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The signal transducing photoreceptors of plants

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ABSTRACT Light signals are amongst the most important environmental cues regulating plant development. In addition to light quantity, plants measure the quality, direction and periodicity of incident light and use the information to optimise growth and development to the prevailing environmental conditions. Red and far-red wavelengths are perceived by the photoreversible phytochrome family of photoreceptors, whilst the detection of blue and ultraviolet (UV)-A wavelengths is conferred by the cryptochromes and phototropins. Higher plants contain multiple discrete phytochromes, the apoproteins of which are encoded by a small divergent gene family. In *Arabidopsis*, two cryptochrome and two phototropin family members have been identified and characterized. Photoreceptor action regulates development throughout the lifecycle of plants, from seed germination through to architecture of the mature plant and the onset of reproduction. The roles of individual photoreceptors in mediating plant development have, however, often been confounded by redundant, synergistic and in some cases mutually antagonistic mechanisms of action. The isolation of mutants null for individual photoreceptors and the construction of mutants null for multiple photoreceptors have therefore been paramount in elucidating photoreceptor functions. Photoreceptor action does not, however, operate in isolation from other signalling systems. The integration of light signals with other environmental cues enables plants to adapt their physiology to changing seasonal environments. This paper summarises current understanding of photoreceptor families and their functions throughout the lifecycle of plants. The integration of light signals with other environmental stimuli is also discussed.

KEY WORDS: *light, phytochrome, cryptochrome, phototropin, shade avoidance*

Introduction

Photoautotrophic higher plants are dependent upon light for their survival. In addition to providing energy for photosynthesis, light signals impart important information about the surrounding environment and can influence not only the timing of seed germination, but the ensuing growth and developmental strategy of a plant. Using specialized photoreceptors, plants can monitor the quantity, quality and direction of incident light. The integration of light signals with the endogenous circadian oscillator provides plants with a means to monitor photoperiod (daylength) and consequently anticipate seasonal changes. Three principal families of signal-transducing photoreceptor have been identified and characterized in higher plant tissues. These are the red (R)/ far-red (FR) – absorbing phytochromes and the blue/UV-A – absorbing cryptochromes and phototropins.

The cryptochromes are chromoproteins that possess a flavin chromophore and a pterin antenna and share protein sequence similarity with prokaryotic DNA photolyases (reviewed in Briggs and Huala, 1999). Two blue/UV-A–absorbing cryptochromes have been characterized in *Arabidopsis*, cry1 and cry2, encoded by the *CRY1* and *CRY2* genes respectively (Koornneef *et al*., 1980., Ahmad *et al*., 1995, Lin *et al*., 1996, 1998). Both cry1 and cry2 are soluble proteins that are present in all organs and tissues of both dark- and light-grown plants (Lin *et al*., 1996, 1998). At the subcellular level, the localization of cry1 is light regulated, with cry1 being largely cytosolic in light-grown seedlings but undergoing dark-induced nuclear import (Guo *et al*., 1999, Yang *et al*., 2000). In contrast, cry2 has been shown to be predominantly localised in the nucleus in the cells of both light- and dark-grown seedlings, although a proportion of the cry2 pool is localised in the cytoplasm (Cashmore *et al*., 1999, Guo *et al*., 1999, Kleiner *et al*., 1999).

The phototropins are the most recently characterized blue/UV-A light-absorbing photoreceptors in plants. The *Arabidopsis* phototropin family comprises two members, phot1 and phot2, showing close sequence similarity. The *PHOT* proteins each have two distinct domains, a C-terminal serine/threonine kinase domain and an N-terminal region which encodes two LOV (Light, Oxygen, Voltage) sub-domains, originally found in proteins acting as light

Abbreviations used in this paper: LOV, light, oxygen, voltage subdomains; R:FR, red: far-red ratio; UV, ultra-violet.

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sensors, oxygen sensors and voltage-gated potassium channel proteins (Huala *et al.*, 1997). The LOV domain peptides of both phot1 and phot2 have been shown to bind the chromophore flavin mononucleotide (FMN) (Christie *et al.,* 1999, Sakai *et al.*, 2001).

Higher plants contain multiple discrete phytochromes, the apoproteins of which are encoded by a small family of divergent genes (Sharrock and Quail 1989). In the model species *Arabidopsis thaliana*, five phytochromes (A-E) have been sequenced and characterized (Clack *et al.,* 1994). The protein products of the *PHYB* and *PHYD* genes share ~80% sequence similarity and these are slightly more related to PHYE than they are to PHYA or PHYC proteins. Phytochromes B, D and E are therefore believed to form a distinct subgroup of the *Arabidopsis* PHY family (Goosey *et al.*, 1997). All higher plant phytochromes are believed to exist as dimers of two identical ~120 kDa polypeptides. Each monomer is attached to a light-absorbing linear tetrapyrrole chromophore, phytochromobilin, via a thioether linkage to a conserved cysteine residue (Furuya and Song, 1994). Phytochromes can exist as either of two relatively stable isoforms: a R-absorbing Pr form, with an absorption maximum at about 660 nm and a FR- absorbing Pfr form, with an absorption maximum at about 730 nm. The Pr form of phytochrome is generally considered to be inactive and accumulates to relatively high levels in dark-grown tissues. Activity is acquired upon photo-conversion to the Pfr form. Photoconversion of Pfr to the Pr isoform upon absorption of FR wavelengths results in an equilibrium of the two forms under most irradiation conditions.

The mechanisms of photoreceptor signal transduction are far from being completely elucidated but are believed to involve both cytosolic and nuclear components. Phosphorylation and dephosphorylation are mechanisms widely used by organisms in signalling cascades. The presence of putative kinase domains within photoreceptor proteins has suggested a role for phosphorylation in light signalling. Phot1 was originally identified as a 120 kDa-membrane associated protein displaying blue light-mediated autophosphorylation (Reymond *et al.,* 1992). The light-dependent autophosphorylation of phot1 is believed to be involved in the early stages of phot1 signal transduction in phototropism (Christie *et al.,* 1998). The action of cry1 and cry2 has also been demonstrated to involve blue light-mediated autophosphorylation (Shalitin *et al.*, 2002, 2003). An *in vitro* assay using an insect cell system showed that cry1 was able to be phosphorylated in a blue light-dependent manner in the absence of an additional protein kinase (Shalitin *et al.*, 2003). Mutant alleles of *cry1* and *cry2* displaying no function were also found to lack phosphorylation. In addition, constitutive phosphorylation was observed in constitutively active C-terminal cry2 fusions (Shalitin *et al.*, 2002). Such data suggest a close association between the blue light-mediated phosphorylation of cry1 and cry2 and their respective functions.

The C-terminal domain of phytochromes contains a region of sequence with homology to histidine kinases, leading to suggestions that phytochrome may act as a light-regulated kinase (Yeh *et al.,* 1997). In addition to autophosphorylation, phyA and phyB also phosphorylate the protein PKS1 (PHYTOCHROME KINASE SUBSTRATE 1) in a light-dependent manner *in vitro* (Fankhauser *et al.*, 1999). The phosphorylation of PKS1 acts to negatively regulate phytochrome function, suggesting an important role for phytochrome kinase activity in light signalling (Fankhauser *et al.*, 1999). In addition, studies in *Arabidopsis* have revealed the binding of phyA Pfr to increase the phosphate exchange activity of nucleoside diphosphate 2 (NDPK2) *in vitro* (Choi *et al.*, 1999). Such studies suggest NDPK2 to be a positive signalling component of the phytochrome-mediated light-signal-transduction pathway in *Arabidopsis*.

Besides initiating signal transduction cascades, phytochromes can also interact directly with the cells transcriptional and posttranscriptional machinery to alter gene expression. The photo-conversion of phytochrome to the Pfr form has been demonstrated to trigger translocation of the photoreceptor to the nucleus (Sakamoto and Nagatani, 1996, Kircher *et al.*, 1999, Yamaguchi *et al.*, 1999). In the nucleus, Pfr can interact with a variety of basic helix-loop helix (bHLH) transcription factors such as PHYTOCHROME INTERACTING FACTOR 3 (PIF3) and control the expression of a number of target genes (Ni *et al.*, 1999, Martinez-Garcia *et al.*, 2000, Khanna *et al.*, 2004). The binding of phytochromes to bHLH transcription factors in the nucleus is believed to form an early signalling step in the de-etiolation of dark grown seedlings. The DNA sequence motif recognised by most bHLH transcription factors is termed the E-box, a hexameric sequence, CANNTG. In *Arabidopsis*, the most commonly recognised type of E-box is the sequence CACGTG, termed the G box (Toledo-Ortiz *et al.*, 2003).

Light also regulates photomorphogenesis via the specific targeting of proteins for ubiquitination and proteasome-mediated degradation. One of the key regulators of this process is the COP1 (constitutive photomorphogenesis 1) E3 ubiquitin protein ligase which acts downstream of both phytochromes and cryptochromes (Ang and Deng, 1994). In the dark, COP1 is associated with a nuclear-localised 12 subunit complex, the COP9 signalosome, involved in targeting proteins for degradation (for review see Wei and Deng, 2003). In the light, COP1 moves out of the nucleus allowing proteins involved in the positive regulation of photomorphogenesis, such as the transcriptional regulator HY5, to accumulate and photomorphogenesis to occur. In addition, the physical interaction of both phytochromes (Wang *et al.*, 2001, Seo *et al.*, 2004) and cryptochromes (Wang *et al.*, 2001, Yang *et al.,* 2000) with COP1 in a light-dependent manner is believed to repress COP1 activity through direct protein:protein interactions.

Light signals regulate the development of plants throughout their lifecycle. In addition to regulating the timing of seed germination and ensuing seedling establishment, photoreceptor action modulates the architectural form and reproductive strategy of plants. Through integrating light signals with other environmental cues, plants can predict changes in the seasonal environment and adjust their development accordingly.

Seed germination

The role of light signals in regulating seed germination is long established. Indeed, early observations showing the R/FR reversible promotion of lettuce seed germination were fundamental in establishing the Pr/Pfr model of phytochrome action (Borthwick *et al.*, 1952b). In natural light environments, the timing of seed germination is influenced by multiple factors. These include ambient temperature, water availability, the position of seeds in the soil profile, soil disturbance and the degree of vegetational shading. Seeds and dark-grown seedlings display three unique modes of phytochrome action, characterised by different fluence rate dependence and R/FR reversibility. These are the very low fluence response (VLFR), the low fluence response (LFR) and the

high irradiance response (HIR). Very low fluence responses are mediated by phyA and are initiated by fluences of light as low as 10^{-9} mol.m^{-2}. These responses are therefore saturated at very low concentrations of Pfr and do not show prototypical R/FR photoreversibility (Smith and Whitelam, 1990). In contrast to other family members, phyA displays extreme light lability and is subject to rapid proteolytic degradation in the Pfr form (Quail, 1994). Seeds that have imbibed water in darkness contain relatively high levels of phyA and consequently display extreme sensitivity to light. It has been estimated that these seeds would be induced to germinate by just a few milliseconds of daylight (Smith, 1982). The VLFR promotion of germination therefore allows seeds to take opportunistic advantage of very brief soil disturbances. Low fluence rate responses are mediated by phytochromes stable in the Pfr form, namely phyB,C,D and E. These responses generally require fluence rates between 0.1-100 μmol.m^{-2}.s^{-1} and are characterised by their robust R/FR reversibility. Studies using *Arabidopsis* mutants null for individual phytochromes revealed roles for both phyA and phyB in the R/FR reversible promotion of seed germination (Shinomura *et al*., 1994, 1996). The residual responsivity of *phyAphyB* double mutant seeds to R and FR pulses, however, suggested the participation of other phytochromes in this response (Poppe and Schäfer, 1997). The isolation of *Arabidopsis* mutants null for phyD (Aukerman *et al*., 1997) and phyE (Devlin *et al*., 1998) enabled the other phytochromes involved in the regulation of seed germination to be identified. Analysis of *phyAphyBphyD* and *phyAphyBphyE* triple mutant combinations uncovered a significant role for phyE in mediating R-induced germination responses (Hennig *et al*., 2002). Surprisingly, given the high sequence similarity between phyB and phyD (Clack *et al*., 1994), the additional absence of phyD did not further impair the germination of *phyAphyB* seeds (Hennig *et al*., 2002). An unexpected finding from this work was the novel discovery that phyE is required for germination responses in continuous FR (Hennig *et al*., 2002). Phytochrome A is generally regarded as the sole mediator of responses to prolonged FR, making the proposed role for phyE somewhat surprising. The possibility exists, however, that for germination responses in FR, the presence of phyE is required for a phyA-mediated response to occur.

Seedling establishment

Following seed germination, light signals act to direct and inhibit hypocotyl extension, whilst promoting the opening and expansion of cotyledons. The concomitant synthesis of chlorophyll, chloroplast development and opening of stomata enable plants to initiate photosynthetic activity and become photoautotrophic. Transfer of dark-grown seedlings to white light results in an inhibition of hypocotyl growth and the opening of cotyledons, a process termed "de-etiolation". The analysis of mutants deficient in multiple photoreceptors has enabled the contribution of each to be assessed under different wavelengths of light.

Cryptochromes and de-etiolation

The establishment of seedlings in natural light environments involves the action of both phytochromes and blue (UV-A) light photoreceptors. The isolation of mutants deficient in cryptochromes 1 and 2 (*cry1* and *cry2*) has revealed roles for these photoreceptors throughout seedling development. Originally designated *hy4*, an *Arabidopsis* mutant deficient in cry1 was isolated based on its long hypocotyl phenotype in blue light with no differences from wild type seedlings observed in R or FR (Koornneef *et al*., 1980., Ahmad *et al*., 1995, Lin *et al*., 1996). In addition to elongated hypocotyls, cry1-deficient seedlings also displayed smaller cotyledons and reduced anthocyanin levels in blue light when compared with wild types (Ahmad *et al.,* 1995, Jackson and Jenkins, 1995). Reductions in anthocyanin content were accompanied by decreases in the blue light-induced transcription of genes encoding enzymes early in the phenylpropanoid pathway, such as chalcone synthase (Ahmad *et al*., 1995, Jackson and Jenkins, 1995). The isolation of an *Arabidopsis* mutant deficient in cry2 and the construction of *CRY2* - overexpressing plants revealed roles for this photoreceptor in blue light signalling. Compared with wild type seedlings, mutants null at the *CRY2* locus display longer hypocotyls in blue light with concomitant reductions in cotyledon expansion (Lin *et al*., 1998). The same study revealed opposite phenotypes in *CRY2* overexpressing plants. Comparison of fluence rate response curves for hypocotyl inhibition revealed an interesting difference between the cry1 and cry2 photoreceptors. Mutants deficient in cry2 displayed loss of sensitivity to blue light at low (< 10 μmol.m^{-2}.s^{-1}) but not high fluence rates, whereas *cry1* mutants behaved oppositely (Lin *et al*., 1998). Expression studies revealed CRY2 protein to be rapidly down-regulated by blue light in an irradiance-dependent manner (Lin *et al*., 1998). Such observations provide a potential molecular mechanism to explain the loss of cry2 function at higher fluence rates. It is therefore possible that cry2 functions to enhance sensitivity to blue light signals during seedling de-etiolation.

Phototropins and phototropism

It is well established that plants respond to the direction of light (Briggs and Christie, 2002). The bending of plant stems towards or away from a light stimulus (termed phototropism) is primarily mediated by blue light detected by the phototropin family of photoreceptors. The identification of an *Arabidopsis* mutant impaired in hypocotyl phototropic curvature lead to the cloning and characterisation of the first phototropin gene (*PHOT1*). Originally designated *nph1* (non-phototropic hypocotyl), mutants failed to grow towards a low intensity blue light stimulus (Liscum and Briggs, 1995). Subsequent observations revealed *phot1* mutants to retain phototropic responsiveness to high irradiance blue light (Sakai *et al*., 2001). The involvement of a second phototropin, phot2, in this response was established following the isolation of a *phot1phot2* double mutant. Plants deficient in both phototropins displayed impaired phototropic responses at all irradiances (Sakai *et al*., 2001). Studies using *cry1cry2* double mutants revealed no impairment of phototropism, confirming a unique role for phototropins in mediating this response (Lascève *et al*., 1999).

Phytochromes and de-etiolation

The unique role of phyA in inhibiting hypocotyl elongation in prolonged FR was established through analysis of phyA-deficient mutants in a variety of species including *Arabidopsis* (Nagatani *et al*., 1993, Parks and Quail, 1993, Whitelam *et al*., 1993), tomato (Van Tuinen *et al*., 1995a) and rice (Takano *et al*., 2001). When

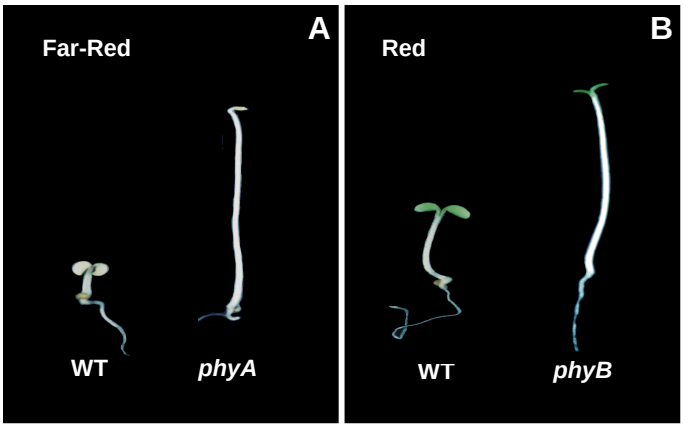

Fig. 1. Phenotypes of *Arabidopsis* phytochrome mutant seedlings. (A) *Wild-type and* phyA *mutant grown in continuous far-red.* **(B)** *Wild-type and* phyB *mutant grown in continuous red.*

grown in continuous FR, *Arabidopsis phyA* mutants display long hypocotyls and are unable to open and expand their cotyledons (Fig. 1A). These plants resemble wild type seedlings that have been grown in continuous darkness and are termed "etiolated". This striking phenotype currently forms the basis for screening mutant populations for lesions in phyA and phyA signalling.

Mutants deficient in phyB have been characterised in a variety of species including *Arabidopsis* (Koornneef *et al*., 1980, Somers *et al*., 1991), *Brassica rapa* (Devlin *et al*., 1992), cucumber (López-Juez *et al*., 1992), tomato (VanTuinen *et al*., 1995b), pea (Weller *et al*., 2000) and *Nicotiana plumbagnifolia* (Hudson *et al*., 1997). Analyses of these mutants have revealed a significant role for phyB in the de-etiolation of seedlings in R. Under these conditions, *phyB* null mutants display elongated hypocotyls and smaller cotyledons when compared to wild type controls (Fig. 1B). Such phenotypes are now universally used as the basis of genetic screens for mutants deficient in phyB and phyB signalling components. In *Arabidopsis* and tomato, it was revealed that mutants deficient in both phyA and phyB displayed longer hypocotyls than either monogenic mutant (Reed *et al*., 1994, Weller *et al*., 2000). Such observations provided early evidence of phyA action in R and established the redundant nature of phytochrome functions. Redundancy between phyA and phyB has also been reported in the R-mediated opening and expansion of cotyledons (Neff and Vanvolkenburgh, 1994, Reed *et al*., 1994, Neff and Chory, 1998). The creation of double, triple and quadruple mutants, deficient in multiple species of phytochrome, have since revealed that all five phytochrome family members promote cotyledon expansion in continuous R (Franklin *et al*., 2003a).

Mutants deficient in phyD were isolated as natural deletions in the Wassilewskija (Ws) ecotype (Aukerman *et al.,* 1997). Despite showing high sequence similarity to phyB, the role of phyD in R-mediated de-etiolation appears minor. When grown in continuous R, monogenic *phyD* mutants displayed marginally longer hypocotyls than plants containing an introgressed *PHYD* gene (Aukerman *et al.,* 1997). The lengths of *phyBphyD* double mutants were greater than the additive increases in both monogenic plants suggesting a synergistic relationship in the control of hypocotyl growth by these two phytochromes (Aukerman *et al.,* 1997). When grown in white light, *phyBphyD* double mutants displayed smaller cotyledons than either monogenic mutant, suggesting both photoreceptors are required for wild-type cotyledon size (Aukerman *et al.,* 1997). Although phytochromes B, D and E form a distinct subgroup within the *Arabidopsis* phytochrome family (Goosey *et al.,* 1997), the role of phyE in seedling de-etiolation appears negligible. When treated with R, FR or white light, etiolated *phyE* mutant seedlings display no obvious mutant phenotype (Devlin *et al.,* 1998).

The recent identification of mutants null at the *PHYC* locus has provided insights into the role of this phytochrome in seedling de-etiolation (Franklin *et al.,* 2003b, Monte *et al.,* 2003). When grown in continuous R, *phyC* mutants displayed elongated hypocotyls, suggesting a role for this phytochrome in modulating extension growth (Franklin *et al.,* 2003b, Monte *et al.,* 2003). The absence of an additive phenotype in a *phyB* mutant background presents the possibility that phyC may operate through modulating phyB function. Despite the relatively close phylogenetic relationship between *PHYA* and *PHYC*, no identifiable role was identified for phyC in FR sensing (Franklin *et al.,* 2003b, Monte *et al.,* 2003).

Development of the light-grown plant

The architectural form of plants is directed, in part, by light signals from the environment. Processes under photoreceptor control include the size, shape and angle of leaves, plant height and degree of axillary branching. The roles of individual photoreceptors in modulating plant architecture are complex and have been largely inferred from studies of loss-of-function mutants in *Arabidopsis*. In addition to performing unique regulatory functions, many photoreceptors operate redundantly, synergistically and in some cases, oppositely to other family members.

Leaf development

Light signals from unfiltered daylight serve to suppress the elongation of stems and petioles whilst promoting the expansion and development of leaves. Such adaptations serve to increase the surface area available for light capture and ultimately photosynthetic productivity. Developing leaves must adapt to fluctuating light levels. Periods of limiting light can reduce photosynthetic activity whereas exposure to excessive light can result in photooxidative damage to chloroplasts. Plants therefore possess adaptive strategies to deal with changes in light quantity. These include light-induced stomatal opening and chloroplast migration. Both are elicited by blue and UV-A light signals mediated through phototropin photoreceptors (Briggs and Christie 2002). Stomatal opening is induced by red light during photosynthetic activity. A separate role for blue light was established through measuring stomatal aperture against a background of saturating red light (Zeiger and Field, 1982). The involvement of phototropins in this response was confirmed using mutant analyses. Whereas single (*phot1, phot2*) mutants displayed increased stomatal aperture in response to blue light, the *phot1phot2* double mutant remained unresponsive (Kinoshita *et al*., 2001). Such observations suggest the blue light control of stomatal aperture to be regulated by phot1 and phot2 acting in a functionally redundant manner. In addition, the leaves of young *phot1phot2* double mutants grown in white light were observed to be smaller than those of wild-type plants and *phot* single mutants and curled downward (leaf epinasty),

suggesting a redundant role for phototropins in regulating leaf expansion (Sakamoto and Briggs, 2002).

At low light irradiances, chloroplasts display an "accumulation response", in which their cellular positioning is optimised for maximum light capture (Sakai *et al*., 2001). At high light irradiances, plants minimise photo-oxidative damage by re-positioning chloroplasts within the cell to maximise mutual shading. Such re-positioning acts to minimise light interception and is termed the "avoidance response" (Sakai *et al*., 2001). Analysis of *phot2* single mutants revealed an impairment in the chloroplast avoidance response to high irradiance unilateral blue light (100 $\mu mol.m^{-2}.s^{-1}$) (Kagawa *et al*., 2001, Jarillo *et al*., 2001). These studies also revealed light-dependent increases in *PHOT2* gene expression, suggesting this phototropin to predominate under high light conditions. Despite displaying a normal avoidance response to high light irradiance, *phot1* single mutants displayed impairments in the accumulation response to low light conditions (Kagawa and Wada, 2000).'The roles of each phototropin in blue light-induced chloroplast migration were clarified through studies using the *phot1phot2* double mutant. In these plants, both chloroplast migration responses were absent (Sakai *et al*., 2001). It can therefore be concluded that both phot1 and phot2 regulate chloroplast accumulation in low irradiance blue light. At higher light irradiances, however, phot2 initiates chloroplast avoidance responses, thus counteracting phot1 action.

In adult *Arabidopsis* plants, leaves are arranged in a compact rosette phenotype. Comparison of multiple phytochrome-deficient mutants revealed the rosette habit of *Arabidopsis* to be regulated by phytochromes A, B and E in a functionally redundant manner (Devlin *et al*., 1998). Indeed, this phenotype formed the basis of a screen from which the *phyE* mutant was isolated (Devlin *et al*., 1998). In these experiments, mutagenized *phyAphyB* double mutant seeds were germinated and examined for phenotypic abnormalities. A plant was identified which displayed elongated internodes between rosette leaves. Molecular characterisation revealed mutations at the *PHYA*, *PHYB* and *PHYE* loci (Devlin *et al*., 1998). The absence of this phenotype in any monogenic or double mutant combination confirmed the redundant nature of this regulation (Devlin *et al*., 1998). When grown in white light, phytochromes A and C act to suppress petiole elongation and promote leaf expansion. Elongated leaves were clearly visible in *phyC* mutants (Franklin *et al*., 2003b, Monte *et al*., 2003), whereas the role of phyA was only visible in a *phyBphyDphyE* null background (Franklin *et al*., 2003a). The latter phytochromes play an important role in determining plant architecture and are the sole mediators of shade avoidance responses in *Arabidopsis*.

R:FR ratio and shade avoidance

One of the most important environmental stimuli directing the development of plants in natural environments is the availability of light. When grown in close proximity to one another, constraints on photosynthetic productivity can lead to competition between individuals for this key resource. Plants have therefore evolved two principle adaptive strategies to enhance their survival in such conditions; shade tolerance and shade avoidance. Successful shade avoidance requires plants to detect the impending threat of shade an initiate avoidance responses before actual shading occurs (Ballaré *et al*., 1990). Plants perceive the presence of neighbouring vegetation as a reduction in the ratio of red to far-red wavelengths in the light reflected from, or transmitted through, green tissues. The R:FR ratio of daylight is typically around 1.15 and varies little with weather conditions (Smith, 1982). The photosynthetic pigments, chlorophylls and carotenoids, absorb light over most of the visible spectrum. Radiation in the FR region is, however, photosynthetically ineffective and very poorly absorbed. Daylight reflected from, or transmitted through, chlorophyllous vegetation is therefore relatively enriched in far-red wavelengths, typically displaying a R:FR ratio of between 0.09-0.7 (Smith, 1982). Changes in R:FR ratio are detected by plants as a change in the relative proportions of Pr and Pfr. Furthermore, the reduction in R:FR ratio is quantitatively related to the density and proximity of neighbouring vegetation (Smith and Whitelam, 1997).

The responses of plants to reduced R:FR ratio were initially characterised in the laboratory through supplementation of white fluorescent light with FR wavelengths (Morgan and Smith, 1976, 1978, 1980). Termed the "shade avoidance syndrome", these responses included multiple architectural changes and pronounced early flowering. The most striking response of plants to a reduction in R:FR is a marked acceleration of stem and petiole elongation, often at the expense of leaf and storage organ development (Fig. 2). Reductions in leaf area are often accompanied by significant decreases in chlorophyll content and, in dicotyledonous plants, reductions in leaf thickness and angle from the stem (leaf hyponasty) (McLaren and Smith, 1978, Smith and Whitelam 1997). In addition, increased apical dominance leads to reduced branching in dicots and reduced tillering in grasses (Casal *et al*., 1986). These adaptations are believed to elevate leaves towards unfiltered daylight, thus increasing the probability of light capture. Such adaptations have been assessed in a number of ecological investigations to confer high relative fitness in dense stands of plants (Schmitt, 1997).

The acceleration of elongation growth in response to reductions in R:FR ratio is extremely rapid. Using transducers and fibre optic light guides, Smith and colleagues were able to measure the extension rate of a single mustard internode. These studies revealed growth rate to increase five fold within 30 minutes of receiving supplementary FR (Morgan *et al*., 1980, Child and Smith, 1987). More recently, it has been demonstrated that a 2 hour reduction in R:FR ratio can result in a 30% increase in *Arabidopsis* hypocotyl length within 24 hours (Salter *et al*., 2003). This response was shown to be gated by the circadian clock with maximum elongation occurring following a low R:FR ratio treatment at subjective dusk (Salter *et al*., 2003). The growth of *Arabidopsis* hypocotyls is believed 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 seedlings natural endogenous rhythm of elongation growth. In contrast, an inhibition of growth was observed in seedlings treated with low R:FR at subjective dawn (Salter *et al*., 2003).

Unlike elongation responses, an acceleration of flowering is only observed following prolonged exposure to the low R:FR signal (Halliday *et al*., 1994). Temporary fluctuations in light quality are a common occurrence in natural environments. When subject to temporary shading, the ability to elongate quickly can

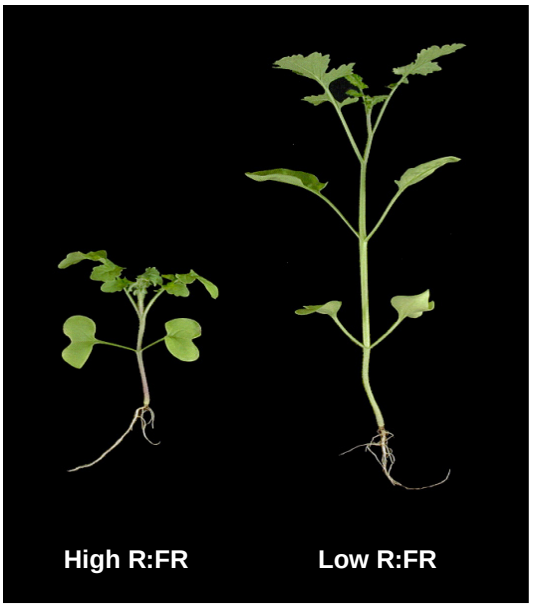

Fig. 2. Responses of Mustard (*Sinapis alba*) to a low red:far-red (R:FR) ratio. *Plants were grown under white light from fluorescent tubes providing equal photosynthetically active radiation (400-700 nm). The plant on the right received supplementary far red (FR) to reduce R:FR ratio.*

confer considerable selective advantage to plants. A rapid transition to flowering would, however, only prove advantageous if plants were unable to overtop competitors. Under these conditions, a precocious transition to reproductive development would promote seed and increase the likelihood of survival under conditions of intense competition (Botto and Smith, 2002, Donohue *et al.*, 2001).

The R/FR photo-reversibility of phytochromes facilitates accurate detection of ambient light quality. In particular, reduction of phyB Pfr in low R:FR ratio light can initiate the shade avoidance syndrome. When grown in white light (ie. high R:FR ratio), phyB-deficient mutants in a variety of plant species display phenotypic traits often referred to as "constitutive shade avoidance". These include increased stem and petiole elongation, decreased leaf size, reduced chlorophyll content and early flowering (Somers *et al.*, 1991, Devlin *et al.*, 1992, López-Juez *et al.*, 1992, Reed *et al.*, 1993). Such observations have confirmed a dominant role for phyB in mediating shade avoidance responses. The retention of responses to reduced R:FR in a *phyB* null mutant, however, suggested the involvement of additional phytochromes (Whitelam and Smith, 1991). The supplementation of white light with FR wavelengths at the end of the day (EOD-FR treatments) is a procedure known to mimic the effects of growth in low R:FR ratio conditions. Using this approach, residual shade avoidance responses were observed in a variety of *phyB* null mutants from multiple species (Robson *et al.*, 1996, Halliday *et al.*, 1994, Devlin *et al.*, 1996). The role of phyD in mediating responses to low R:FR ratio was confirmed through comparison of a *phyBphyD* double mutant with its monogenic parents. Mutants deficient in phyD displayed wild-type responses to low R:FR ratio and EOD FR treatments (Aukerman *et al.*, 1997, Devlin *et al.*, 1999). Analysis of *phyBphyD* double mutants, however, revealed greater petiole elongation and earlier flowering than *phyB* null plants grown in high R:FR (Aukerman *et al.*, 1997, Devlin *et al.*, 1999). Such observations established a redundant role for phyD in mediating shade avoidance, a proposal substantiated by their sequence similarity and similar patterns of gene expression (Mathews and Sharrock, 1997, Goosey *et al.*, 1997). These studies also revealed *phyAphyBphyD* triple mutants to retain an early flowering response to EOD-FR treatment, indicating the participation of another phytochrome in this response (Devlin *et al.*, 1999). The subsequent creation of *phyBphyDphyE* triple and *phyAphyBphyDphyE* quadruple mutants confirmed phytochromes B, D and E to be the sole mediators of shade avoidance responses (Franklin *et al.*, 2003a). These plants displayed no response to low R:FR ratio or EOD-FR treatments, thereby excluding a role for phyC in the regulation of shade avoidance. This notion was supported by analyses of a *phyC* null mutant which showed no impairment of R:FR ratio perception, alone, or in combination with other phytochrome mutations (Franklin *et al.*, 2003b).

In FR-rich light environments, the action of phyA in the HIR response mode acts to inhibit hypocotyl extension, thus antagonising shade avoidance. Observations that *phyA* mutant seedlings displayed longer hypocotyls than wild-type controls when grown in continuous low R:FR ratio supported this proposal (Johnson *et al.*, 1994). More recent investigations have revealed the phyA-mediated inhibition of hypocotyl extension in low R:FR ratio to be gated by the circadian clock. Maximum inhibition occurred at subjective dawn, a time when phyA levels are highest (Salter *et al.*, 2003). The importance of phyA in antagonising elongation responses to reduced R:FR ratio was illustrated by Yanovsky and colleagues who demonstrated conditional seedling lethality of the *phyA* mutation (Yanovsky *et al.*, 1995). When grown in the field under dense vegetational shade, many *phyA* seedlings displayed extreme hypocotyl elongation and died. The over-expression of *PHYA* is therefore a feasible strategy to curtail the unwanted elongation growth of densely planted crops. This approach has been successfully implemented in transgenic tobacco, which displayed a greater harvest index than wild type plants at high planting densities (Robson *et al.*, 1996).

Despite elucidation of the phytochromes involved, relatively little is known about the signalling components involved in transducing the R:FR ratio signal. The most frequently cited examples of genes whose expression regulated by R:FR ratio are the homeodomain ZIP transcription factors *ATHB-2* (previously *HAT4*) and *ATHB-4*. Both these genes show significant increases in transcript levels upon transfer to low R:FR ratio (Carabelli *et al.*, 1993, 1996). Analysis of phytochrome-deficient mutants has revealed *ATHB-2* expression to be regulated redundantly by phyB and phyE (Franklin *et al.,* 2003a). The possible involvement of ATHB-2 in shade avoidance was proposed following observations that transgenic plants over-expressing *ATHB-2* displayed phenotypes similar to wild-type plants grown in low R:FR ratio (Schena and Davis, 1992, Steindler *et al.*, 1999). These findings were supported by studies showing transgenic plants with decreased levels of *ATHB-2* to behave oppositely (Carabelli *et al.*, 1996, Steindler *et al.*, 1999). More recently, microarray studies in *Arabidopsis* have revealed two genes, *PIL1* (*PIF3-LIKE 1*) and *PIL2* (*PIF3-LIKE 2*), to display rapid and significant increases in transcript upon transfer of plants to low R:FR ratio (Salter *et al.*, 2003). Both genes encode basic helix-loop-helix (bHLH) transcription factors with significant protein sequence similarity to the

phytochrome interacting factor PIF3 (Ni *et al.*, 1998). The de-repression of *PIL1* is extremely rapid, with significant increases in transcript being recorded within 8 minutes of low R:FR ratio treatment. In contrast, exposures of up to 2 hours were required for detectable increases in *PIL2* transcript (Salter *et al.*, 2003). The de-repression of both genes was also shown to be gated by the circadian clock, with maximum de-repression occurring at subjective dawn. Mutants deficient in PIL1 displayed an attenuated hypocotyl elongation response to transient reductions in low R:FR ratio, confirming a role for this protein in rapid shade avoidance (Salter *et al.*, 2003).

In addition to reductions in R:FR ratio, vegetational shading can also limit the total amount of photosynthetically active radiation (PAR) reaching a plant. It is therefore not surprising that, in addition to R:FR ratio signals, plants monitor the amount of blue light in their ambient environment. Reductions in both PAR and blue light have been shown to initiate shade avoidance responses in both cucumber hypocotyls (Balláre *et al.*, 1991) and tobacco stems (Casal and Sánchez, 1994). Studies using transgenic tobacco, insensitive to the plant hormone ethylene, revealed delayed shade avoidance responses to neighbouring vegetation (Pierik *et al.*, 2004a). The behaviour of transgenic plants to reductions in R:FR ratio was, however, similar to wild-type controls. Further investigation revealed the delayed shade avoidance phenotypes observed to result from insensitivity to reduced fluence rates of blue light (Pierik *et al.*, 2004a). Such findings confirm the importance of blue light signals in shade avoidance and suggest ethylene to be an important regulatory component in these responses (Pierik *et al.*, 2004a). Exposure to increasing concentrations of ethylene has been shown to initiate shade avoidance responses in wild-type tobacco plants (Pierik *et al.*, 2003, 2004b). Furthermore, production of the hormone ethylene was significantly increased in these plants in response to low R:FR treatment (Pierik *et al.,* 2004b). Such studies suggest that, in addition to light signals, increases in atmospheric ethylene may signal to plants the proximity of neighbouring vegetation.

Photoperiodic regulation of flowering

In addition to changes in R:FR ratio, the timing of reproductive development can be influenced by changes in daylength, or photoperiod. Sensitivity to the timing of light and darkness, termed photoperiodism, can provide a reliable indicator of seasonal changes. In photoperiodically sensitive species, the onset of sexual or vegetative reproduction is governed by the relationship between the daylength received and a critical or threshold daylength (Thomas and Vince Prue 1997). Plants in which flowering is accelerated by short days (Short-Day-Plants, SDP) generally flower in the autumn before the adverse temperatures of winter. Plants in which flowering is accelerated by long days (Long-Day-Plants, LDP) generally flower in the favourable climate of late spring. Daylength measurement involves the integration of temporal information, provided by the circadian oscillator, with light/dark discrimination, provided by photoreceptors. The timing of reproductive development in SDP's is dependent on the length of the dark rather than the light period (Thomas 1991). Two common experimental approaches for studying the regulation of floral initiation are manipulation of daylength using day extension and "night break" treatments. In day extension experiments, light of low fluence rate is applied to the end of a short-day photoperiod. This procedure enables manipulation of daylength without significant alterations in PAR. In night break experiments, light exposure is given in the middle of a long night, thus mimicking long-day conditions. A night break treatment given during the perceived night period can therefore prevent flowering in SDP (Borthwick *et al.*, 1952a).

Observations that *phyA* mutants of *Arabidopsis* (a LDP) flowered later than wild-type plants in long days suggested phyA to function as a promoter of flowering. The reduced sensitivity of *phyA* mutants to night breaks (Reed *et al.*, 1994) and day extensions (Johnson *et al.*, 1994, Neff and Chory, 1998) provided support for this notion. Similar responses were observed in the LDP pea, whereby phyA deficiency resulted in reduced photoperiodism and an inability to detect day extensions (Weller *et al.*, 1997). Phytochrome B is believed to be an inhibitor of flowering. Early flowering and decreased photoperiodic sensitivity were observed in phyB-deficient mutants of *Arabidopsis* (Goto *et al.*, 1991), pea (Weller and Reid, 1993) and the SDP Sorghum (Childs *et al.*, 1997). In apparent contradiction to these findings, an early flowering phenotype was observed in transgenic *Arabidopsis* plants over-expressing *PHYB* (Bagnall *et al.*, 1995).

An early flowering phenotype was reported in Columbia *phyC-2* mutants grown in short days, suggesting a role for phyC in inhibiting flowering under these conditions (Monte *et al.*, 2003). No effect of the *phyC* mutation was observed in a *phyB* null background, suggesting phyC function to require the presence of phyB (Monte *et al.*, 2003). An early flowering response was not, however, observed in *phyC-1* mutants in the Ws ecotype (Franklin *et al.*, 2003b). These differences may represent natural variation between Columbia and Ws accessions. Alternatively, the additional deficiency of phyD in Ws plants may contribute to this discrepancy.

The inductive effect of blue light on floral initiation in *Arabidopsis* suggested the involvement of blue light absorbing photoreceptors (Mozely and Thomas, 1995). A role for cry1 was proposed based on observations that some *cry1* alleles flowered later than wild-type plants in short days (Bagnall *et al.*, 1996, Mozely and Thomas, 1995). Analyses of *cry2* alleles have implicated a predominant role for this photoreceptor in perception of long day photoperiods (Guo *et al.*, 1998). Under long day conditions, *cry2* mutants flowered significantly later than wild-type plants (Koornneef *et al.*, 1991, Guo *et al.*, 1998). Transcript levels of the floral activator *CONSTANS* (*CO*) were significantly reduced in *cry2* mutants grown in long day photoperiods, suggesting cry2 to function as a positive regulator of *CO* (Guo *et al.*, 1998). The precise role of photoreceptors in the photoperiodic regulation of flowering was established as a "co-incidence model" of light and *CO* expression (Yanovsky and Kay, 2002). These studies revealed *CO* expression to be gated by the circadian clock with high daytime levels observed only in long days. The authors propose that the co-incidence of light signals (perceived through cry2 or phyA) with elevated levels of *CO* transcript lead to the activation of expression of the floral promoter *FLOWERING LOCUS T* (*FT*) and ultimately flowering.

The late flowering response of *cry2* mutants in white light was phenocopied by growth in continuous red and blue wavelengths, but not by red or blue light alone (Guo *et al.,* 1998). The authors propose that phyB mediates the red light-inhibition of flowering,

whereas blue light acts to inhibit phyB function. The late flowering phenotype of *cry1cry2* double mutants grown in monochromatic blue light revealed additional redundant roles for these photoreceptors in a phyB-independent promotion of flowering (Mockler *et al.,* 1999). Unlike other family members, phyA displays significant activity in continuous blue light (Whitelam *et al*., 1993, Neff and Chory, 1998). Under these conditions, *cry1*, *cry2* and *phyA* mutants display similar flowering responses to wild-type plants (Mockler *et al*., 2003). Late flowering was, however, observed in all double mutant combinations, implicating redundancy of function between these photoreceptors in mediating the direct blue light promotion of flowering (Mockler *et al*., 2003).

Crosstalk in photoreceptor signalling

Crosstalk between red and blue light sensing photoreceptors is not restricted to the regulation of flowering. Indeed, integration of red and blue light signals occurs at all stages of plant development. Although the exact nature of co-action has yet to be elucidated, it is accepted that blue light-mediated de-etiolation involves the interaction of both phytochrome and cryptochrome signalling (Yanovsky *et al*., 1995, Ahmad and Cashmore 1997, Casal and Mazzella, 1998). Comparisons of mutants deficient in multiple combinations of phyA, phyB and cry1 revealed numerous genetic interactions between these photoreceptors during seedling development (Neff and Chory, 1998, Casal and Mazzella, 1998). Physical interactions have been demonstrated between CRY1 and PHYA proteins *in vitro* (Ahmad *et al.,* 1998) and between cry2 and phyB photoreceptors *in vivo* (Más *et al*., 2000). In the latter study, functional interactions were also observed in the regulation of hypocotyl elongation, flowering time and input to the circadian clock (Más *et al*., 2000). Mutants deficient in cry2 displayed a longer period length in *CAB2*:*LUCIFERASE* gene expression in white light, a phenotype not observed in red light and severely attenuated in blue light. Such observations suggest cry2 function to depend on the activation of phytochromes. This notion was supported by observations that supplementation of white light with FR wavelengths could abolish the late flowering phenotype of *cry2* mutants (Más *et al*., 2000). It is, however, possible that removal of phytochrome Pfr over-rides the cry2 regulation of flowering in a separate pathway mediated by light quality. In addition, fluorescence resonance energy transfer (FRET) microscopy revealed phyB and cry2 to form light-dependent nuclear speckles. The translocation of phyB to the nucleus in red light is well established (Sakamoto and Nagatani, 1996, Yamaguchi *et al*., 1999, Kircher *et al*., 1999) and suggests that the cellular compartmentalization of photoreceptors may be important in mediating light-induced physiological responses.

Phytochromes C and D have also been reported to show functional interactions with cryptochromes. A role for phyC in blue light sensing was proposed following observations that *phyC* mutants displayed long hypocotyls in low fluence rates of blue light (Franklin *et al*., 2003b). Under these conditions, cry2 function has been shown to predominate in the regulation of hypocotyl extension (Lin *et al*., 1998). The hyposensitivity of *phyC* mutants to low fluence rates of blue light therefore suggests a possible functional interaction between phyC and cry2 (Franklin *et al*., 2003b). A functional interaction between phyD and cryptochrome was reported following observations that the red light mediated inhibition of hypocotyl elongation following a white light pre-treatment required the presence of either phyD or cry1 (Hennig *et al.,* 1999).

Integration of light signals with other environmental stimuli

In addition to interactions between photoreceptors, plants integrate light signals with other environmental stimuli to produce a coordinated response to environmental changes. The integration of light and gravity signals enables plants to orientate themselves within the soil and adjust their architecture for optimum photosynthetic activity (Hangarter 1997). Gravity provides a constant and unidirectional signal to developing plants which is integrated with light signals from phytochrome and phototropin photoreceptors. In white and blue light, *Arabidopsis* roots display negative phototropism, mediated by phototropins (Okada and Shimura, 1992, Briggs and Christie, 2002). In contrast, red light has been observed to induce a weak positive phototropism response in roots (Ruppel *et al*., 2001, Kiss *et al*., 2003). Mutant analyses revealed significant roles for phytochromes A and B in mediating this response (Kiss *et al*., 2003). In addition to directing the growth of shoots and roots through the soil, gravity signals can also regulate the orientation of multiple plant organs. A red light pre-treatment, mediated by phytochromes A and B, has been demonstrated to “enhance” phototropic curvature of *Arabidopsis* hypocotyls in blue light (Parks *et al*., 1996, Janoudi *et al*., 1997a,b). This appears to be a discrete response and is not related to phytochrome-mediated agravitropism, regulated by phyA and phyB (Liscum and Hangarter 1993, Robson and Smith, 1996).

The integration of light and temperature signals provides plants with important seasonal information. The promotion of germination (stratification) or flowering (vernalization) following a period of cold treatment can synchronize physiological processes with favourable environmental conditions, thus conferring considerable selective advantage. Periods of cold temperature and reduced daylength provide plants with a reliable indicator of seasonal progression and are important environmental cues regulating the transition from vegetative to reproductive development (Simpson and Dean, 2002). Mutants of *Arabidopsis* displaying a delayed flowering response have been grouped into three independent promotory pathways. These are the long-day pathway, the autonomous pathway and the gibberellic acid (GA)-dependent pathway (Koornneef *et al*., 1998). More recently, a separate light quality pathway has been suggested (Cérdan and Chory, 2003, Halliday *et al*., 2003). The vernalization response acts similarly to the autonomous pathway to reduce transcript levels of the floral repressor *FLC* and requires a nuclear localised protein VRN2 (Michaels and Amasino, 1999, Gendall *et al*., 2001). The requirement for vernalization is conferred by dominant alleles of the *FRI* gene, the product of which promotes *FLC* accumulation (Johanson *et al*., 2000). Floral integrators such as *FT* and *SOC1* have been shown to act downstream of *FLC* (Rouse *et al*., 2002). Vernalization is a quantitative response with increasing periods of low temperature resulting in progressively earlier flowering. Assays investigating the DNaseI sensitivity of *FLC* revealed altered chromatin organisation in cold treated plants (Gendall *et al*., 2001). More recently, vernalization has been shown to involve epigenetic silencing of *FLC* by histone

methylation (Bastow *et al*., 2004, Sung and Amasino, 2004). In addition to vernalization, a novel thermosensory pathway controlling flowering time has been identified in *Arabidopsis* (Blázquez *et al*., 2003, Halliday *et al*., 2003). Growth of wild-type plants at reduced temperatures (16ºC) resulted in significantly delayed flowering, a response exaggerated in *cry2* mutants (Blázquez *et al*., 2003). An absence of this response was observed in the autonomous pathway mutants, *fca-1* and *fve-1* suggesting the possible involvement of these proteins.

Growth of plants at 16ºC also abolished the previously characteristic early flowering phenotype of *phyB* mutants, suggesting complex crosstalk between light and temperature signalling mechanisms (Halliday *et al*., 2003). These plants retained elongation phenotypes characteristic of the shade avoidance syndrome, indicating no general impairment of phytochrome function at reduced temperatures. The early flowering response at 16ºC was shown to correlate with elevated levels of the floral promoter *FT*, signifying the existence of discrete pathways controlling flowering and elongation responses to shade (Halliday *et al*., 2003). Analysis of mutants deficient in multiple phytochromes has revealed more prominent roles for phyD and phyE in regulating flowering at cooler temperatures (Halliday and Whitelam, 2003). These studies also revealed the elongated internode phenotype of the *phyAphyBphyE* triple mutant to require higher growth temperatures. When grown at 16ºC, these plants displayed a normal rosette habit. It is therefore possible that our current understanding of phytochrome functions has been determined, in part, by the temperature at which plants were grown. Many *Arabidopsis* accessions grow throughout the northern hemisphere and would subject to mean monthly temperatures below 16ºC for much of the year. A complete characterisation of phytochrome responses at different ambient growth temperatures should therefore provide a more refined picture of phytochrome functions in natural light environments.

Conclusion

In conclusion, the use of photoreceptor mutants has proved invaluable in the elucidation of photoreceptor functions. In addition to redundant interactions between family members, numerous physical and functional interactions occur between red and blue light sensing systems. The construction of a *phyAphyBphyCphyDphyE* quintuple null mutant should ultimately enable the question of whether blue light signalling can operate completely independently of phytochromes to be addressed. The integration of light signals with temperature and gravity sensing mechanisms confers significant adaptive plasticity to plants growing in natural communities, enabling co-ordinated physiological responses to the ambient surroundings and anticipation of seasonal changes. Advances in molecular technology and judicious experimental design should hopefully yield the sites of signal crosstalk and the molecular mechanisms involved.

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