acid and ethylene production in petioles and leaves of wild type and ACC deaminase transgenic *Brassica napus* seedlings. *Plant Growth Regulation* **52**, 53–60.
- Lau OS, Deng XW.** 2012. The photomorphogenic repressors COP1 and DET1: 20 years later. *Trends in Plant Science* **17**, 584–593.
- Leivar P, Tepperman JT, Cohn MM, Monte E, Al-Sady B, Erickson E, Quail PH.** 2012. Dynamic antagonism between phytochromes and PIF family basic helix-loop-helix factors induces selective reciprocal responses to light and shade in a rapidly responsive transcriptional network in *Arabidopsis*. *The Plant Cell* **24**, 1398–1419.
- Li L, Ljung K, Breton G, et al.** 2012. Linking photoreceptor excitation to changes in plant architecture. *Genes and Development* **26**, 785–790.
- Lian H, He S, Zhang Y, Zhu D, Zhang J, Jia K, Sun S, Li L, Yang H.** 2011. Blue-light-dependent interaction of cryptochrome 1 with SPA1 defines a dynamic signaling mechanism. *Genes and Development* **25**, 1023–1028.
- 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. *Proceedings of the National Academy of Sciences, USA* **95**, 2686–2690.
- Liu B, Zuo Z, Liu H, Liu X, Lin C.** 2011. *Arabidopsis* cryptochrome 1 interacts with SPA1 to suppress COP1 activity in response to blue light. *Genes and Development* **25**, 1029–1034.
- 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. *The Plant Journal* **53**, 312–323.
- Mas P, Devlin PF, Panda S, Kay SA.** 2000. Functional interaction of phytochrome B and cryptochrome 2. *Nature* **408**, 207–211.
- Millenaar FF, Cox MCH, de Jong van Berkel YEM, Welschen RAM, Pierik R, Voeselek LACJ, Peeters AJM.** 2005. Ethylene-induced differential growth in petioles of *Arabidopsis thaliana*: analyzing natural variation, response kinetics and regulation. *Plant Physiology* **137**, 998–1008.
- Millenaar FF, van Zanten M, Cox MCH, Pierik R, Voeselek L, Peeters AJM.** 2009. Differential petiole growth in *Arabidopsis thaliana*: photocontrol and hormonal regulation. *New Phytologist* **184**, 141–152.
- Morelli G, Ruberti I.** 2000. Shade avoidance responses. Driving auxin along lateral routes. *Plant Physiology* **122**, 621–626.
- Moreno JE, Tao Y, Chory J, Ballaré CL.** 2009. Ecological modulation of plant defense via phytochrome control of jasmonate sensitivity. *Proceedings of the National Academy of Sciences, USA* **106**, 4935–4940.
- Morgan D, Smith H.** 1978. Function of phytochrome in natural-environment. 7. Relationship between phytochrome photoequilibrium and development in light grown *Chenopodium-album* L. *Planta* **142**, 187–193.
- Morgan D, Smith H.** 1979. Function of phytochrome in the natural-environment. 8. Systematic relationship between phytochrome-controlled development and species habitat, for plants grown in simulated natural radiation. *Planta* **145**, 253–258.
- Mullen JL, Weinig C, Hangarter RP.** 2006. Shade avoidance and the regulation of leaf inclination in *Arabidopsis*. *The Plant Cell and Environment* **29**, 1099–1106.
- Nagashima H, Hikosaka K.** 2012. Not only light quality but also mechanical stimuli are involved in height convergence in crowded *Chenopodium album* stands. *New Phytologist* **195**, 803–811.
- Ninkovic V.** 2003. Volatile communication between barley plants affects biomass allocation. *Journal of Experimental Botany* **54**, 1931–1939.
- Pierik R, Cuppens MLC, Voeselek LACJ, Visser EJW.** 2004a. Interactions between ethylene and gibberellins in phytochrome-mediated shade avoidance responses in tobacco. *Plant Physiology* **136**, 2928–2936.
- Pierik R, Djakovic-Petrovic T, Keuskamp DH, de Wit M, Voeselek L.** 2009. Auxin and ethylene regulate elongation responses to neighbor proximity signals independent of gibberellin and DELLA proteins in *Arabidopsis*. *Plant Physiology* **149**, 1701–1712.
- Pierik R, Whitelam GC, Voeselek LACJ, de Kroon H, Visser EJW.** 2004b. Canopy studies on ethylene-insensitive tobacco identify ethylene as a novel element in blue light and plant–plant signalling. *The Plant Journal* **38**, 310–319.

- Pierik R, Mommer L, Voeselek LA.** 2013. Molecular mechanisms of plant competition: neighbour detection and response strategies. *Functional Ecology* **27**, 841–853.
- 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 Phytologist* **193**, 339–348.
- Rizzini L, Favory J, Cloix C, et al.** 2011. Perception of UV-B by the *Arabidopsis* UVR8 protein. *Science* **332**, 103–106.
- Roig-Villanova I, Bou-Torrent J, Galstyan A, Carretero-Paulet L, Portoles S, Rodriguez-Concepcion M, Garcia JFM.** 2007. Interaction of shade avoidance and auxin responses: a role for two novel atypical bHLH proteins. *EMBO Journal* **26**, 4756–4767.
- Rolauffs S, Fackendahl P, Sahn J, Fiene G, Hoecker U.** 2012. *Arabidopsis* COP1 and SPA genes are essential for plant elongation but not for acceleration of flowering time in response to a low red light to far-red light ratio. *Plant Physiology* **160**, 2015–2027.
- Runyon JB, Mescher MC, De Moraes CM.** 2006. Volatile chemical cues guide host location and host selection by parasitic plants. *Science* **313**, 1964–1967.
- Salisbury FJ, Hall A, Grierson GS, Halliday KJ.** 2007. Phytochrome coordinates *Arabidopsis* shoot and root development. *The Plant Journal* **50**, 429–438.
- Sasidharan R, Chinnappa CC, Staal M, Elzenga JTM, Yokoyama R, Nishitani K, Voeselek LACJ, Pierik R.** 2010. Light quality-mediated petiole elongation in *Arabidopsis* during shade avoidance involves cell wall modification by xyloglucan endotransglucosylase/hydrolases. *Plant Physiology* **154**, 978–990.
- Sasidharan R, Chinnappa CC, Voeselek L, Pierik R.** 2008. The regulation of cell wall extensibility during shade avoidance: a study using two contrasting ecotypes of *Stellaria longipes*. *Plant Physiology* **148**, 1557–1569.
- Schmitt J.** 1997. Is photomorphogenic shade avoidance adaptive? Perspectives from population biology. *Plant, Cell and Environment* **20**, 826–830.
- 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. *American Naturalist* **146**, 937–953.
- Sellaro R, Crepy M, Ariel Trupkin S, Karayekov E, Sabrina Buchovsky A, Rossi C, Casal JJ.** 2010. Cryptochrome as a sensor of the blue/green ratio of natural radiation in *Arabidopsis*. *Plant Physiology* **154**, 401–409.
- Sellaro R, Hoecker U, Yanovsky M, Chory J, Casal JJ.** 2009. Synergism of red and blue light in the control of *Arabidopsis* gene expression and development. *Current Biology* **19**, 1216–1220.
- Sessa G, Carabelli M, Sassi M, Ciolfi A, Possenti M, Mitterpergher F, Becker J, Morelli G, Ruberti I.** 2005. A dynamic balance between gene activation and repression regulates the shade avoidance response in *Arabidopsis*. *Genes and Development* **19**, 2811–2815.
- Smalle J, Haegman M, Kurepa J, Van Montagu M, Van der Straeten D.** 1997. Ethylene can stimulate *Arabidopsis* hypocotyl elongation in the light. *Proceedings of the National Academy of Sciences, USA* **94**, 2756–2761.
- Smith H.** 1982. Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology and Plant Molecular Biology* **33**, 481–518.
- Smith H.** 2000. Phytochromes and light signal perception by plants—an emerging synthesis. *Nature* **407**, 585–591.
- Smith H, Holmes MG.** 1977. Function of phytochrome in natural-environment. 3. Measurement and calculation of phytochrome photo-equilibria. *Photochemistry and photobiology* **25**, 547–550.
- Sorin C, Salla-Martret M, Bou-Torrent J, Roig-Villanova I, Martinez-Garcia JF.** 2009. ATHB4, a regulator of shade avoidance, modulates hormone response in *Arabidopsis* seedlings. *The Plant Journal* **59**, 266–277.
- Stamm P, Kumar PP.** 2010. The phytohormone signal network regulating elongation growth during shade avoidance. *Journal of Experimental Botany* **61**, 2889–2903.
- 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.
- Tanaka SI, Nakamura S, Mochizuki N, Nagatani A.** 2002. Phytochrome in cotyledons regulates the expression of genes in the hypocotyl through auxin-dependent and -independent pathways. *Plant and Cell Physiology* **43**, 1171–1181.
- Tao Y, Ferrer JL, Ljung K, et al.** 2008. Rapid synthesis of auxin via a new tryptophan-dependent pathway is required for shade avoidance in plants. *Cell* **133**, 164–176.
- Valladares F, Niinemets U.** 2008. Shade tolerance, a key plant feature of complex nature and consequences RID A-3816-2008. *Annual Review of Ecology Evolution and Systematics* **39**, 237–257.
- Vermeulen PJ, Anten NPR, Schieving F, Werger MJA, During HJ.** 2008. Height convergence in response to neighbour growth: genotypic differences in the stoloniferous plant *Potentilla reptans*. *New Phytologist* **177**, 688–697.
- Weijsschede J, Antonise K, de Caluwe H, de Kroon H, Huber H.** 2008. Effects of cell number and cell size on petiole length variation in a stoloniferous herb. *American Journal of Botany* **95**, 41–49.
- 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*. *Journal of Cell Biology* **145**, 437–445.
- Zhang T, Maruhnich SA, Folta KM.** 2011. Green light induces shade avoidance symptoms. *Plant Physiology* **157**, 1528–1536.
- Zheng X, Wu S, Zhai H, et al.** 2013. *Arabidopsis* phytochrome B promotes SPA1 nuclear accumulation to repress photomorphogenesis under far-red light. *The Plant Cell* **25**, 115–133.
- Zuo Z, Liu H, Liu B, Liu X, Lin C.** 2011. Blue light-dependent interaction of CRY2 with SPA1 regulates COP1 activity and floral initiation in *Arabidopsis*. *Current Biology* **21**, 841–847.