Photomorphogenesis and Photoperiodism in Plants

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19.1 Introduction

It has long been observed that light affects the way plants grow. Effects of light can be observed on processes and phenomena throughout the plant life cycle, including seed germination, apical hook opening, stem elongation, leaf expansion, the synthesis of photosynthetic and protective pigments, stomatal regulation, lateral branching, bud dormancy and flowering. The vast majority of these effects are unrelated to the use of light for photosynthesis and are mediated through a specialised system of photoreceptors that informs the plant about its surroundings and directs it to develop appropriately.

Photomorphogenesis is a general term encompassing all responses to light that affect plant form. Two specific classes of photomorphogenic response are sometimes distinguished. *Phototropic* responses involve the reorientation of plant organs with respect to an asymmetry in the incident light, as in the case of shoot tips bending to grow towards the light. *Photoperiodic* responses are those in which various aspects of development are modified in response to changes in the daily light/dark cycle and involve a circadian timing mechanism. Developmental features commonly subject to photoperiodic control include flowering, bud dormancy and leaf senescence.

This chapter will give an overview of our current knowledge about the way in which these different responses are achieved. We will discuss the discovery and nature of the photoreceptors involved in these phenomena, their physiological roles as determined in the laboratory and their possible significance in the natural environment. Although lower plants also show clear photomorphogenic responses, they have in general been less intensively studied, and we will restrict this discussion to higher plants.

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19.2 Photomorphogenetic Photoreceptors

As with other photobiological responses, an initial step in the investigation of photomorphogenic responses was the determination of action spectra. Early measurements identified the blue (BL), red (R) and far-red (FR) regions of the spectrum as being particularly important for the control of plant growth (e.g. Went 1941; Parker et al. 1949) and formed the point of departure in the search for specific photoreceptor pigments for light in these wavebands. Relatively rapid progress was made in biochemical characterisation of the photoreceptor responsible for R and FR responses (Sage 1992). In contrast, progress towards identification of a specific BL photoreceptor was limited due to the large number of different BL-absorbing compounds in the plant with the potential to serve as a photoreceptor chromophore and to the lack of a distinctive photophysiological assay.

However, the advent of molecular genetic approach from around 1990 brought rapid developments in our understanding of the nature, diversity and functions of the photoreceptor pigments involved in informational light sensing. Five classes of higher plant photoreceptors have now been characterised in detail; the *phytochrome* family of R- and FR-absorbing photoreceptors, three different photoreceptor families mediating responses in the BL and UV-A regions of the spectrum (*cryptochrome*, *phototropin* and *ZTL/FKF1* families) and the UV-B photoreceptor UVR8 (Fig. 19.1). We will discuss each of these in turn.

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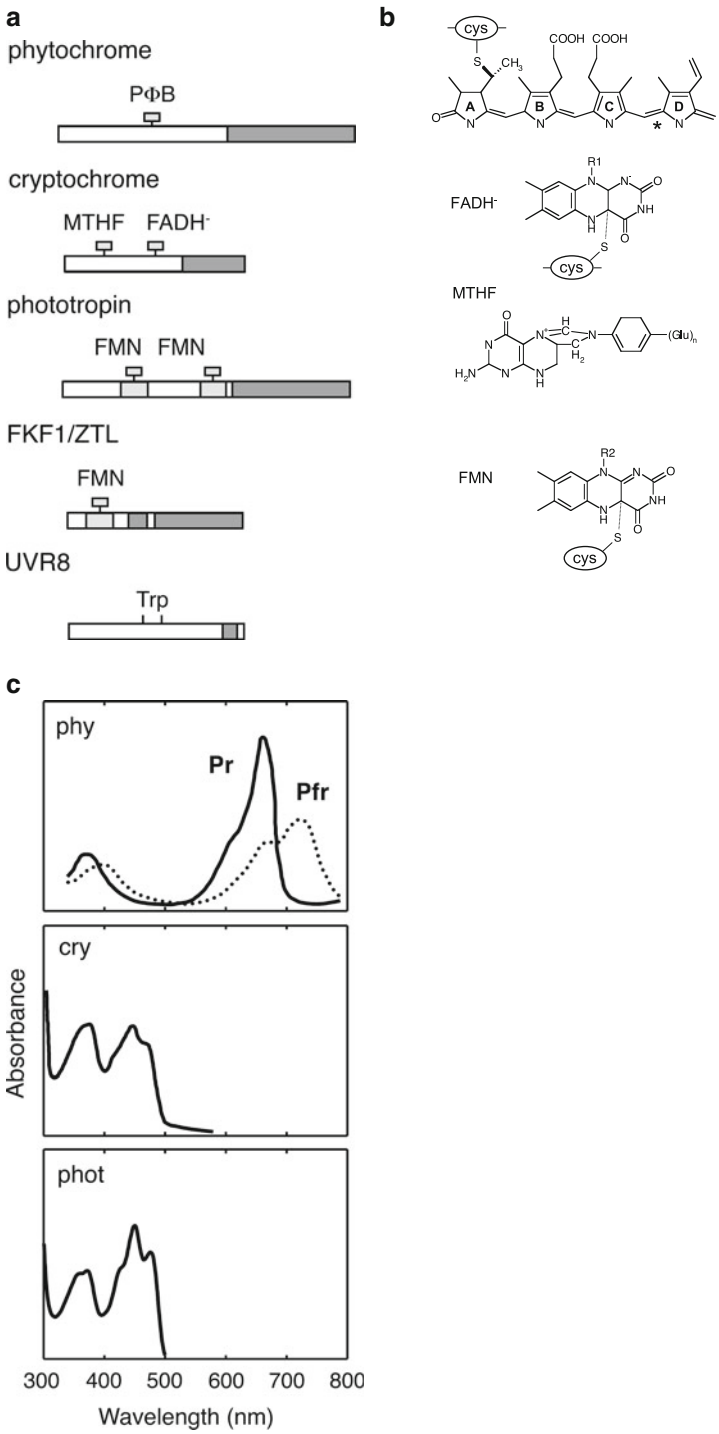

Fig. 19.1 Characteristics of plant photoreceptors. (**a**) Illustrates protein domain structures for the five classes of photoreceptor proteins. (**b**) Shows the structures and approximate attachment sites of chromophores for each class of photoreceptor, except UVR8. The asterix indicates the double bond involved in photoisomerization of the phytochrome chromophore. (**c**) Shows *in vitro* absorption spectra for phytochrome, cryptochrome and phototropin redrawn from Butler et al. (1964), Lin et al. (1995) and Christie et al (1999)

19.2.1 Phytochromes

19.2.1.1 Isolation

The main impetus in the early search for photoreceptors came from observations that the inductive effects of R on several aspects of plant development could be reversed by irradiation with FR. The fact that this R/FR reversibility occurred for diverse responses suggested that it might be a property of a single photoreceptor (Withrow et al. 1957). This was proven by the purification of a protein that exhibited R-/FR-reversible absorption changes. The protein was named *phytochrome*, a name derived from the Greek words for *plant* and *colour*. The two forms of phytochrome are characterised by absorption peaks at around 660 and 730 nm and are referred to as Pr and Pfr, respectively (Fig. 19.1). Both Pr and Pfr also have secondary absorption peaks in the BL region of the spectrum but

can to some extent absorb light across the visible and near UV spectrum. These two forms of phytochrome can be repeatedly interconverted by light pulses, and continuous light establishes a dynamic equilibrium between them that depends on the composition of the light.

19.2.1.2 Genes and Gene Family

The first phytochrome-encoding gene was identified from oat seedlings in 1984 by expression screening (Hershey et al. 1984), and phytochrome genes have been subsequently identified in many other flowering plants, as well as gymnosperms, ferns, mosses and algae (Mathews 2006). Phytochrome-related sequences have also been found in a wide range of microbes, including cyanobacteria, fungi and diatoms, suggesting a very ancient origin (Kehoe and Grossman 1996; Davis et al. 1999; Karniol et al. 2005). In higher plants, phytochromes are encoded by a small gene family. Three ancient branches, phyA, phyB and phyC, date back to the origin of flowering plants and possibly as far back as the origin of seed plants (Mathews 2010). Within angiosperms an additional duplication within the phyB lineage giving rise to phyE seems to be relatively ancient and widespread, and independent duplications within the phyA and phyB subfamilies have occurred within various taxa (Sharrock and Mathews 2006). In other cases such as poplar and some legumes, the phyC and phyE lineages subsequently appear to have been lost (Howe et al. 1998; Platten et al. 2005a). Nevertheless, the control of photomorphogenesis appears to be dominated by phyA and phyB in most species that have been studied in detail, and it is possible that additional phytochromes merely refine this basic programme.

19.2.1.3 Gene/Protein Structure

The generic phytochrome apoprotein has a molecular mass of around 125 kDa and consists of two domains; an N-terminal domain of 75 kDa that binds the chromophore and a C-terminal domain of 55 kDa that consists of two regions with homology to histidine kinases (Fig. 19.1) (Rockwell et al. 2006). The first of these C-terminal regions contains two PAS domains, which are implicated in protein-protein interactions. This region also contains a small domain that is essential for the regulatory activity of the molecule. Gene and protein structure are in general highly conserved across the phytochrome family, with the most notable difference being small poorly conserved N- and C-terminal extensions in phyB-type phytochromes (Sharrock and Mathews 2006). Phytochromes are synthesised in cytosol in the red-light-absorbing (Pr) configuration and form dimers in vivo. Deletion and point mutation studies have given some indication of areas of importance for determination of the absorption spectrum, photochromicity, dimerisation and signal transduction for both phyA and phyB (Rockwell et al. 2006).

19.2.1.4 Chromophore

The phytochrome chromophore, phytochromobilin (PΦB), is an open-chain bilitriene (Fig. 19.1), similar to the chromophore for the photosynthetic pigment C-phycocyanin in cyanobacteria. Feeding studies combined with analysis of chromophore-deficient mutants have shown that phytochromobilin is formed in plastids by a pathway which branches from the pathway for chlorophyll synthesis with the chelation of Fe^{2+} rather than Mg^{2+} to protoporphyrin IX (Rockwell et al. 2006; Davis 2006). Heme is then oxygenised to biliverdin resulting in the opening of the tetrapyrrole ring. This is followed by reduction of the A-ring to form PΦB. Free PΦB assembles autocatalytically to the phytochrome apoprotein and attaches at its C3 position to a cysteine residue in the middle of the N-terminal domain via a thioether linkage (Rockwell et al. 2006). Photoreversibility of the phytochrome holoprotein derives from isomerisation of bound PΦB about the double bond between rings C and D. It is worth noting that the absorption peaks of the Pr and Pfr are red shifted 35 and 100 nm, respectively, relative to that of free phytochromobilin conformers. This illustrates the importance of the protein environment for the light-absorbing properties of the chromophore and hence for the spectral characteristics of the photoreceptor. PΦB-deficient mutants have been isolated in a range of species and shown to carry mutations in structural genes for enzymes in PΦB biosynthesis (Muramoto et al. 1999; Kohchi et al. 2001). As a consequence of PΦB deficiency, these mutants have reduced levels of spectrally active phytochrome and exhibit strong defects in responses to light that are attributable to reduced activity of multiple members of the phytochrome family (Parks and Quail 1991; Weller et al. 1997b). All *Arabidopsis* phy apoproteins can assemble with PΦB in vitro (Eichenberg et al. 2000), and it is assumed that all higher plant phytochromes utilise PΦB as their sole chromophore in vivo. Some lower plant phytochromes may use a related bilin phycocyanobilin (PCB), and microbial phy also utilise a wider range of chromophores including biliverdin (bacteria) and PCB (cyanobacteria) (Rockwell and Lagarias 2010; Ulijasz and Vierstra 2011).

19.2.2 Cryptochromes

The contribution of a BL-specific photoreceptor system to de-etiolation was first inferred from observations that BL could promote de-etiolation, even in plants grown under continuous red light (i.e. under conditions which are saturating for phytochrome activity). In addition, mutants strongly deficient in phytochrome chromophore synthesis (and hence in the activities of all phytochromes) were shown to retain substantial responsiveness to BL (Briggs 2006). The unidentified BL photoreceptor was often referred to as *cryptochrome*,

from the Greek words for *hidden* and *colour*, reflecting its elusive nature. The primary BL photoreceptor in de-etiolation was finally identified in 1994, after cloning of the defective gene in an *Arabidopsis* mutant (*hy4*) specifically impaired in de-etiolation under BL (Ahmad and Cashmore 1994). This photoreceptor is now known as cryptochrome 1 (cry1). A second member of the cryptochrome family, cryptochrome 2 (cry2), was identified by its homology to cry1 (Lin et al. 1998). As in the case of the phytochromes, these two cryptochrome subfamilies have undergone independent duplication in certain taxa (Perrotta et al. 2000; Platten et al. 2005a; Hirose et al. 2006).

The CRY1 and CRY2 apoproteins are around 75 kDa in molecular mass and have two distinct parts (Fig. 19.1). The N-terminal half shows similarity to enzymes called photolyases, which are activated by BL and UV light to repair certain kinds of damage to DNA. In contrast, the C-terminal halves of cry1 and cry2 show only a very low degree of similarity to each other and to other known proteins. When expressed in *E. coli*, the photolyase-like domain binds the same two chromophores as photolyases (Fig. 19.1) – a flavin (flavin adenine dinucleotide) and a pterin (methenyltetrahydrofolate) (Lin et al. 1995; Malhotra et al. 1995) – although it has yet to be confirmed that the latter chromophore is utilised in planta. It has been speculated that the pterin chromophore may serve as a kind of antenna and may predominantly determine the UV-A/BL-absorbing properties of the molecule, while the flavin chromophore may be essential to the initial signalling reaction (Chaves et al. 2011). The FAD chromophore is thought to undergo a light-driven redox cycle between the oxidised form, which absorbs BL most effectively, and a reduced form, which characteristically absorbs green light (GL) (Liu et al. 2011). This interpretation is consistent with observations that GL can antagonise some cryptochrome-dependent responses to BL (Chaves et al. 2011).

19.2.3 Phototropin

Despite the substantial problems encountered in the biochemical search for a BL photoreceptor, this approach did prove successful in the identification of the photoreceptor for BL-induced phototropism. Work in the lab of Winslow Briggs identified a 120 kDa membrane protein that underwent autophosphorylation after irradiation with BL. The action spectrum and various kinetic aspects of this reaction showed a close correlation to those for phototropism, suggesting that the protein itself might function as a photoreceptor (Briggs 2006). The physiological significance of the protein was confirmed by its absence in aphototropic *nph1* mutants of *Arabidopsis* (Liscum and Briggs 1995), and cloning of the *NPH1* gene in 1997 subsequently revealed a protein with clear characteristics of a BL receptor (Huala et al. 1997). This protein is now known as phototropin 1 (phot1). A second *NPH1*-like gene (*NPL1*) was also identified and subsequently also shown to encode an active phototropin photoreceptor (phot2) that functions together with phot1 in the BL regulation of phototropism, chloroplast movement, stomatal opening and leaf expansion (Kagawa et al. 2001; Kinoshita et al. 2001; Sakai et al. 2001; Sakamoto and Briggs 2002). Phot2 is present in all plants, whereas phot1 appears restricted to spermatophytes (Galvan-Ampudia and Offringa 2007).

The phot molecules consist of two distinct halves; a C-terminal domain with clear homology to classical serine/threonine kinases, and an N-terminal half containing two domains that each bind a flavin mononucleotide (FMN) chromophore (Fig. 19.1). These domains have been termed LOV domains for their presence in a range of proteins involved in the sensing of *l*ight, *o*xygen or *v*oltage (Christie et al. 1999). Both FMN chromophores undergo a photocycle that involves formation of a cysteinyl adduct and loss of BL absorption upon BL exposure. Mutational studies have shown that the majority of phot activity depends on the photochemical activity of the LOV2 domain, while the role of LOV1 domain is less clear (Christie and Murphy 2013).

19.2.4 Other LOV-Domain Blue-Light Photoreceptors

Following the isolation of phototropins, sequence homologies and forward genetics identified a second small family of LOV-domain proteins encoded in the *Arabidopsis* genome (Nelson et al. 2000; Somers et al. 2000). However, outside their single LOV domain, these proteins show no similarity with the phototropins, but instead incorporate an F-box domain (implicated in protein-protein interactions) and a kelch repeat domain (Fig. 19.1). Most higher plants have a basic complement of two such proteins (ZTL and FKF1) although *Arabidopsis* itself has an additional protein (LKP2) more closely related to ZTL (Schultz et al. 2001). It has subsequently been shown that LOV domains from these proteins attach FMN chromophore, and they are now known to act as photoreceptors regulating light-dependent protein turnover in photoperiodic and circadian regulation (see Sect. 19.5.2.1 below).

19.2.5 UV-B Photoreceptors

In addition to the effects of BL and UV-A mediated by the phytochrome and cryptochrome families, shorter wavelength UV (UV-B) also affects plant growth. At high irradiances this is due to the effects of DNA damage, but at low irradiances photomorphogenic effects are also observed (Kim

et al. 1998). Although phytochromes and cryptochromes can contribute to these low-irradiance effects, in some cases they have been shown to be independent of known photoreceptors, suggesting the existence of a distinct photoreceptor for UV-B (Ulm 2006). However, it is only recently that this photoreceptor was identified (Rizzini et al. 2011) as UVR8, a beta-propeller protein with homology to the mammalian guanine nucleotide exchange factor RCC1.

UVR8 was first identified in screens for *Arabidopsis* mutants showing increased sensitivity to UV-B damage and shown to be absolutely required for developmental responses to UV-B under conditions that exclude contribution from other known photoreceptors (Kliebenstein et al. 2002; Favory et al. 2009). UVR8 exists as a dimer in the absence of UV-B light but reversibly dissociates into monomers after light absorption. UVR8 expression does not show conspicuous regulation by light, but it does become enriched in the nucleus in response to UV-B (Kaiserli and Jenkins 2007; Favory et al. 2009).

Unlike many other photoreceptors, UVR8 does not appear to require a covalently bound chromophore, and the primary perception mechanism seems instead to depend on UV absorbance by certain tryptophan residues in the protein itself, which are clustered at the dimerisation interface (Christie et al. 2012). Mutational studies have established that substitution of three specific tryptophans is sufficient to confer constitutive dimerisation and loss of signalling interactions, but only partial loss of biological activity, suggesting that momomerisation alone is not sufficient for function (O'Hara and Jenkins 2012).

19.3 Physiological Roles of Photoreceptors

Considering the number and nature of plant photoreceptors, it is easy to see how early attempts to interpret physiological observations of photomorphogenesis were hampered by the diversity and functional overlap of the photoreceptors involved. The identification of photoreceptor-specific mutants has been essential for the characterisation of the functions and interactions of the photoreceptors, and mutants continue to be an important tool in dissection of signalling pathways. Null mutants have now been identified for each of the 13 known photoreceptors in *Arabidopsis*, and photoreceptor-specific mutants have also been identified in other higher plant species, notably tomato, rice and pea. These have been useful in testing generalisations about photoreceptor function and in studying processes not easily studied in *Arabidopsis*. Sense and antisense transgenic lines expressing altered levels of specific photoreceptors have also been of use in exploring photoreceptor functions where no mutants have been available and in species not convenient for mutant analysis. In recent years the availability of genome scale approaches has also facilitated analysis of photoreceptor involvement in natural variation.

As the number of known plant photoreceptors has grown, it is becoming clear that many light-regulated processes are controlled by multiple photoreceptors, which may interact in different ways in different developmental contexts (Casal 2006, 2013). The following sections present an overview of what is known about the photocontrol of several of the better-studied processes in higher plants. The exception is flowering, which is dealt with in Sect. 19.5.

19.3.1 Germination

In species that exhibit seed dormancy, germination can often be induced by a light treatment given to imbibed seed. In general, small-seeded species are more responsive than large-seeded ones. In a classic study on lettuce seed germination in the 1930s, Flint and MacAlister found that R was particularly effective at inducing germination, while FR and BL were inhibitory (Sage 1992). It was shown subsequently that the effect of R could be reversed by FR. In some highly sensitive seeds, including *Arabidopsis*, a distinct non-FR-reversible phase can be identified. Three hours after imbibition, germination of *Arabidopsis* seeds can be induced by R in a fully FR-reversible manner, and this response is absent in the *phyB* mutant (Shinomura et al. 1996). After longer periods of imbibition, the sensitivity to light increases and, at 48 h germination, can be induced by very small amounts of light, including FR, and is therefore no longer FR reversible. This second phase is absent in the *phyA* mutant (Shinomura et al. 1996).

These two responses illustrate some more general features of phyA and phyB function. PhyB controls responses which can be induced by low-fluence R in the order of 1–1,000 μmol m^{-2} and which are reversible by FR. These are called low-fluence responses (LFR) and are a function of the amount of phyB in the Pfr form (Fig. 19.2). PhyA-mediated responses are much more sensitive to light and have a range in threshold fluence approximately four orders of magnitude lower than LFR (0.1–100 nmol m^{-2}). These very-low-fluence responses (VLFR) require only a very small proportion of phyA (<0.1 %) to be converted to the Pfr form. They can therefore be induced by light of any wavelength from 300 to 750 nm and are not reversible by FR (Fig. 19.2). The molecular basis for the difference between these two forms of response is not yet understood.

19.3.2 Seedling Establishment

The development of the germinating seedling and its establishment as a fully autotrophic plant require the coordination

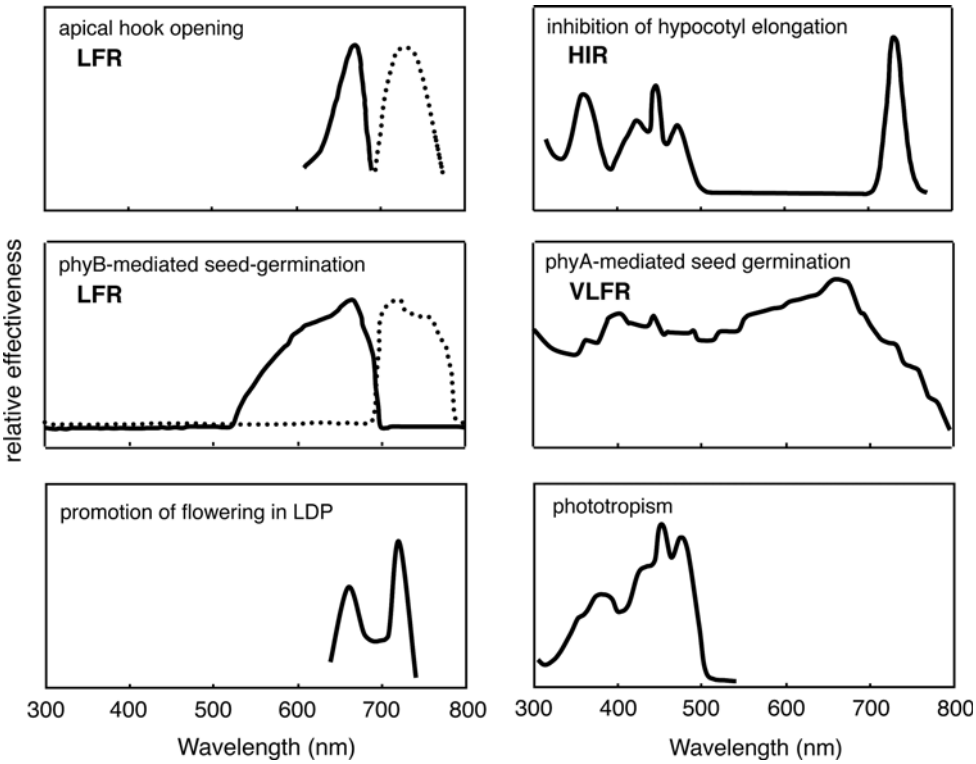

Fig. 19.2 Action spectra for representative photomorphogenic responses. *LFR*-low-fluence response, *HIR*, high-irradiance response, *VLFR*, very-low-fluence response. Broken lines represent reversal of response (Redrawn from Withrow et al. 1957; Hartmann 1967; Baskin and Iino 1987; Carr-Smith et al. 1989; Shinomura et al. 1996)

of several different light-regulated processes. These include inhibition of stem or hypocotyl elongation, apical hook opening, opening and expansion of cotyledons and leaves and the induction of accumulation of photosynthetic and protective pigments. The regulation of these processes by light, which is often termed *de-etiolation*, can be dramatically demonstrated by the exposure of etiolated (dark-grown) seedlings to brief R pulses. Experiments of this kind show roles for phyA and phyB that are generally consistent with the LFR and VLFR response modes identified in the control of germination. These responses also manifest in coordinated changes in the expression of many different genes, both nuclear and plastidic (Tepperman et al. 2001, 2004).

Light responses during seedling establishment are more commonly studied by growing plants under different irradiances of continuous monochromatic light. The responses induced under these conditions are often stronger than those observed in response to a single light pulse and are termed high-irradiance responses (HIRs). HIRs to continuous BL, R and FR have all been reported. The FR-HIR is in most cases controlled entirely by phyA, whereas the R-HIR is controlled mainly by the phyB-type phytochromes (Fig. 19.3) (Franklin et al. 2003). The exception is in rice, where phyC may also contribute to de-etiolation in response to continuous FR (Takano et al. 2005). PhyA can also act under continuous R, but its contribution can often only be seen at lower irradiances, where the phyB-type phytochromes are not active (Kerckhoffs et al. 1997; Mazzella et al. 1997).

The HIRs can be considered as a series of responses to pulses of light, and the fundamental photoreactions have been explored by replacing the continuous irradiation with intermittent pulses. R-HIR can be effectively induced by an R pulse every 4 h in an FR-reversible manner, suggesting that the R-HIR is effectively a continuous activation of LFR. In contrast, the FR-HIR can be replaced only by FR pulses given every 3 min. Under this regime, the effect of the FR pulses is reversible by R (Shinomura et al. 2000). The FR-HIR is therefore distinct from the phyA-mediated VLFR and operates by a mechanism fundamentally different from phyB-mediated LFR. The molecular basis for these differences is not yet understood, although recent results suggest that the dynamics of degradation and intracellular transport play an important role (see Sect. 19.4.1).

De-etiolation can also be induced by BL. Under high-irradiance continuous BL, cry1 is the main photoreceptor for de-etiolation responses, with a threshold for activity of around 5 $\mu mol \cdot m^{-2} \cdot s^{-1}$, whereas at lower irradiances, phyA becomes the predominant BL photoreceptor (Fig. 19.3). PhyB-type phytochromes also make a minor contribution under high-irradiance BL that becomes more evident in the absence of phyA and cry1 (Poppe et al. 1998; Weller et al. 2001b; Platten et al. 2005b). In *Arabidopsis*, the second cryptochrome, cry2, is also reported to have a minor role in

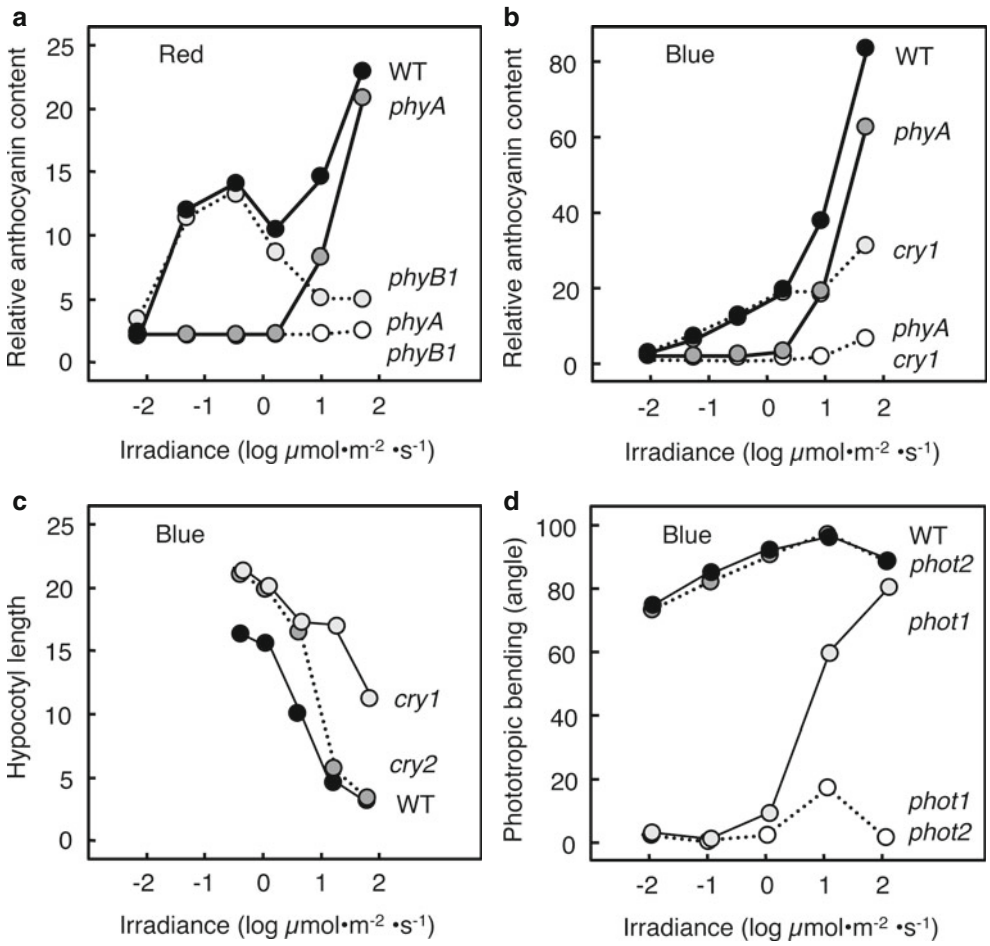

Fig. 19.3 Irradiance dependence for various photomorphogenic responses in wild-type and photoreceptor mutant seedlings of tomato (**a**, **b**) and Arabidopsis (**c**, **d**), exposed for 24 h to monochromatic red or blue light. (Redrawn from Kerckhoffs et al. 1997, Weller et al. 2001b, Guo et al. 1998, Sakai et al. 2001)

the control of seedling light responses under lower-irradiance BL (Fig. 19.3) (Lin et al. 1998).

Temporal differences in the action of different photoreceptors are also observed. Immediately following exposure of etiolated seedlings to R, phyA is the main photoreceptor controlling inhibition of hypocotyl elongation, and phyB only becomes predominant after several hours of exposure (Parks and Spalding 1999). This functional separation is similar to the temporal phases observed for phyA- and phyB-mediated germination and may be due in part to phyA degradation. Similar analyses have shown that inhibition of elongation in response to blue light is mediated initially by phot1 for the first 30 min following exposure and then subsequently by cry1 and cry2 (Folta and Spalding 2001).

19.3.3 Phototropism

Detailed action spectra indicated that the photoreceptor responsible for seedling phototropism has an absorption peak in the UV-A and a 3-component peak in the BL region of the spectrum. Fluence-response curves for induction of phototropism by BL pulses resolved two components (Liscum and Stowe-Evans 2000). The "first-positive" component can be induced by fluences of 0.1–500 μmol m^{-2} and shows reciprocity within a certain fluence range. The "second-positive" component has a similar fluence threshold but is also time dependent, with a minimum time requirement of around 10 min. *phot1* mutants lack the first-positive response and are completely aphototropic under low irradiances of continuous BL, suggesting that they are also deficient in the second-positive response. However, under continuous BL of higher irradiance (>10 μmol m^{-2} s^{-1}), *phot1* mutants show a normal phototropic response (Sakai et al. 2000), implying the action of another photoreceptor, subsequently shown to be phot2 (*NPL1*) (Fig. 19.3) (Sakai et al. 2001). The function of phototropin in the control of hypocotyl elongation was initially thought to be restricted to the perception of unilateral B, because *nph1* plants exhibit grossly normal de-etiolation responses (Liscum and Briggs 1995). However, more detailed analyses have shown that phototropins can mediate a more general inhibition of elongation in response to B (Folta and Spalding 2001; Sakamoto and Briggs 2002).

Although phyA, phyB, cry1 and cry2 have all been proposed to contribute to the B phototropic response, it is now clear that these photoreceptors are neither necessary nor sufficient for directional light sensing, at least in *Arabidopsis* hypocotyls. Nevertheless they can modulate expression of the phototropic response, by increasing its amplitude or speeding up its development. In addition, absorption of R by phytochrome can enhance the subsequent phototropin-mediated response to unilateral B (Parks et al. 1996). One suggestion is that this may an indirect effect resulting from phytochrome suppression of gravitropism (Lariguet and Fankhauser 2004).

19.3.4 Shade Avoidance

Light responses in established, fully autotrophic seedlings are often referred to as shade-avoidance responses. In response to shading, stem elongation increases, development of lateral organs such as leaves and branches is suppressed, and flowering is accelerated (Casal 2013). Vegetational shading involves changes in both irradiance and spectral quality of the light reaching the plant. The main difference in spectral quality is an effective enrichment for FR, which is due to the fact that leaves transmit FR but absorb BL and R. The term shade avoidance as applied to laboratory experiments refers specifically to responses induced by manipulation of the FR content against a constant background of photosynthetically active radiation (Fig. 19.4).

Once again, the availability of multiple photoreceptor mutants has allowed the control of shade-avoidance responses to be dissected in detail. These analyses show that phyB/(E)-type phytochromes dominate the response, with mutants deficient in these phytochromes appearing as strongly shade-avoiding plants even when grown under high-irradiance light of high R:FR (Devlin et al. 1998, 1999; Weller et al. 2000). This indicates that these phytochromes act as a simple developmental switch in which Pfr formed under light of high R:FR actively initiates photomorphogenic responses and this activation is proportionately reduced as the photoequilibrium is shifted back towards the Pr form by increasing FR supplementation.

It was initially assumed that phyA was unlikely to be important for shade avoidance, as phyA-deficient mutants show no substantial difference from WT seedlings when grown in white light (Whitelam et al. 1993, Weller et al. 1997a). However, phyA can in fact oppose the phyB-mediated shade-avoidance response by inhibiting stem elongation under light of low R:FR ratio (Smith et al. 1997; Weller et al. 1997a), and it is clear that the balance of phyA to phyB is therefore important in determining the degree of responsiveness to changes in R:FR.

In addition to changes in R:FR, canopy shade also clearly represents a reduction in overall irradiance. This is thought to act through both phytochrome and cryptochrome systems (Keller et al. 2011).

Fig. 19.4 Shade-avoidance response of wild-type tomato seedlings simulated by addition of high irradiance far-red light to the white light source, lowering the ratio of red to far-red light from 6.3 to 0.1

19.3.5 Chloroplast Movement

One important physiological mechanism for short-term acclimation to altered light levels is the relocation of chloroplasts within mesophyll tissues. Under high irradiances, chloroplasts move towards anticlinal cell walls thus reducing the amount of intercepted light, whereas under low irradiances, they accumulate along the periclinal walls to maximise light absorption. These "avoidance" and "accumulation" responses occur within 2 h of a change in light conditions. In angiosperms these movements are primarily responses to the BL spectral region and are mediated exclusively by phototropins but can be modified or enhanced by phytochromes (DeBlasio et al. 2003; Luesse et al. 2010). Interestingly, whereas both phot1 and phot2 contribute to the accumulation response, the avoidance response is controlled only by phot2 (Sakai et al. 2001).

19.3.6 Stomatal Opening

In general plant stomata tend to be closed in darkness and open in response to light, particularly light in the blue region of the spectrum. This means that CO_2 uptake and fixation

occur while energy from the light reactions of photosynthesis is available Both phototropins and cryptochromes appear to contribute independently to this response with phototropins functioning across a wide irradiance range and cryptochromes mainly at higher irradiances (Kinoshita et al. 2001; Mao et al. 2005).

19.4 Photoreceptor Regulation and Early Signalling

Most of the classical photomorphogenic responses listed above are whole-plant responses and occur on a scale of hours to days after first exposure to the light stimulus. Recent molecular and genetic dissections are revealing shorter-term cellular and molecular and hormonal events underlying these responses. While each photoreceptor and photoreceptor group participates in distinct signalling networks, it is clear that transcriptional regulation, sub-cellular partitioning and control of protein stability are common themes across these networks. Details of specific components within light signalling networks are covered in Chap. 14. Here we will restrict our discussion to regulation of photoreceptor expression and early events in photoreceptor signalling.

19.4.1 Phytochrome

Two features considered characteristic of phytochrome in early studies were its presence at much higher levels in dark-grown than in light-grown seedlings and its rapid disappearance after exposure to light. These features are now known to mainly reflect the properties of phyA. PhyA accumulates as Pr in the cytosol and conversion to Pfr after light exposure initiates both a rapid proteasome-mediated degradation of the protein and a rapid downregulation of *PHYA* transcription (Rockwell et al. 2006; Hennig 2006). PhyA degradation is mainly dependent on the CUL1-RING ubiquitin ligase pathway (Debrieux et al. 2013). Other phytochromes are expressed at a much lower level than phyA in dark-grown seedlings and are not strongly light regulated. In light-grown plants, phytochrome genes are widely expressed around the plant at generally similar level across different tissues (Goosey et al. 1997; Hauser et al. 1997) and show regulation by the circadian clock (Toth et al. 2001).

Both phyA and phyB are synthesised in the cytosol in darkness and show light-dependent nuclear transport, with response modes typical of VFLR and FR-HIR for phyA and LFR for phyB (Kircher et al. 1999, 2002; Hisada et al. 2000; Gil et al. 2000). This implies a major role in transcriptional regulation, and indeed, major genome-wide changes in transcription occur within an hour of phytochrome activation (Tepperman et al. 2001, 2004). Other phytochrome responses, such as osmotic changes leading to organ movement and cell growth, occur much more rapidly, indicating a role for phytochrome in the cytoplasm (Hughes 2013).

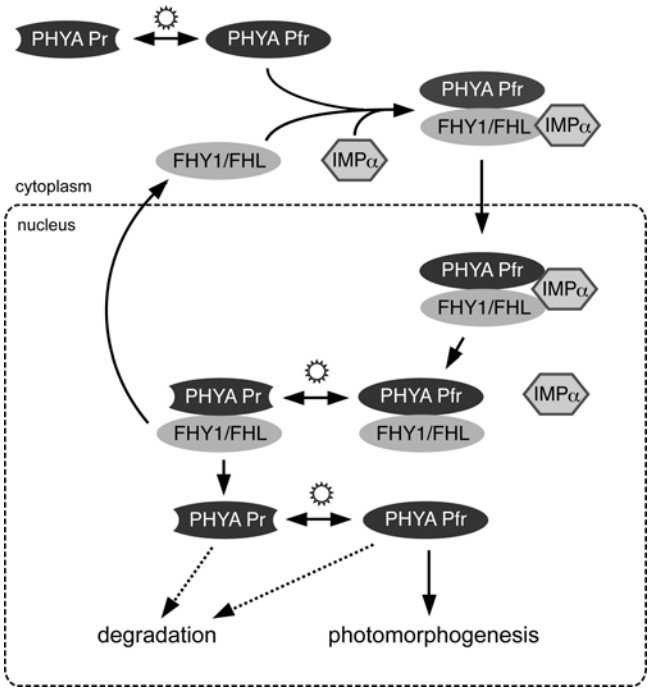

Fig. 19.5 Model for light-induced nuclear transport of phyA, (Adapted from Kircher et al. 2011; Rausenberger et al. 2011). Following irradiation, phyA in the cytoplasm is converted to the Pfr form and interacts with FHY1/FHL proteins. These proteins in turn interact with importin α, which facilitates the transport of the complex into the nucleus. In the nucleus the complex dissociates, and an equilibrium between photoconversion and degradation is established that depends on the spectral quality of the light. The highest levels of the active Pfr form are thought to occur under far-red wavelengths, due to the fact that these conditions minimize overall phyA degradation by protecting it in the inactive but more stable Pr form

Differences in the dynamics of intracellular transport are thought to be a key factor explaining how phytochromes with very similar absorbance properties can mediate responses with quite different spectral sensitivities. In recent years it has become clear that phytochrome nuclear transport is facilitated by interaction with proteins that themselves possess a nuclear localisation signal (Pfeiffer et al. 2012). PhyB-type phytochromes undergo relatively slow nuclear import, which is facilitated by the PIF family of bHLH transcription factors (Pfeiffer et al. 2012), which also act in phytochrome signalling (Leivar and Quail 2010; see Chap. 14). In contrast, phyA is much more rapidly imported after light exposure. This import depends on two related proteins, FHY1 and FHL, which physically interact with phyA and can shuttle it in both directions across the nuclear membrane (Fig. 19.5). These two proteins are indispensible for phyA nuclear import and for the HIR mode of phyA action (Hiltbrunner et al. 2006; Genoud et al. 2008; Kircher et al.

2011). The most advanced explanation for the distinct action spectrum of phyA HIR has invoked an interaction between facilitated transport, photoconversion and degradation that leads to accumulation of phyA in the nucleus under continuous FR but not continuous R (Rausenberger et al. 2011).

In addition to their roles in nuclear import of phyA, the FHY1 and FHL proteins may guide nuclear phyA into signalling complexes involving a number of transcription factors, including LAF1 (Myb type) and HFR1 (bHLH type) (Yang et al. 2009). The retention of certain responses to FR in a *phy1 fhl* double mutant, which is unable to import phyA to the nucleus, has provided additional evidence that phyA can also act in the cytoplasm (Rösler et al. 2007).

Despite homology of phytochrome C-terminal domains to histidine kinases, and the histidine kinase activity of prokaryotic phytochromes (Rockwell et al. 2006), plant phytochromes instead show light-dependent autophosphorylation characteristic of ser/thr kinase activity (Yeh and Lagarias 1998), although functionally significant tyrosine phosphorylation has also recently been reported (Nito et al. 2013). A range of functions have been ascribed to phytochrome autophosphorylation. For example, phyA autophosphorylation in the N-terminal region impedes the degradation of phyA (Han et al. 2010), while phosphorylation of one particular residue in *Arabidopsis* phyB may influence signalling by increasing the rate at which the active Pfr form reverts to the inactive Pr form (Medzihradszky et al. 2013).

Other studies have identified targets of phytochrome phosphorylation. Some of these target proteins have also been shown to interact physically with phy (Ahmad et al. 1998; Fankhauser et al. 1999; Choi et al. 1999; Colon-Carmona et al. 2000), but in most cases, evidence is still lacking about whether this phosphorylation is direct and whether it is functionally significant (Quail 2006). Two exceptions may be the PIF family of transcription factors (Leivar and Quail 2011; see Chap. 14) and FHY1 (Chen et al. 2012).

19.4.2 Cryptochrome

CRY transcription is regulated by the circadian clock (Toth et al. 2001; Platten et al. 2005b; Zhang et al. 2008), and in some species, a strong repression by light has also been reported (Platten et al. 2005b). The *Arabidopsis* cry2 protein differs from cry1 in being unstable under high-irradiance BL (Lin et al. 1998). This is reminiscent of the rapid light-induced degradation of phyA but, in contrast, depends mainly on the COP1 ubiquitin ligase pathway (see Chap. 14; Lau and Deng 2012; Weidler et al. 2012). Both cry1 and cry2 have been shown to localise to the nucleus (Kleiner et al. 1999; Matsumoto et al. 2003), although studies of a number of BL-induced phenomena involving changes in ion fluxes across cell membranes (e.g. Spalding 2000) suggest that cryptochromes could also be involved in light-driven redox reactions outside the nucleus.

To date, there is little known about the primary reactions of cryptochromes. Autophosphorylation occurs rapidly in response to light exposure (Shalitin et al. 2003), and the prevailing interpretation of the primary light reaction is that light absorption initiates electron transport from the FAD chromophore to ATP, which is bound in an adjacent pocket (Brautigam et al. 2004), and this then facilitates phosphotransfer to residues in the C-terminal domain. This phosphorylation may be supplemented by other protein kinases and causes a change in conformation of the molecule such that the C-terminal domain becomes exposed to interaction with signalling partners, one of which is COP1 (Wang et al. 2001; Zhang et al. 2006; Lau and Deng 2012; see Chap. 14).

19.4.3 Phototropin

In etiolated seedlings, phot1 is much more abundant than phot2 and is downregulated by light, whereas phot2 levels increase (Christie and Murphy 2013). This may explain the greater photosensitivity of phot1 relative to phot2 inferred from mutant analyses (Sakai et al. 2001). Both phot1 and phot2 are predominantly associated with the plasma membrane in dark-grown epidermal and subepidermal cells of the hypocotyl and in guard cells (Sakamoto and Briggs 2002; Harada et al. 2003) and partially relocalise to the cytosol in response to light (Aihara et al. 2008; Wan et al. 2008). Localisation of phot2 to the Golgi apparatus has also been reported (Kong et al. 2006), but the significance of this is not clear. *PHOT1* gene expression shows circadian regulation in *Arabidopsis* and in several other species is strongly downregulated in response to light (Kanegae et al. 2000).

The primary structure of the phototropin C-terminal domain clearly identifies it as a classical ser/thr kinase, and single substitutions at a number of conserved residues indicate that autophosphorylation in the kinase activation loop is essential for phot function (Inoue et al. 2008a, 2011; Sullivan et al. 2010). As in the case of cryptochromes, the activity of the C-terminal domain of the photoreceptor is constrained in darkness by the light-sensing N-terminal half. In darkness the phototropin FMN chromophore is bound in a non-covalent manner in a hydrophobic pocket of the LOV domain but upon light exposure forms a covalent bond with an adjacent cysteine residue (Salomon et al. 2000). This causes a conformational change within the LOV domain, which disrupts its interaction with an adjacent alpha-helical region and releases activity of the kinase domain (Harper et al. 2003). Autophosphorylation is implicated in the binding of phototropin to several interacting proteins, and several targets of transphosphorylation have also been identified that may

variously act to modulate phototropism (Demarsy et al. 2012) or mediate phototropin control of stomatal opening (Takemiya et al. 2013).

19.5 Photoperiodism

The importance of the duration of the daily photoperiod for plant development was first noted over 90 years ago. Using changes in day length, plants can monitor the time of year and predict seasonal change in other environmental variables. A number of processes exhibit photoperiodic regulation, including the induction of flowering, the formation of storage organs such as bulbs and tubers and the onset of bud dormancy. Of these, it is the induction of flowering that has been studied most intensively. Clear differences in photoperiodic responsiveness were first documented by Garner and Allard (1920), who classified plants according to whether flowering was preferentially induced under long days (long-day plants (LDP)) or short days (short-day plants (SDP)) (Fig. 19.6). Other early observations indicated that flowering responses could be dramatically altered by low irradiances or short exposures to light. This suggested that the light served as a source of information rather than of energy and showed photoperiodism to be a truly photomorphogenic phenomenon.

19.5.1 Light and the Circadian Clock

Endogenous rhythms have been observed in plants for more than 200 years. However, the importance of an endogenous circadian rhythm for the timekeeping aspect of photoperiodism was first suggested in the 1930s by Erwin Bünning (1964). In fact, photoperiodism can be thought of as the adaptation of circadian timekeeping to the measurement of day length. As such it must involve interaction of light signalling ("input") and specific flower induction ("output") pathways with a circadian oscillator or "clock". One characteristic feature of circadian rhythms is that they show a free-running period that is close to but not exactly 24 h. However, under daily light/dark (L/D) cycles, the rhythmic outputs become synchronised or *entrained* to a period of 24 h exactly.

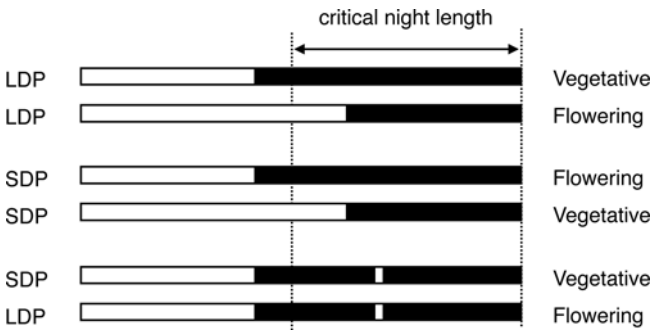

Fig. 19.6 Summary of differences in flowering responses of short day plants (*SDP*) and long-day plants (*LDP*). Open and filled bars represent light and dark periods, respectively

There are generally considered to be two basic models for the way in which light might interact with the clock (Thomas and Vince-Prue 1997). In the *internal coincidence* model, photoperiodic induction results from the increasing overlap in phase of two distinct circadian output rhythms. Light interacts with the induction process solely by controlling the phase and/or period (i.e. entrainment) of the two rhythms. In the *external coincidence* model, developed from ideas first proposed by Bünning, the circadian clock generates an output rhythm in light sensitivity and photoperiodic induction results from the coincidence of an inductive light signal with the light-sensitive phase of this rhythm. In this model, light has two roles: entrainment of the clock and direct interaction with downstream components necessary for the response. A third effect of light in photoperiodism may be to influence output responses directly, without the involvement of a timing component. The challenge is to understand how the plant is able to integrate these signals and generate the appropriate response.

19.5.1.1 Physiological Approaches

Detailed physiological investigations of the relationship between light and the circadian clock have been performed across a wide variety of different species, both SDP and LDP (see Thomas and Vince-Prue 1997). These studies have generated a large amount of complex and often contradictory literature. However, there is reasonable agreement on some of the more general conclusions, and these are summarised below.

Short-Day Plants

In a fixed daily cycle, it is clear that changes in day length could in theory be detected either as changes in length of the light period or of the dark period. It has been established that for many SDP it is mainly the length of the night that is measured, suggesting that processes necessary for floral induction can only take place if the night is longer than a certain *critical night length*. Interruption of an inductive long night with a short-light treatment prevents its effect and delays flowering. In many species, this night-break (NB) response is relatively sensitive and has thus been amenable to pulse experiments and a detailed photobiological analysis (Thomas and Vince-Prue 1997).

NB responses in SDP show action spectra typical of phytochrome-mediated LFR, for which R is inhibitory to flowering and subsequent FR cancels this inhibition. In this response, phytochrome in its Pfr form is clearly acting to inhibit flowering. In addition to the light quality of the NB, its timing can also be important, and several different SDP species show circadian rhythmicity in the responsiveness to

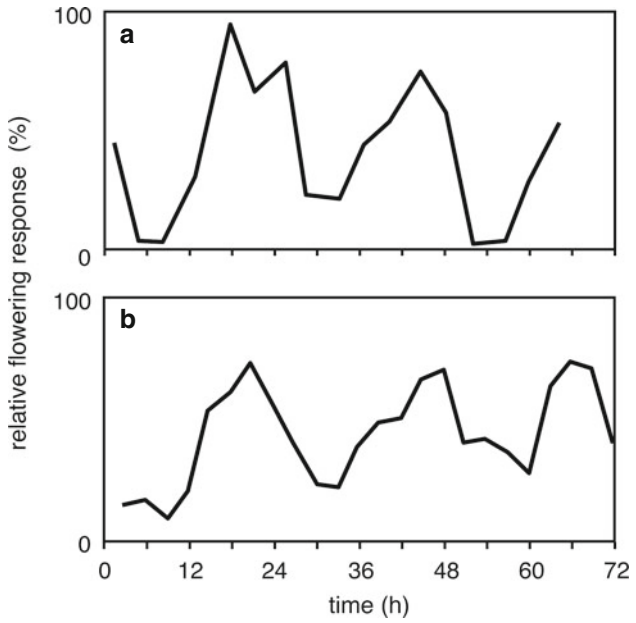

Fig. 19.7 Circadian rhythms in flowering responses to light treatments in SDP and LDP. (**a**) Rhythmic response of the SDP *Glycine max* (soybean) to a 4 h night-break with white light given at various times during an extended night following an 8-h photoperiod (redrawn from Coulter and Hamner, 1964). (**b**) Rhythmic response of the LDP *Hordeum vulgare* (barley) to 6 h of far-red light added at various times during an extended photoperiod of continuous white light (redrawn from Deitzer et al. 1982)

a NB (Fig. 19.7), consistent with the external coincidence model (Thomas and Vince-Prue 1997). Other light treatments can reset the phase of this rhythm. In some cases, the phase-setting effects of light were shown to occur independently of effects on flower induction, and R was also the most effective wavelength for inducing phase shifts. Phase shifting has generally been found to require longer exposures to light than the NB response. With even longer periods of light exposure (>6 h), the phase of the rhythm is no longer shifted but suspended and only released approximately 9 h after transfer to darkness (Thomas and Vince-Prue 1997).

Other studies have shown that in addition to the strong inhibitory effect of R shown in the NB response, FR is also effective for inhibition of flowering when given at the end of the day or early in the dark period. This clearly suggests the action of a second phytochrome, which promotes flowering in its Pfr form. This response does not affect the timing of NB sensitivity.

Long-Day Plants

Until recently, less was known about light requirements in LDP photoperiodism. As for SDP, light reactions governing flowering in LDP occur in both light and dark periods, although one or the other may predominate in any one species. The concept of a critical night length is again relevant, but for LDP, nights must be shorter than the critical length for plants to flower. In some LDP, R NB is effective for promotion of flowering. Their effectiveness varies during the night, and the response can be partially reversed by FR. However, unlike in SDP, a clear rhythmicity in responsiveness is not observed, and in general, longer periods of light are required to elicit a response (Thomas and Vince-Prue 1997).

Light reactions during the photoperiod have also been demonstrated in LDP. For example, FR added to a photoperiod of R or white light (WL) can promote flowering, with rhythmic variation in effectiveness (Fig. 19.7). Although phase-shifting experiments are much more difficult to perform in LDP and less conclusive, light-induced changes in phase of the rhythm of FR responsiveness have been reported (e.g. Deitzer et al. 1982).

Photoperiodic responses in LDP have more often been investigated using extensions of a short, non-inductive photoperiod. Action spectra for the promotion of flowering by photoperiod extensions most commonly show peaks at around 710–720 nm, well above the absorbance peak of Pr and clearly below that of Pfr (Thomas and Vince-Prue 1997). This peak is similar to that seen for the FR-HIR in seedling de-etiolation, suggesting the involvement of phyA. However, in other species, action spectra with peaks in both R and FR have also been reported (Carr-Smith et al. 1989), indicating that a second phytochrome is probably involved (Fig. 19.2). In some species, notably crucifers, BL is also effective as a day extension.

19.5.1.2 Genetic Approaches

The most detailed understanding of photoperiod response has come from studies in *Arabidopsis* (a LDP) and rice (a SDP). A number of flowering mutants or genetic variants have also been characterised in other photoperiodic species, including the LDP wheat, barley and garden pea and the SDP soybean and potato. Not surprisingly, studies of photoperiod response mutants and other genetic variants have identified photoreceptor, light signalling and circadian clock-related genes, as well as a number of other genes that integrate the light and clock inputs through output pathways for photoperiodic flower induction. Molecular and physiological analyses of these mutants are providing invaluable information about molecular components important for photoperiodic responsiveness.

Photoreceptor Mutants

Early flowering is also a well-known feature of shade-avoidance responses, suggesting that low R:FR acts to deactivate a phytochrome normally acting to inhibit flowering under high R:FR. Mutants for *phyB*-like genes in both SDP and LDP species show early flowering under both SD and LD, suggesting that these photoreceptors confer general inhibition of flowering in their Pfr form (Devlin et al. 1998,

1999; Weller et al. 2001a; Takano et al. 2005). The fact that relatively long periods of light are necessary for promotion of flowering in LDP, and the similarity of action spectra for this promotion to that seen for the FR-HIR in seedling de-etiolation, has for some time suggested that phyA might have a significant flower-promoting role in LDP. This has been confirmed in *phyA* mutants of *Arabidopsis* and pea (Weller et al. 2001a; Yanovsky and Kay 2002). In the SDP rice and soybean, phyA mutants instead confer early flowering (Takano et al. 2005; Liu et al. 2008).

As a generalisation, it thus appears that phyA is associated with photoperiod sensing and has opposite effects in SDP and LDP. In contrast, phyB acts to inhibit flowering in both LDP and SDP and under natural conditions is not directly involved in time measurement, with a role instead in sensing shade.

In *Arabidopsis*, an important role in the photoperiodic control of flowering has also been demonstrated for the cryptochrome photoreceptor family. Cry2, despite a relatively minor effect on seedling photomorphogenic responses, has a strong promotive effect on flowering under LD (Guo et al. 1998) that is dependent on the activation of phyB (Mockler et al. 2003). This suggests that the perception of day length has become the dominant function of this photoreceptor in *Arabidopsis*. However, in general, relatively few species show strong control of flowering by BL, and the importance of cry2 in photoperiodism may not be widespread.

Finally, the ZTL/FKF1 photoreceptors are also intimately involved in photoperiod sensing through light-dependent regulation of core circadian clock and output components (see below). Although this mechanism has primarily been elucidated in *Arabidopsis*, it seems likely to be conserved, and recent evidence in potato does point to a conserved role for FKF1 in photoperiod sensing (Kloosterman et al. 2013).

Photoreceptor Mutants and the Circadian Rhythm

Studies of circadian clock properties in photoreceptor mutants have shown that multiple photoreceptors contribute to the control the circadian period in a manner that closely parallels their roles in the control of de-etiolation. In *Arabidopsis*, phyB-type phytochromes are responsible for period shortening under high-irradiance R, while phyA acts under low-irradiance R and BL. Cry1 and cry2 act redundantly to shorten the circadian period under BL across a wide irradiance range (Somers et al. 1998). These results suggest that all of these photoreceptors may have the ability to contribute to entrainment of the clock under certain circumstances. However, the significance of this for plants growing under high WL irradiances is unclear. Under such conditions, phyB and cry1 would be expected to be the predominant photoreceptors controlling clock period, although a quadruple mutant lacking phyA, phyB, cry1 and cry2 can entrain normally to WL/D cycles (Yanovsky et al. 2000a).

Circadian Rhythm Mutants

Numerous genes essential for correct maintenance of circadian rhythms under light/dark cycles have now been identified in *Arabidopsis* (Nagel and Kay 2012), and many of these were first isolated in mutant screens for altered flowering time, emphasising the importance of normal circadian regulation for photoperiodism. The key feature of these genes is that they affect multiple clock outputs, including rhythmic control of gene expression and leaf movement.

The *Arabidopsis* circadian clock was initially envisaged as a simple transcriptional feedback loop involving three components: the closely related myb transcription factors *LHY* and *CCA1* and the pseudo-response regulator (PRR) homologue *TOC1* (Alabadi et al. 2002; Mizoguchi et al. 2002). Other genes have subsequently been identified that are also necessary for circadian rhythmicity under constant conditions, including *LUX*, *GI*, *ELF3*, *ELF4* and other *PRR* genes (e.g. Park et al. 1999; Fowler et al. 1999; Hazen et al. 2005; Farré et al. 2005; Nakamichi et al. 2005; McWatters et al. 2000). Inclusion of these genes has necessitated a gradual shift to a more complex model involving multiple interlocking negative feedback loops (Nagel and Kay 2012) and multiple points for light input. Interestingly these components have also been identified in other species by virtue of their effects on photoperiod response (Turner et al. 2005; Hecht et al. 2007; Liew et al. 2009; Watanabe et al. 2011; Faure et al. 2012; Matsubara et al. 2012; Weller et al. 2012).

As described above, light influences the clock in a number of different ways. Some of the mechanisms by which this occurs are now known. For example, the *LHY* and *CCA1* genes both identified as early targets of phytochrome action in transcript profiling of seedling responses to R and FR (Martinez-Garcia et al. 2000). Both genes contain G-box light-regulated elements in their promoters and are transcriptionally activated by the binding of phytochrome and PIF3. Three positive factors in light signalling, FHY3, FAR1 and HY5, bind to the promoter of *ELF4* and activate its expression (Li et al. 2011). Phytochrome-dependent light input to the clock may also occur through ELF3, a multifunctional protein with a role in control of light signalling to the clock (McWatters et al. 2000; Kolmos et al. 2011): potentially by direct physical interaction of phytochromes with ELF3 (Liu et al. 2001). In a third example, the ZTL and FKF1 blue-light receptors have been shown to regulate the stability of TOC1 by targeting it for proteasome-dependent degradation (Mas et al. 2003; Baudry et al. 2010).

19.5.2 Signalling in Photoperiodism

19.5.2.1 Long-Distance Signalling in Evocation of Photoperiod Responses

The sensitivity to flower-inducing light signals varies tremendously among different species. In many cases the site at

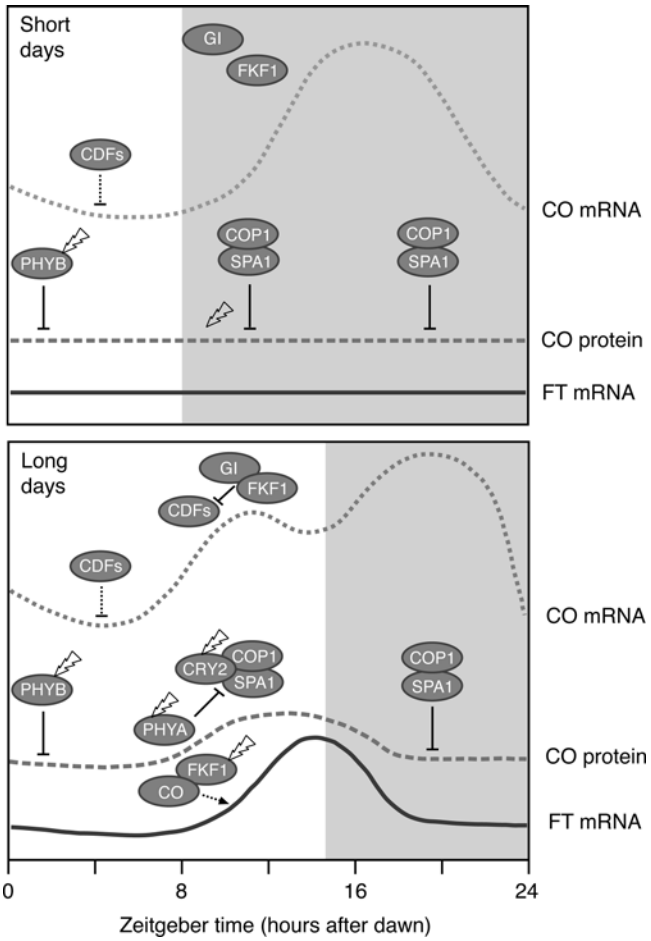

Fig. 19.8 Model depicting the molecular basis for the photoperiod response in Arabidopsis. Light influences the rhythmic induction of FT through transcriptional and post-translational regulation of CONSTANS. At least four photoreceptors play a significant role in this regulation (Redrawn from Andres and Coupland (2012))

which light is perceived can be separated from the eventual site of flower formation, indicating the existence of some form of long-distance communication. This has been studied in classic physiological experiments involving grafting, leaf-removal and differential exposure of different parts of the plant and more recently through transgenic approaches to drive gene expression in specific tissues. Experiments of this kind have provided evidence for a promoter of flowering (often called "florigen") as the main long-distance signal in the photoperiod response, although a role for inhibitory signals has not been definitively excluded.

Speculations about the nature of the floral regulators have considered known plant hormones (gibberellins, cytokinins), various metabolites (sugars, polyamines) and, more recently, specific RNA molecules and proteins. Over recent years, numerous detailed studies have identified a major role for genes in the *FT* family as integrators of multiple external and internal signals controlling flowering, including photoperiod. *FT* genes encode small proteins with homology to mammalian phosphatidylethanolamine-binding proteins, and in *Arabidopsis* and rice, it has been conclusively established that FT proteins act as florigens (Andres and Coupland 2012; Brambilla and Fornara 2013). In *Arabidopsis*, *FT* transcription is low under SD but is activated in vascular bundles under LD, and FT protein is translocated from phloem companion cells to the shoot apex, where it enters the shoot apical meristem (Corbesier et al. 2007; Jaeger and Wigge 2007; Mathieu et al. 2007). In rice, two distinct *FT*-like genes, *Hd3a* and *RFT1*, are, respectively, activated under inductive SD and non-inductive LD and encode SD- and LD-specific florigens (Tamaki et al. 2007; Komiya et al. 2009; Tsuji et al. 2011).

In both *Arabidopsis* and rice, FT proteins reaching the SAM enter the nucleus and bind to the bZIP transcription factor FD to induce expression of inflorescence identity genes in the MADS-domain family (Abe et al. 2005; Wigge et al. 2005; Taoka et al. 2011). In rice, a more detailed picture has recently emerged in which FT proteins after entering cells in the SAM first bind to 14-3-3 proteins in the cytoplasm before moving to the nucleus and forming a ternary complex with FD (Taoka et al. 2011).

19.5.2.2 Genetic Analysis of the Photoperiod Response Mechanism Measurement

Over the past 10 years, there has also been intense interest in the mechanisms by which photoperiod regulates *FT* genes and, in particular, how light and the circadian clock may interact. These mechanisms have been elucidated in two species, rice and *Arabidopsis*, and this comparison provides the first detailed molecular understanding of how plants can respond in an opposite manner to photoperiod cues. However, the taxonomic distance between these two species for the moment gives only limited insight into how these different mechanisms may have evolved.

Arabidopsis

In *Arabidopsis*, attention has focused mainly on *CONSTANS*, a nuclear protein with motifs suggestive of a role in regulation of transcription and/or protein-protein interaction. CO is a potent promoter of flowering, and its direct and major regulatory target is *FT* itself (Samach et al. 2000; Wigge et al. 2005). CO protein binds to the *FT* promoter in association with other transcription factors (Song et al. 2012a; Kumimoto et al. 2010; Tiwari et al. 2010) and is therefore likely to activate *FT* expression directly. A series of studies have provided evidence that a high level of CO protein is necessary for activation of *FT* expression and only occurs when high levels of *CO* expression coincide with light, which in turn occurs only in the afternoon of LD photoperiods, and is thought to explain the LD flowering response of *Arabidopsis* (Fig. 19.8).

It is now known that both transcriptional and post-transcriptional mechanisms contribute to the regulation of

CO protein level. *CO* transcription is controlled by the circadian clock, with a peak around dusk in LD and early in the night in SD, and consistent with this, *CO* transcript levels and/or rhythms are altered in many of the clock mutants described above. In addition, the FKF1 photoreceptor promotes *CO* expression in the afternoon through blue-light-dependent degradation of CDF proteins, which are Dof-type transcription factors that bind to the *CO* promoter and inhibit *CO* transcription (Fig. 19.8) (Imaizumi et al. 2005). Several other proteins that regulate *CO* transcription have been described, but their function is not yet well understood (Morris et al. 2010; Ito et al. 2012).

Other studies have shown that post-transcriptional regulation of CO is also important for the photoperiod response (Valverde et al. 2004; Zuo et al. 2011). In the middle of a LD photoperiod, a phyB-dependent mechanism promotes the proteasome-dependent degradation of CO protein, but in the evening this degradation is opposed by light through the action of phyA and cry2, stabilising CO and allowing the activation of *FT* (Fig. 19.8). While the mechanism by which phytochromes regulate CO stability is not yet clear, two mechanisms for BL-dependent stabilisation of CO have been outlined. Cry2 antagonises the dark-dependent degradation of CO by the COP1/SPA E3 ubiquitin ligase complex (Zuo et al. 2011, Chap. 14), while the FKF1 photoreceptor stabilises CO through a direct interaction (Song et al. 2012b). As both FKF1 and CRY2 proteins are most abundant in the afternoon under LD, both of these mechanisms contribute to maintaining a high level of CO protein specifically under LD.

The photoperiod response in *Arabidopsis* therefore depends on circadian regulation of CO expression, and on complex interactions between multiple photoreceptor inputs, that act to entrain the circadian clock (phyA, phyB, cry1, cry2), to otherwise regulate clock components (ZTL), to activate CO transcription (FKF1) and to regulate CO protein stability (phyA, phyB, cry2, FKF1).

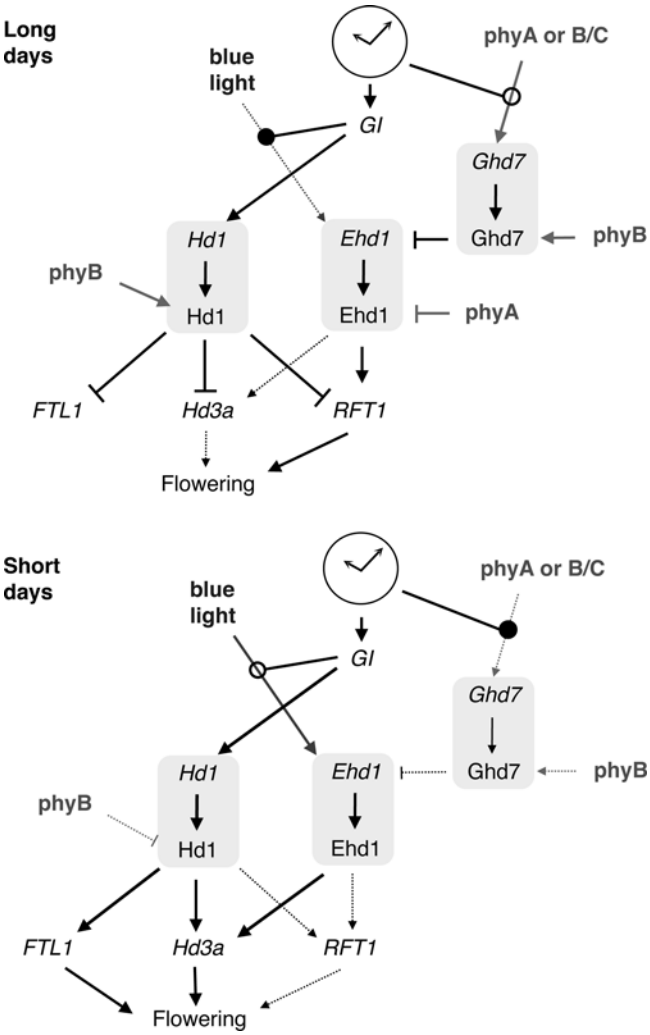

Fig. 19.9 Genetic model depicting the network controlling photoperiod-responsive flowering in rice (Redrawn from Itoh and Izawa 2013; Brambilla and Fornara 2013). Weak and strong effects are indicated by dashed and solid lines respectively. Circles indicate gating of light signals by the circadian clock

Rice

In rice, the *CO*-like gene *Hd1* has also been shown to be important for photoperiod responsiveness. However, in contrast to *Arabidopsis* CO, Hd1 has a dual role, contributing to upregulation of *Hd3a* and induction of flowering under SD but also acting to repress *Hd3a* and inhibit flowering under non-inductive LD (Hayama et al. 2002). *Hd1* expression shows a diurnal expression rhythm, but in contrast to *Arabidopsis CO*, the coincidence of light and *Hd1* expression that occurs under LD represses rather than promotes flowering (Fig. 19.9). *Hd1* expression during the light phase in SD can be increased, and flowering delayed by overexpression of the rice *GI* ortholog (Hayama et al. 2003; Ishikawa et al. 2011), suggesting a conserved role for *GI* and clock regulation of *Hd1*. Interestingly, Hd1 requires phyB to inhibit flowering, but the nature of this interaction is not yet clear (Ishikawa et al. 2011).

In addition to this *Hd1*-dependent pathway, the photoperiod response in rice also involves an Hd1-independent pathway. This pathway features two other genes not conserved in *Arabidopsis*: *Ehd1*, a B-type response regulator that promotes flowering and *Hd3a*/*RFT1* expression in SD, and *Ghd7*, a CCT-domain protein that represses *Ehd1* expression in LD (Fig. 19.9). In SD, *Ehd1* is upregulated in the morning through a BL-dependent mechanism involving *GI* (Itoh et al. 2010), whereas in LD, *Ehd1* is repressed in the morning by phytochrome-dependent induction of *Ghd7*. A shift in the sensitive phase for phytochrome induction of *Ghd7* from morning in LD to midnight in SD explains both the SD-specific *Ehd1* expression and the ability of a short night break to repress this expression and promote flowering (Itoh et al. 2013).

The photoperiodic control of flowering in rice thus essentially consists of two linked external coincidence mechanisms

and at least two photoreceptor systems. Given the importance of diurnal expression rhythms in these mechanisms, it is not surprising that roles for other clock components such as *ELF3* are also beginning to emerge (Saito et al. 2012).

It is clear that powerful molecular genetic studies combined with careful physiological studies have enabled substantial recent progress in answering several of the long-standing questions in higher plant photoperiodism: the molecular mechanisms underlying the photoperiod response, the basis for the difference between LDP and SDP responses, and nature of mobile signalling in photoperiodism. We can look forward to continued rapid progress on all three fronts.

19.6 Photomorphogenesis and Phototropism in the Natural Environment

In discussing the significance of photomorphogenesis in the natural environment, several things must be kept in mind. We need to consider the changes that may occur in the properties of light reaching the plant, the kind of information plants may extract from these changes, and the way in which this information might be converted into an appropriate developmental response.

Most plants have adopted a sedentary habit and are therefore committed to adapt to changes in their environment by developmental plasticity. Natural selection is therefore likely to have favoured modifications of development that maximise energy capture or that improve the ability of the plant to resist detrimental effects of light. In addition, correlation between changes in light environment and other environmental variables such as cold or drought are also likely to have favoured crosstalk between light signalling and other signalling pathways and the exploitation of light information as a predictive signal. Conditions of continuous selection would also result in pressure to extract increasing amounts of information from light, through an ability to monitor more subtle changes. This in turn could conceivably have supported the evolution of multiple photoreceptors with diverse light-sensing properties.

Speculations about the importance of photoreceptors in the natural environment have been largely based on studies of mutants and transgenic lines grown as single plants in controlled-environment conditions, combined with an intuitive appreciation for the developmental predicament of the plant. However, they have recently begun to receive solid support from experiments conducted under natural and/or competitive conditions (Ballare 1999).

19.6.1 Improving Energy Capture

In general, higher plants have two strategies to increase their capture of energy. They can either gain access to more energy by extending their growth into areas of stronger light, or they can more efficiently capture the energy already reaching them.

Measurements of light quality in the natural environment have shown that changes in the amount of light due to cloud cover or the time of day are accompanied by relatively small changes in its spectral distribution (Franklin and Whitelam 2005). In contrast, chlorophyll-containing tissues absorb efficiently in the R and B region of the spectrum but transmit and reflect a substantial proportion of light in the FR waveband. Thus, the presence of plants affects the local light environment by causing a measurable decrease in the ratio of R to FR light energy. This may occur by the filtering out of R and/or by increased lateral reflection of FR. However, it is particularly significant that increases in lateral reflection of FR from neighbouring plants occur prior to any reduction in the amount of photosynthetically active R and BL wavelengths (Ballare et al. 1990). An increase in the amount of FR is thus an unambiguous signal to the plant that potential competitors are growing nearby. Where this signal is unidirectional, the appropriate response of the plant is obviously to redirect its growth away from the other plants. In a denser population, the gradient in FR will not be as great, and the response may also include an increase in overall growth rate. Although the horizontal and lateral components of the response to shading are often treated separately as phototropism and shade avoidance, it is more appropriate to consider both responses as aspects of a strategy in which the plant is actively "foraging" for light (Ballare et al. 1997).

A negative phototropism in response to increases in lateral FR reflected from neighbouring plants has been demonstrated in cucumber. This response is completely lacking in a phyB-deficient mutant, indicating that in addition to its role in shade avoidance, phyB is also important for the detection of non-shading neighbours (Ballare et al. 1992). The existence of additional phyB-type phytochromes with differing roles at different stages of development suggests that plants are still evolving to fine-tune their capacity for shade avoidance and neighbour detection and emphasises the importance of these responses for the plant.

As the canopy closes or population density increases, increases in the leaf area index also occur, and as a result the light energy in the R and BL wavebands decreases. Under such circumstances, a plant may also be exposed to a lateral gradient in BL and show a positive phototropic response. The phyB-deficient mutant of cucumber retains the ability to respond to such a gradient (Ballare et al. 1991), implying the action of a BL photoreceptor, which is most probably phototropin, under conditions of deep shade, where it is likely that the observed growth responses result from a reduction in activity of several photoreceptors including the phyB-type phytochromes, cry1 and phototropin (Ballare 1999). Without phyA however, seedlings cannot sense the FR transmitted through the canopy and do not de-etiolate, indicating that

phyA may be essential for maintaining a degree of de-etiolation in highly competitive situations (Yanovsky et al. 1995).

Under shade conditions many plants may also increase their efficiency of light capture, by modifying various features of their photosynthetic organs. Depending on the species, this may include modification of light harvesting complex composition, chloroplast organisation, orientation or position and leaf shape, size or thickness (Terashima and Hikosaka 1995; Vogelmann et al. 1996; Mullineaux and Karpinski 2002). Acclimation to shade is therefore a complex phenomenon but does at least in some cases involve responses that can be considered photomorphogenic such as leaf reorientation (Inoue et al. 2008b). The fact that phototropins control chloroplast orientation and stomatal aperture also clearly implies an important role in the regulation of photosynthesis (Boccalandro et al. 2012). However, in general the contribution of photomorphogenic photoreceptors to photosynthetic acclimation is not yet well understood.

19.6.2 Light and the Seed Habit

Other adaptive responses to light seem to have arisen with the development of the seed habit. Control of seed germination is important to allow seedling to develop in favourable light environment. Particularly for small-seeded species germinating under the soil surface, seedlings must be able to emerge into full light before the seed energy reserves are exhausted. The extremely low fluences of light needed to induce germination of some species can be understood as a signal to the seed that it is near the soil surface before making the irreversible commitment to germinate. In other species, the higher light requirement and R/FR reversibility of germination may reflect a strategy to preferentially promote germination under gaps in the canopy (Casal and Sanchez 1998).

Investment of energy in the seed has allowed a period of time in which seedlings can develop independently of the need to photosynthesise. In effect this provides a longer period of time over which the seedling can integrate information about its light environment and adjust its development appropriately. In combination with the seed habit, many species have developed a growth strategy of etiolation in which they are able to suppress normal light-regulated leaf development and elongate rapidly growing in darkness. This could conceivably have been favoured in evolution because it increases the efficiency with which the plant uses stored seed reserves but also because its rapid emergence into the light after germination will maximise competitive advantage. However, along with this strategy comes the need for anticipation of imminent emergence into the light environment, and a rapid response immediately following emergence. PhyA does appear to serve this purpose under natural conditions, and it is conceivable that some of the distinct features of phyA could have arisen in response to this pressure (Mathews 2006).

19.6.3 Avoidance or Survival of Unfavourable Conditions

In addition to useful light for photosynthesis, sunlight also contains potentially damaging UV wavelengths. Various phenylpropanoid pigments including sinapates and flavonoids absorb UV and reduce its damaging effects on the plant (Bieza and Lois 2001). The production of these pigments in many cases is strongly induced by light as a result of increased expression of certain genes in phenylpropanoid metabolism (Shirley 1996; Ryan et al. 2001). In many cases, this induction is strongest in young seedlings and immature leaves, which are more susceptible to UV damage.

It is also possible that light can also serve as an indirect signal of other adverse aspects of the environment. For example, the fact that in some species light can act to inhibit germination can be understood in terms of the need for a damp environment and a correlation between reduced water availability near the soil surface and increased light levels. A similar association could explain the negative phototropism of some roots, and experimental evidence supporting this has recently been reported (Galen et al. 2007). The action of phot1 allows roots near the surface to reorient and grow downwards into the soil, with consequences for the availability of water to those roots and performance under drought conditions (Galen et al. 2007).

A more complicated kind of correlative selection may underlie many seasonal responses. Factors such as temperature and water availability can clearly become limiting at certain times of year in some environments, and many plants are able to avoid the deleterious effects of these seasonal extremes through suppression of normal growth and the adoption of various survival strategies. These include seed and bud dormancy, formation of storage organs and initiation of flowering, which can be timed so as to allow the reproductive cycle to be completed before unfavourable conditions return. Changes in limiting factors of temperature and water availability can act directly as triggers for these changes (as seen in cold temperature requirements for germination or flowering). However, although seasonal, these factors are also subject to irregular short-term variation, whereas change in day length is a much more constant and reliable indicator of season from year to year. In general, the degree of photoperiod responsiveness is an important aspect of adaptation to growth at a given latitude (Thomas and Vince-Prue 1997).

As the molecular basis for light and photoperiod responses has become better understood, increasing numbers of studies are turning towards an investigation of the ecological

significance of observed genetic variation or the genetic basis for natural variation in plant responses. Notable recent examples include demonstrations of the contribution of the phyC photoreceptor to natural variation in *Arabidopsis* flowering time (Balasubramanian et al. 2006), the role of *FT* homologues in latitudinal variation in seasonal dormancy in poplar (Böhlenius et al. 2006) and the fitness consequences of genetic variation in *Arabidopsis* circadian clock function (Michael et al. 2003).

19.7 Concluding Remarks

Considering that plants are fixed in one place and dependent on light as an energy source, it is not surprising that sophisticated mechanisms have evolved enabling them to modify their development in response to light and thus to better compete with their neighbours. Persistent selective pressures for extracting more subtle information from the light environment have favoured the evolution of several distinct photoreceptor systems. For the most part, these systems act synergistically, increasing the general sensitivity of the plant to light. However, some photoreceptors have developed discrete light-sensing abilities, which may be linked to specific physiological and ecological roles.

The past 30 years have seen major advances in our understanding of the photoreceptors involved in photomorphogenesis and the definitive identification of some of the molecular and cellular processes required for expression of light responses. We still do not fully understand the complexities of signal transduction or the network of interactions between light, plant hormones and other factors. Nevertheless, the genetic and molecular tools are now available to enable a thorough analysis of these aspects of photomorphogenesis over the coming years. Greater understanding of photomorphogenesis will bring an increased ability to manipulate plant light responses for practical purposes, such as in the control of density-dependent shading, flowering and yield in horticultural and crop plants. It will also help us to better understand the origins and adaptive significance of natural variation in growth habit and flowering phenology.

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