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BOTANICAL BRIEFING

Phytochromes and Shade-avoidance Responses in Plants

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• *Background and Aims* The ability to detect and respond to the impending threat of shade can confer significant selective advantage to plants growing in natural communities. This Botanical Briefing highlights (*a*) the regulation of shade-avoidance responses by endogenous and exogenous factors and (*b*) current understanding of the molecular components involved in red to far-red ratio signal transduction.
• *Scope* The Briefing covers: (*a*) the shade-avoidance syndrome in higher plants; (*b*) the adaptive significance of shade avoidance in natural light environments; (*c*) phytochrome regulation of shade-avoidance responses; (*d*) the role of blue light signals in shade avoidance; (*e*) gating of rapid shade-avoidance responses by the circadian clock; (*f*) potential signalling components and future perspectives.

Key words: Phytochromes, red light, far-red light, red to far-red ratio, blue light, elongation growth, early flowering, circadian clock, ethylene.

INTRODUCTION

Natural plant communities, as well as agricultural crops, are frequently resource-limited, and competition between individuals often results in plastic developmental responses to the specific resource shortage. As photoautotrophs, higher plants depend upon the acquisition of light energy for their survival and competition for light is characteristic of plant communities. Being sessile organisms that cannot choose their surroundings, plants must adapt their growth and development to the ambient light environment. Monitoring changes in the quantity, quality and direction of light enables plants to optimize both the timing of germination and their subsequent growth and development for the optimal acquisition of light energy to drive photosynthesis. In addition, through interactions with the central circadian oscillator, light signals enable plants to monitor day length (photoperiod) and adapt their growth and development, especially the timing of the transition from vegetative to reproductive development, in relation to changing seasonal environments. Such developmental plasticity in response to light signals is conferred by specialized information-transducing photoreceptors. In higher plants, three major families of such photoreceptors have been identified and characterized. These are the red (R)/far-red (FR) light-absorbing phytochromes and the blue/UV-A light-absorbing cryptochromes (Cashmore *et al*., 1999) and phototropins (Briggs and Huala, 1999).

R : FR RATIO AND SHADE AVOIDANCE

Plants have evolved mechanisms that enable them to respond to the presence of neighbours. The spectral energy distribution of daylight is dramatically altered by vegetation. The photosynthetic pigments, chlorophylls and carotenoids, absorb light over most of the visible spectrum, although some green light is reflected or transmitted. Radiation in the FR region is very poorly absorbed and, consequently, the light that is transmitted through, or reflected, from vegetation is depleted in R and significantly enriched in FR wavelengths. A useful parameter to describe the natural light environment is therefore the ratio of photon irradiance in the R, to that in the FR (R : FR ratio). This parameter is often directly defined as follows:

$$\text{R : FR ratio} = \frac{\text{photon irradiance between 655 and 665 nm}}{\text{photon irradiance between 725 and 735 nm}}$$

The R : FR ratio of daylight is around 1·15 and varies little with weather conditions or time of year (Smith, 1982). Reported R : FR ratios underneath canopies of vegetation are typically in the range 0·05–0·7 (Smith, 1982). A spectral photon distribution of both incident and reflected daylight is shown in Fig. 1.

Changes in light quality in the red and far-red regions of the spectrum (i.e. R : FR ratio) are detected by the phytochromes. Higher plants contain multiple phytochromes, the apoproteins of which are encoded by a small divergent gene family (Quail, 1994). Three major phytochromes exist in angiosperms, phyA, phyB and phyC, encoded by the genes *PHYA*, *PHYB* and *PHYC*. Two additional phytochromes exist in dicotyledonous plants, phyD and phyE, and likely represent the products of more recent gene duplication events (Mathews and Sharrock, 1997). In the model plant species *Arabidopsis thaliana*, five apophytochrome-encoding genes (*PHYA–PHYE*) have been sequenced and characterized (Sharrock and Quail, 1989; Clack *et al*., 1994). The protein products of the *PHYB* and *PHYD* genes share approx. 80 % sequence identity and are slightly more related to PHYE than they are to either PHYA or PHYC. Thus, the *PHYB*, *PHYD* and *PHYE* genes are considered to form a distinct subgroup within the arabidopsis *PHY* gene family (Goosey *et al*., 1997).

Phytochromes exist as a homodimer of two independently reversible subunits. Each subunit consists of a polypeptide (approx. 124 kDa) covalently linked to a light-absorbing,

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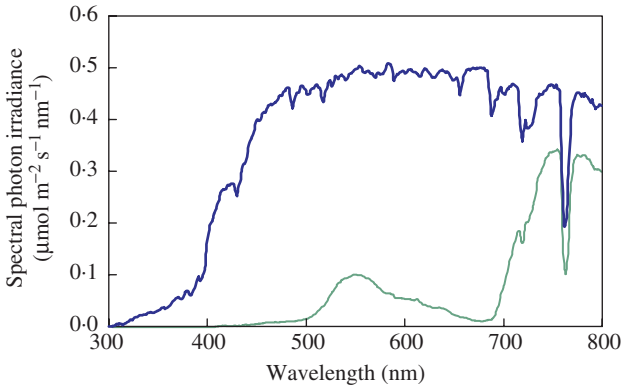

FIG. 1. The spectral photon distributions of daylight (blue line) and light reflected from leaves of *Fallopia japonica* (green line).

linear tetrapyrrole chromophore, phytochromobilin, via a thioether linkage (Furuya and Song, 1994). In the dark, phytochrome is synthesized in the red light-absorbing (Pr) form (absorption maximum approx. 660 nm) and is generally regarded to be biologically inactive. Activity is acquired upon photo-conversion to the far red light-absorbing (Pfr) form (absorption maximum approx. 730 nm). Under almost all irradiation conditions, an equilibrium mixture of the two forms will exist. The relative amounts of R and FR light in incident radiation will be translated by the phytochromes into different relative concentrations of the active Pfr form of phytochrome. A reduced R : FR ratio, leading to relatively low concentrations of Pfr, is considered to be a key signature of light reflected from, or transmitted through, neighbouring vegetation.

In response to low R : FR ratio signals, many plants display a rapid and pronounced increase in the elongation growth rate of stems and petioles, often at the expense of leaf and storage organ development. This is demonstrated in Fig. 2, which shows arabidopsis and *Brassica rapa* plants grown in prolonged irradiation of both high and low R : FR ratios. In addition to reduced chlorophyll content, a reduction in leaf thickness is often observed in plants receiving low R : FR ratio signals (McClaren and Smith, 1978). These architectural modifications are accompanied by elevated leaf angles (hyponasty) and an increase in apical dominance leading to reduced branching in dicots and reduced tillering in grasses (Casal *et al*., 1986). Such responses, collectively termed the shade-avoidance syndrome, serve to elevate leaves towards unfiltered daylight and provide an essential survival strategy in rapidly growing populations.

Shade-avoidance responses are typically initiated in advance of canopy closure and light becoming limiting. Thus, plants respond predominantly to the reduction in R : FR ratio of light reflected from surrounding vegetation (a proximity signal) and therefore initiate escape responses in anticipation of being shaded (Ballaré *et al*., 1990). The morphology, size and distribution of leaves are key factors in the generation of these proximity signals (Gilbert and Smith, 2001). If the reduced R : FR ratio signal persists and the plant is unable to overtop competing vegetation, flowering is accelerated, thereby promoting seed set and enhancing the probability of reproductive success (Halliday *et al*., 1994; Smith and Whitelam, 1997; Dorn *et al*., 2000).

THE ADAPTIVE SIGNIFICANCE OF SHADE AVOIDANCE

The adaptive significance of shade avoidance has been assessed in a number of ecological investigations. Such studies have suggested that the ability of stems and petioles to elongate in response to proximity-to-vegetation signals can confer high relative fitness in dense stands of plants (Schmitt *et al*., 2003). Constitutive expression of an oat *PHYA* gene has previously been used to suppress shade-avoidance responses in transgenic tobacco plants (McCormac *et al*., 1991, 1992). In these plants, persistence of a normally transient phyA-mediated inhibition of stem elongation resulted in an inability of plants to increase stem elongation in response to low R : FR ratio signals. When grown in dense stands, these transgenic plants displayed decreased fitness compared with wild-type tobacco plants (Schmitt *et al*., 1995; Robson *et al*., 1996). A similar finding was obtained from a recent study using transgenic tobacco plants that are insensitive to ethylene (see 'The role of blue light and other signals in shade avoidance'). Compared with wild types, the transgenic plants display a significant delay in the key shade-avoidance traits—increased leaf hyponasty and stem elongation in response to reduced R : FR ratio. When grown in mixed populations alongside wild-type seedlings, the ethylene-insensitive transgenic plants suffered a severely reduced competitive ability compared with their wild-type neighbours (Pierik *et al*., 2003). However, when grown in crowded monocultures, biomass accumulation in the ethylene-insensitive transgenic plants was comparable with that of crowded wild-type monocultures. This suggests that when all neighbouring plants suffer the same disruption of shade-avoidance responses, there are no obvious fitness consequences (Pierik *et al*., 2004*a*).

Although shade avoidance may have major fitness benefits in crowded communities, in the absence of competition for light, the reallocation of resources towards elongation growth that typifies the shade-avoidance response may reduce the competitive success of an individual as well as leading to an increased risk of lodging and mechanical injury (Casal and Smith, 1989). Experiments in which mutants that are constitutively elongated have been grown at low densities, in either the glasshouse or in the field, support this notion. Under these conditions, the *elongated internode* (*ein*) mutant of *Brassica rapa* displayed decreased dry biomass and a reduction in the number of reproductive structures compared with wild-type plants (Schmitt *et al*., 1995). Likewise, seedlings of the *long hypocotyl* (*lh*) mutant of cucumber were subject to increased stem damage compared with wild-type cucumber seedlings (Casal *et al*., 1994).

PHYTOCHROME REGULATION OF SHADE AVOIDANCE

The roles of individual phytochromes in mediating responses to low R : FR ratios have been largely inferred

FIG. 2. The R : FR ratio-mediated shade-avoidance response. The appearance of arabidopsis (A) and *Brassica rapa* (B) plants grown under high or low R : FR ratio conditions. All plants were grown under white fluorescent light providing equal photosynthetically active radiation (400–700 nm). For each species, the plants on the right received supplementary FR to reduce the R : FR ratio.

from studies using mutants deficient in one or more family members. When grown in white light (i.e. high R : FR ratio conditions), phytochrome B-deficient mutants of a number of plants species characteristically display elongated stems/petioles, reduced leaf size, decreased chlorophyll content and early flowering—responses often described as 'constitutive shade avoidance' (Somers *et al*., 1991; Devlin *et al*., 1992; López-Juez *et al*., 1992; Reed *et al*., 1993). Such studies have confirmed a major role for phyB in transducing the low R : FR ratio signal, although the retention of some, attenuated shade-avoidance responses in phytochrome B-deficient null mutants indicated the involvement of additional phytochromes (Whitelam and Smith, 1991). Daytime reductions in R : FR ratio and end-of-day (EOD) FR treatments, known to mimic the effects of growth in reduced R : FR ratio conditions, were subsequently shown to elicit small, yet significant, shade-avoidance responses in *phyB* mutants of multiple species (Robson *et al*., 1993; Halliday *et al*., 1994; Devlin *et al*., 1996). The discovery of a naturally occurring *phyD* mutation in the Wassilewskija (Ws) ecotype of arabidopsis enabled the role of this phytochrome in shade avoidance to be examined. Adult mutants deficient in phyD displayed wild-type responses to both low R : FR ratio and EOD FR treatments (Aukerman *et al*., 1997; Devlin *et al*., 1999). Comparison of a *phyBphyD* mutant with a *phyB* mutant, however, revealed the double mutant to display greater petiole elongation and earlier flowering, phenotypes reminiscent of the shade-avoidance syndrome (Devlin *et al*., 1999). These findings suggested a redundancy of function between phyB and phyD in regulating shade avoidance, a proposal supported by their sequence similarity and similar patterns of expression of their genes (Goosey *et al*., 1997; Mathews and Sharrock, 1997).

A pronounced acceleration of flowering and internode growth between rosette leaves were observed in arabidopsis *phyAphyB* mutants subject to EOD FR treatments, forming the basis of a screen from which the *phyE* mutation was isolated (Devlin *et al*., 1998). These phenotypes were constitutively displayed by the *phyAphyBphyE* triple mutant, implicating phyE in the regulation of these responses (Devlin *et al*., 1998). The subsequent creation of mutants null for multiple phytochrome species led to confirmation that the shade-avoidance syndrome is regulated exclusively by phytochromes B, D and E, all acting together in a functionally redundant manner (Franklin *et al*., 2003*a*). These phytochromes represent the most recently evolved members of the phytochrome family, forming a distinct subgroup (Mathews and Sharrock, 1997). It can therefore be speculated that competition for light may have provided the selective pressure for their evolution (Devlin *et al*., 1998).

The elongated appearance and early flowering response displayed by *phyB* mutants grown in high R : FR ratio, phenotypes not displayed by *phyD* or *phyE* monogenic mutants, have implicated phyB as the major regulator of shade-avoidance responses in Arabidopsis. Recent studies have, however, revealed evidence that action of different

phytochromes is modified by other environmental signals, particularly ambient growth temperature (Blázquez *et al*., 2003; Halliday *et al*., 2003). For instance, a modest reduction in ambient temperature from 22 °C to 16 °C was sufficient to completely abolish the early flowering phenotype of *phyB* mutants. Accelerated flowering responses in low R : FR were, nevertheless, still observed in wild-type plants grown at 16 °C, suggesting that phytochromes, other than phyB, play a more dominant role in repressing flowering in plants growing at lower temperatures. Studies using mutants null for multiple phytochromes revealed that phyE, and to a lesser extent phyD, do indeed play greater roles in the control of flowering under cooler conditions (Halliday and Whitelam, 2003; Halliday *et al*., 2003).

In contrast to the other phytochromes, phyA is subject to rapid proteolytic degradation upon photoconversion to Pfr and therefore only accumulates to high levels in etiolated seedlings (Quail, 1994). A major role for phyA, and the basis upon which *phyA* mutants were identified, is mediating FR high irradiance responses in de-etiolating seedlings (Smith and Whitelam, 1990). Despite being present at reduced levels in light-grown plants, phyA performs an important role in the regulation of hypocotyl elongation in response to changes in R : FR ratio. When grown in continuous low R : FR ratio light, *phyA* mutant seedlings displayed enhanced hypocotyl elongation compared with wild-type controls (Johnson *et al*., 1994). These observations led to the suggestion that in wild-type plants, phyA action was antagonizing phyB-mediated shade avoidance by constraining hypocotyl extension. This notion is supported by observations showing that the hypocotyls of *phyAphyB* double mutants display enhanced elongation growth when compared with monogenic *phyB* mutants (Johnson *et al*., 1994). In the field, the action of phyA in constraining shade-avoidance elongation responses has been shown to be of fundamental importance in seedling establishment under dense natural vegetational shade. Under these conditions, *phyA* mutants display an extreme hypocotyl elongation response, with many seedlings failing to become established and dying prematurely (Yanovsky *et al*., 1995). The growth-inhibitory action of phyA in low R : FR ratio conditions has been successfully exploited in the production of transgenic tobacco plants which overexpress *PHYA*, thus leading to the elimination of unwanted elongation responses in more densely planted crops (Robson *et al*., 1996).

A role for phyC in mediating shade-avoidance responses was excluded following observations that *phyBphyDphyE* triple mutants were blind to the reduced R : FR ratio signal and EOD FR treatments (Franklin *et al*., 2003*a*). This proposal was endorsed by the isolation of mutants, null at the *PHYC* locus, which displayed no aberrancy in R : FR ratio perception, alone, or when present in combination with other phytochrome mutations (Franklin *et al*., 2003*b*).

THE ROLE OF BLUE LIGHT AND OTHER SIGNALS IN SHADE AVOIDANCE

In addition to changes in R : FR ratio, reductions in total light quantity can provide information to plants about the proximity of neighbours in closed canopies (Ballaré *et al*., 1991*a*; Ballaré, 1999). Indeed, reductions in both photosynthetically active radiation and blue light can induce shade-avoidance responses in cucumber hypocotyls (Ballaré *et al*., 1991*b*) and tobacco stems (Casal and Sánchez, 1994). Changes in blue light quantity are sensed by the blue light photoreceptors cryptochromes and phototropins (Briggs and Huala, 1999; Cashmore *et al*., 1999). Studies using transgenic tobacco plants that are insensitive to ethylene revealed their delayed shade-avoidance responses to the presence of neighbouring vegetation were the result of insensitivity to reduced fluence rates of blue light (Pierik *et al*., 2004*b*). The ethylene insensitive plants displayed more or less wild-type responses to reductions in R : FR ratio. Such observations indicate that reductions in incident blue light play an important role in shade avoidance in dense communities and suggest that ethylene is an important regulatory component in these blue light-mediated responses (Pierik *et al*., 2004*b*). In addition to reductions in R : FR ratio and blue light irradiance, exposure to low concentrations of ethylene has also been shown to initiate shade-avoidance responses in wild-type tobacco plants (Pierik *et al*., 2003). This, together with the finding that ethylene concentrations increase in the canopy atmosphere, suggest that ethylene accumulation in crowded stands may provide a further warning to plants that competitors are nearby (Pierik *et al*., 2004*b*).

SIGNALLING IN SHADE AVOIDANCE

Proximity perception in natural light environments is achieved through the convergence of multiple signals. Of these, a reduction in R : FR ratio may be considered to be the most effective (Holmes and Smith, 1975; Ballaré *et al*., 1990; Smith and Whitelam, 1997). Although the individual phytochrome species involved in the perception of R : FR ratio signals have been defined, relatively little is known about the molecular mechanisms involved in transducing the signal into changed patterns of growth and development. Phytochrome B plays a major role in R : FR ratio perception and an understanding of the molecular mechanisms underlying phytochrome B signal transduction in relation to its role in seedling de-etiolation is emerging. The isolation of multiple phytochrome B-interacting factors and observations of light-induced translocation of the Pfr form of phyB (and indeed other phytochromes) to the nucleus suggest that phytochrome signal transduction is a highly complex network of events occurring in multiple cellular compartments (for reviews, see Møller *et al*., 2002; Schäfer and Bowler, 2002). As yet, no direct experimental evidence exists to link the nuclear translocation of Pfr or the binding of phyB to interacting factors with R : FR ratio signalling. These events are beyond the scope of this review and will not be discussed further here.

The transition to flowering in arabidopsis is controlled by multiple regulatory pathways which converge to regulate the expression of meristem identity genes such as *LFY* (Simpson and Dean, 2002). This is achieved using a number of floral pathway integrating genes such as *FT* and *SOC1*. These are, in turn, regulated by transcriptional regulators

such as *FLC* and *CO* (Simpson and Dean, 2002). The concept of an independent light quality (i.e. R : FR ratio) pathway was suggested by the discovery that the early flowering phenotype of *phyB* mutants involved regulation of *LFY* expression, in a manner that was independent from *CO*, the floral regulator implicated in the photoperiodic regulation of flowering (Blázquez and Weigel, 1999). More recent studies have revealed this pathway involves regulation of *FT* (Cerdán and Chory, 2003; Halliday *et al*., 2003) in a temperature-conditional manner (Halliday *et al*., 2003). Mutant screening has resulted in the identification of *pft1*, a recessive mutation which suppresses the early flowering phenotype associated with phyB deficiency (Cerdán and Chory, 2003). The *PFT1* gene encodes a nuclear-localized protein with structural similarity to some transcriptional regulators (Cerdán and Chory, 2003). Petiole length was largely unaffected in *pft1phyB* double mutants, whilst the *pft1* mutation led to a significant impairment of the flowering response to EOD FR treatments. Taken together, these data suggest that the major role of PFT1 is to regulate flowering time downstream of phytochromes B, D and E (Cerdán and Chory, 2003).

Reports of genes whose expression is strongly regulated by changes in R : FR ratio are limited. The most cited examples to date include the homeodomain ZIP transcription factors *ATHB-2* (also known as *HAT4*) and *ATHB-4*. Both these genes show a rapid increase in transcript abundance upon transfer of arabidopsis plants to low R : FR ratio (Carabelli *et al*., 1993, 1996). Analyses of mutants deficient in multiple phytochrome combinations have revealed the regulation of *ATHB-2* transcript abundance to be controlled by phyB and phyE acting in a functionally redundant manner (Franklin *et al*., 2003*a*). The possible involvement of *ATHB-2* in shade avoidance has been inferred from studies using plants with altered levels of *ATHB-2* expression (Schena and Davis, 1992; Steindler *et al*., 1999). Transgenic plants with elevated levels of *ATHB-2* displayed some phenotypes similar to those of wild-type plants grown in reduced R : FR ratio. Plants with decreased levels of *ATHB-2* behaved oppositely, suggesting a role for *ATHB-2* in the regulation of shade avoidance (Carabelli *et al*., 1996; Steindler *et al*., 1999).

More recently, microarray analyses in arabidopsis have revealed two genes, *PIL1* (***PI****F3-****L****IKE 1*) and *PIL2* (***PI****F3-****L****IKE 2*) to show rapid and significant increases in transcript abundance upon transfer of plants to low R : FR ratio (Salter *et al*., 2003). Both genes encode basic helix–loop–helix transcription factors with high protein sequence similarity to the phytochrome-interacting protein *PIF3* (Ni *et al*., 1998). The increase in *PIL1* transcript level is extremely rapid, with quantitative reverse transcription polymerase chain reaction (qRT-PCR) revealing detectable increases in *PIL1* transcript after just 8 min of low R : FR ratio treatment (Salter *et al*., 2003). The kinetics of *PIL2* transcript abundance appear slightly different, with longer exposures to low R : FR required for maximum de-repression of its expression (Salter *et al*., 2003). More detailed expression studies of *PIL1* and *PIL2* showed de-repression of both genes to be gated by the circadian clock, with maximum increases occurring at subjective dawn (Salter *et al*., 2003). The role of PIL1 in shade avoidance was established following observations that a *pil1* null mutant was impaired in rapid hypocotyl elongation in response to transient reductions in R : FR ratio (Salter *et al*., 2003).

The gating of *PIL1* and *PIL2* gene de-repression by the circadian clock led to speculation that physiological responses to low R : FR ratio may be regulated in a similar manner. It was subsequently revealed that a 2-h transient reduction in R : FR ratio was sufficient to induce a 30 % increase in arabidopsis hypocotyl extension within the following 24-h period. This response was also gated by the circadian clock, with maximum elongation occurring at subjective dusk (Salter *et al*., 2003). A considerably attenuated response was observed in *pil1* null mutants, suggesting that the presence of PIL1 is required. Paradoxically, an inhibition of hypocotyl length was observed in seedlings treated with low R : FR ratio at subjective dawn, a time when maximum de-repression of *PIL1* transcript occurs (Salter *et al*., 2003). This response was absent in *phyA* mutants, confirming the role of this phytochrome family member in antagonizing shade-avoidance elongation growth responses. The growth of arabidopsis hypocotyls is reported to be under circadian control, with a daily arrest at dawn and a period of rapid elongation at dusk (Dowson-Day and Millar, 1999). Hypocotyl extension in rapid shade avoidance therefore coincides with the seedling's natural endogenous rhythm of elongation growth. Observations that *pil1* null mutants appear phenotypically similar to wild-type plants in prolonged low R : FR ratios suggest that PIL1 only plays a role in rapid responses to shade (Salter *et al*., 2003).

FUTURE PERSPECTIVES

Although the photoreceptors involved in mediating shade-avoidance responses are well established, a thorough understanding of this important biological phenomenon requires elucidation of the molecular components involved. The use of microarray technology has already enabled the identification of novel genes whose expression is strongly regulated by R : FR ratio (Salter *et al*., 2003). The rapid and transient phenotypes of *pil1* null mutants suggest redundancy of function to exist in the regulation of elongation responses to shade. Future investigations of multiple physiological responses will undoubtedly reveal further candidates and ultimately the signal transduction processes involved.

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