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INVITED REVIEW

Phytochrome-mediated development in land plants: red light sensing evolves to meet the challenges of changing light environments

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Abstract

Phytochromes are photoreceptors that provide plants with circadian, seasonal, and positional information critical for the control of germination, seedling development, shade avoidance, reproduction, dormancy, and sleep movements. Phytochromes are unique among photoreceptors in their capacity to interconvert between a red-absorbing form (absorption maximum of ~660 nm) and a far-red absorbing form (absorption maximum of ~730 nm), which occur in a dynamic equilibrium within plant cells, corresponding to the proportions of red and far-red energy in ambient light. Because pigments in stems and leaves absorb wavelengths below about 700 nm, this provides plants with an elegant system for detecting their position relative to other plants, with which the plants compete for light. Certain aspects of phytochrome-mediated development outside of flowering plants are strikingly similar to those that have been characterized in *Arabidopsis thaliana* and other angiosperms. However, early diverging land plants have fewer distinct phytochrome gene lineages, suggesting that both diversification and subfunctionalization have been important in the evolution of the phytochrome gene family. There is evidence that subfunctionalization proceeded by the partitioning among paralogues of photosensory specificity, physiological response modes, and light-regulated gene expression and protein stability. Parallel events of duplication and functional divergence may have coincided with the evolution of canopy shade and the increasing complexity of the light environment. Within angiosperms, patterns of functional divergence are clade-specific and the roles of phytochromes in *A. thaliana* change across environments, attesting to the evolutionary flexibility and contemporaneous plasticity of phytochrome signalling in the control of development.

Keywords: *Arabidopsis*, development, gene duplication, green algae, land plants, phytochrome, rice, shade

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Introduction

Photoreceptors function at the interface between organisms and their environments, providing information that is critical for the appropriate timing of growth and developmental transitions. The exquisite fine-tuning of land plants to their light environments is manifest in numerous phenomena, from the coordinated control by three distinct photoreceptor systems of branching in the filamentous protonemata of a moss (Uenaka *et al*. 2005) to the preconditioning by a single photoreceptor that enables germinating *Arabidopsis* seedlings to anticipate their most likely environment (Mazzella *et al*. 2005). Such responsiveness to environmental signals is useful only if it is not lost when new environments are encountered, and when plant form and life histories change. In order to promote survival, photoreceptor systems must be robustly linked to the signalling networks that ensure suitable responses. At the same time, both information gathering and processing must be flexible enough to change when new challenges are presented. In the case of phytochromes, the principal photosensory function is to detect

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the relative proportions of red (R) and far-red (FR) energy in ambient light (Smith 1982). While this basic function has been conserved through millions of years of prokaryotic and eukaryotic evolution, the organisms in which they are found have diversified profoundly. The responses induced by light signals are concomitantly diverse, shaped by the morphologies, life histories, and environments of the photoreceptor-bearing organisms. The diversity of phytochrome-mediated regulatory functions in major clades of green plants (green algae and land plants) reveals how a single photosensory function has evolved to meet many specific needs and reveals the ecological importance of phytochromes for all plants. Phytochromes control cellular responses and tropisms such as chloroplast movement, cytoplasmic motility, endoreduplication, and nyctinastic movements, and of tropisms such as gravitropism, polarotropism, and phototropism (e.g. Wada & Kadota 1989; Kim *et al*. 1993; Haupt & Häder 1994; Hangarter 1997; Gendreau *et al*. 1998; Takagi *et al*. 2003). However, it is the role of phytochromes in the major developmental pathways of germination, de-etiolation, shade avoidance, and flowering that is likely to have had the biggest impact on the establishment and ecological success of the major clades of land plants. A review of the literature reveals the surprisingly early appearance of several responses considered to be important in the ecology of angiosperms, including differential control of germination in open and shaded habitats, delay of development in the dark coupled with rapid developmental responses to light signals, and shade avoidance. Moreover, the gene phylogeny suggests that functional diversification in red- and far-red sensing, perhaps coinciding with increasing complexity in the light environment due to the origin of canopy shade, has been important in ferns, gymnosperms, and angiosperms.

Characteristics of phytochrome action and structure

Photosensory specificity, physiological response modes and light lability

After three centuries of written observations on the impact of light and light quality on plant form (reviewed in MacDougal 1903), breakthroughs occurred in 1920, when it was noted that short-day plants require sufficiently long nights to flower (Garner & Allard 1920) and in 1946, when it was noted that R was the most effective wavelength for interrupting a long night in order to inhibit flowering (Parker *et al*. 1946). In certain cases, the effect of an R pulse in the night could be cancelled by a subsequent pulse of FR. Similarly, the germination of light-sensitive, or photoblastic, seeds was found to be induced by R and inhibited by FR (Flint & McAlister 1935, 1937; Borthwick *et al*. 1952). Moreover, repeated alternating pulses of R and FR could be given, with the last pulse determining the response. From these observations, a model of a single pigment, activated by R and inactivated by FR was derived. Determination of action spectra for the R induction and FR reversal led to the identification of phytochrome in crude plant extracts (Butler *et al*. 1959), the first pigment for plant photomorphogenesis to be characterized. Phytochrome is synthesized in the R-absorbing form (Pr, absorption maximum ~660 nm) and is converted to the FR-absorbing form (Pfr, absorption maximum ~730 nm) when irradiated with R. Irradiation with FR converts Pfr back to Pr. There is evidence that Pfr, Pr, and the photoconversions between them promote biological responses (e.g. Shinomura *et al*. 2000), and that biological outputs reflect the ratio of Pr to Pfr, which is dynamically determined by the relative proportions of R and FR in ambient light, the forward and reverse rates of photoconversion, and the rates of thermal interconversion (Rockwell *et al*. 2006).

Because all phytochrome present in dark-imbibed seeds or in dark-grown seedlings is in the Pr form, extremely low fluences of light in most regions of the visible spectrum raise the level of Pfr. Responses saturated by the low levels of Pfr (10^{-6}–10^{-3} Pfr/Ptotal) that are established by such low fluences are called very low fluence responses (VLFR) and the role of phytochromes in these cases apparently is to sense the quantity or presence of light rather than its quality (Smith & Whitelam 1990). Responses saturated at intermediate fluences (1–1000 μmol m^{-2} s^{-1}) are low fluence responses (LFR), and are characterized by repeated reversibility, with R inducing the response and FR reversing it. The relationship between Pfr/Ptotal and LFR is logarithmic, and saturation of the response often occurs at low levels of Pfr/Ptotal (10^{-2}–0.87 Pfr/Ptotal; Smith & Whitelam 1990). In contrast to VLFR and LFR, which require transient exposures of lesser or greater duration, respectively, high-irradiance responses (HIR) require continuous, long-term irradiation and they are dependent on wavelength; maximum response usually occurs at wavelengths that maintain low levels of Pfr for long periods of time (Smith & Whitelam 1990), such as occurs in FR-rich environments.

VLFR may have important consequences for buried seeds and seedlings, allowing them to respond rapidly to the very brief exposures to light caused by soil disturbance (Smith 1995; Casal *et al*. 1997). In contrast, R/FR reversible LFR are critical at all stages of development. They include transient responses such as chloroplast movement, nyctinasty, and ion fluxes, as well as growth and developmental responses such as seed germination, de-etiolation, stem growth, leaf expansion, and the induction of flowering (e.g. Mancinelli 1994). The longer exposures required for LFR suggest that they are important responses for development in relatively open habitats (Smith 1995), where the higher ratio of R:FR reliably indicates the absence of competitors (see below). The dependence of HIR on the maintenance of low levels of Pfr for long periods of time, indicating prolonged

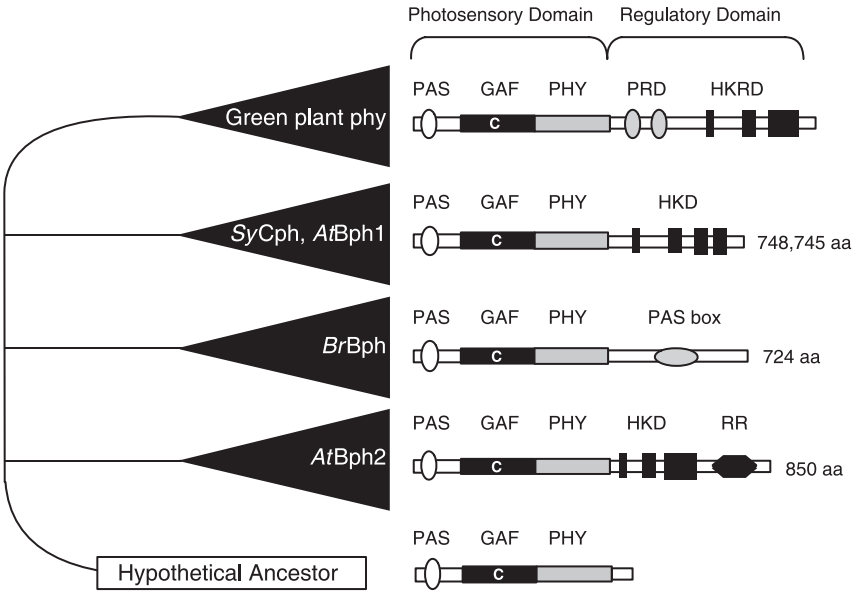

Fig. 1 Phytochrome structures in green plants and prokaryotes. N-terminal photosensory domains of green plant phytochromes are homologous with photosensory domains of bacteriophytochromes, but the relationships among gene lineages remain unresolved. Regulatory domains of the lineages represented are not closely related. *Sy*Cph1, *Synechocystis* sp. PCC6803 Cph1; *At*BphP1 and *At*BphP2, *Agrobacterium tumefaciens* BphP1 and BphP2; *Br*Bph*P*, *Bradyrhizobium* sp. ORS278 BphP; PAS domain (Ponting & Aravind 1997); GAF domain (Aravind & Ponting 1997); PHY domain (Montgomery & Lagarias 2002); PRD, PAS-related domain; HKD, histidine kinase domain; HKRD, histidine kinase related domain; RR, response regulator.

exposure to FR, suggests that they are important responses for development in more closed habitats, such as in deep canopy shade or in the first few millimeters of soil below ground level, which are characterized by reduced ratios of R:FR (Smith 1982, 1995; Yanovsky *et al*. 1995). HIR are important in germination, de-etiolation, and long-day (LD) induction of flowering.

Among the most important of light cues used by plants are those that indicate where they are relative to neighbouring plants that might impinge on their access to photosynthetically active radiation. Because pigments in stems and leaves absorb wavelengths below about 700 nm, canopy shade has a lower R:FR ratio (0.05–1.15, Smith 1982) than direct light (1.05–1.25, Smith 1982). Phytochromes, with their absorption maxima of 660 nm and 730 nm for Pr and Pfr, respectively, are well suited to serve as indicators of changes in the R:FR ratio of ambient light, and thus as indicators of their proximity to neighbours. Because small changes in the R:FR ratio lead to large changes in the ratio of Pfr to Ptotal (Smith 1982), even very small changes in the R:FR ratio are detectable, such as those that occur in the light reflected from stems of neighbouring plants while they are still small (Ballaré *et al*. 1990). Such positional information allows plants to germinate in habitats appropriate to their ecologies and to alter their morphologies when this will facilitate their success in reaching the light, or alternatively, in their early entry into the reproductive phase.

Before it became apparent that there were multiple phytochromes in single genomes (Sharrock & Quail 1989), it was recognized that flowering plants contain two physiologically distinct pools of phytochrome, one relatively stable in light and one more labile in light. Because light labile phytochrome is abundant in dark-imbibed or dark-grown tissues and is rapidly degraded and down-regulated in the light (Somers *et al*. 1991), it has an enhanced capacity to serve a transient role in conditions when extremely high sensitivity may be advantageous (Furuya & Schäfer 1996), such as in VLFR. Differential control of abundance by light also provides a mechanism for coordinating potentially antagonistic activities of paralogous phytochromes by temporally restricting the activities of the light labile types.

Phytochrome structure

Green plant phytochromes have remarkably conserved primary and secondary structures. With few exceptions, coding sequences are interrupted by three introns positioned at conserved sites (Sharrock & Mathews 2006). The large apoproteins (~1100 amino acids) comprise an N-terminal photosensory region and a C-terminal regulatory region, each of approximately 500–600 amino acids (Fig. 1; Fankhauser 2001; Montgomery & Lagarias 2002). The N-terminal photosensory core comprises a PAS domain, a GAF domain that harbours the conserved cysteine to which a linear tetrapyrrole chromophore covalently binds, and a GAF-related PHY domain unique to phytochromes, which also have been referred to as P2, P3, and P4 (Montgomery & Lagarias 2002). The first insight into the structure of the PAS and GAF folds came only recently, from a 2.5-Å crystal structure of these domains from the bacteriophytochrome of *Deinococcus radiodurans* (Wagner *et al*. 2005), which is likely to be very similar in important details to structures found widely in phytochromes (Rockwell & Lagarias 2005; Wagner *et al*. 2005). The surprising nature of the interaction between the PAS and GAF folds, a trefoil knot, rare among protein structures, has profound implications for phytochrome activities, perhaps resulting in a much more rigid structure than is typical of interdomain interactions,

increasing the efficiency of photoconversion between Pr and Pfr (Rockwell & Lagarias 2005). At the same time, the D-ring of the chromophore, which rotates during photoconversion, is strikingly less packed by protein residues than the rest of the chromophore, which is buried deeply in the GAF fold (Wagner *et al*. 2005). These results further confirm the uniqueness of phytochromes among all known light-sensing pigments. The regulatory region comprises a PAS-related domain (PRD) of two PAS repeats and a histidine kinase-related domain (HKRD). Phytochrome activity requires dimerization of two holoprotein monomers, and recent data have revealed the presence of both homodimers and heterodimers *in planta* (Sharrock & Clack 2004).

Evolution of phytochrome structure

The origin of green plant phytochromes

Detection of phytochrome-like sequences in the genome of the cyanobacterium *Synechocystis* sp. that were cloned and expressed in *Escherichia coli* provided the first evidence of phytochromes in prokaryotes (Hughes *et al*. 1997; Lamparter *et al*. 1997b). Subsequent biochemical studies of cyanobacterial phytochromes have been important in defining the minimum structural determinants of phytochrome activity. Analyses of *Synechocystis* Cph1 revealed that fragments consisting only of the PAS, GAF, and PHY domains are sufficient for bilin lyase activity (chromophore attachment) and for R/FR reversibility (Wu & Lagarias 2000). Cph1 has an active histidine kinase domain (HKD) fused C-terminal to its PHY domain (Fig. 1) that modulates signalling through a phosphorelay with response regulators (Yeh *et al*. 1997). In contrast, the large C-termini of the green plant phytochromes have two PAS repeats positioned between the photosensory domain and the HKRD lacks histidine kinase activity (Fankhauser 2001). The C-termini of green plant phytochromes have nonetheless been viewed as critical to signalling based on analyses of deletion and point mutants (Fankhauser 2001). However, it has been shown that the HKRD is dispensable (Krall & Reed 2000), and that 650-amino acid N-terminal fragments of phyB are sufficient for both photosensory and regulatory functions (Matsushita *et al*. 2003). Analyses of a smaller N-terminal fragment lacking the PHY domain indicates that signalling occurs through the PHY domain (Oka *et al*. 2004), which is also necessary for R/FR reversibility (Wu & Lagarias 2000). The 650-amino acid fragments induced phyB responses with much higher sensitivity to light than full-length phyB, suggesting that while the C-terminus of green plant phytochromes may not be required for light signalling, it appears to be important in modulation of light signals (Matsushita *et al*. 2003).

The structures in Fig. 1 represent a subset of the diversity in C-termini of bacteriophytochromes and fungal phytochromes (e.g. Fankhauser 2001; Lamparter 2004; Blumenstein *et al*. 2005; Karniol *et al*. 2005), suggesting there is a complex history of phytochrome lineages involving the acquisition of different C-termini and the use of different signalling mechanisms. Understanding the evolutionary history of phytochromes will first require sampling and analyses of the PAS, GAF, and PHY domains from representative prokaryotic and eukaryotic (fungal, diverse algal groups, plants) lineages. Published trees based on analyses of GAF domain sequences (Montgomery & Lagarias 2002; Lamparter 2004; Karniol *et al*. 2005) lack sufficient phylogenetic information to achieve a robust hypothesis of relationships among the bacteriophytochrome lineages and of their relationships with the lineages in various eukaryotes. Second, distinctive C-termini may serve as markers of clade membership, and may help to identify relatives of green plant phytochromes. One analysis indicates that C-termini of currently sequenced cyanobacterial phytochromes are not closely related to those of green plant phytochromes, but the results do not suggest a robust alternative hypothesis (Lamparter 2004). Together these data suggest that R/FR-sensing phytochromes originated in bacteria, where they function as sensors of bilin and oxygen as well as of light (Montgomery & Lagarias 2002), and perhaps with a streamlined structure comprising only the PAS-GAF-PHY sequence that is homologous with the photosensory core of green plant phytochromes.

Phytochrome phylogeny within land plants

Due to the high degree of structural conservation throughout their length, green plant phytochromes have a history that is readily traced in land plants. Results from phylogenetic analyses of nucleotide sequences are summarized in the tree depicted in Fig. 2. This reveals that near the origin of seed plants the phytochrome trunk lineage split into two major gene lineages (Fig. 2, #1) that have descendants in all extant seed plants. One lineage includes *PHYP* of gymnosperms and *PHYB* and *PHYB*-related genes of angiosperms; the other lineage includes *PHYO* and *PHYN* of gymnosperms and *PHYA* and *PHYC* of angiosperms. While it is clear that *PHYP* is the gymnosperm orthologue of *PHYB*, the relationships among *PHYA, PHYC, PHYN* and *PHYO* are less clear. Either *PHYN*/*A* split from *PHYO*/*C* before the radiation of extant seed plants (Fig. 2, #2a) or two separate duplications occurred, one on the branch leading to extant gymnosperms and one on the branch leading to angiosperms (Fig. 2, #2b). Analyses of the currently available published and unpublished data yield conflicting trees (Fig. 3a, b), both of which are incompatible with the body of evidence that suggests that angiosperms and extant gymnosperms are monophyletic sister groups, as in Trees 3c and 3d (reviewed in Burleigh & Mathews 2004). A different rooting of Trees 3a and 3b gives gene phylogenies that are compatible with

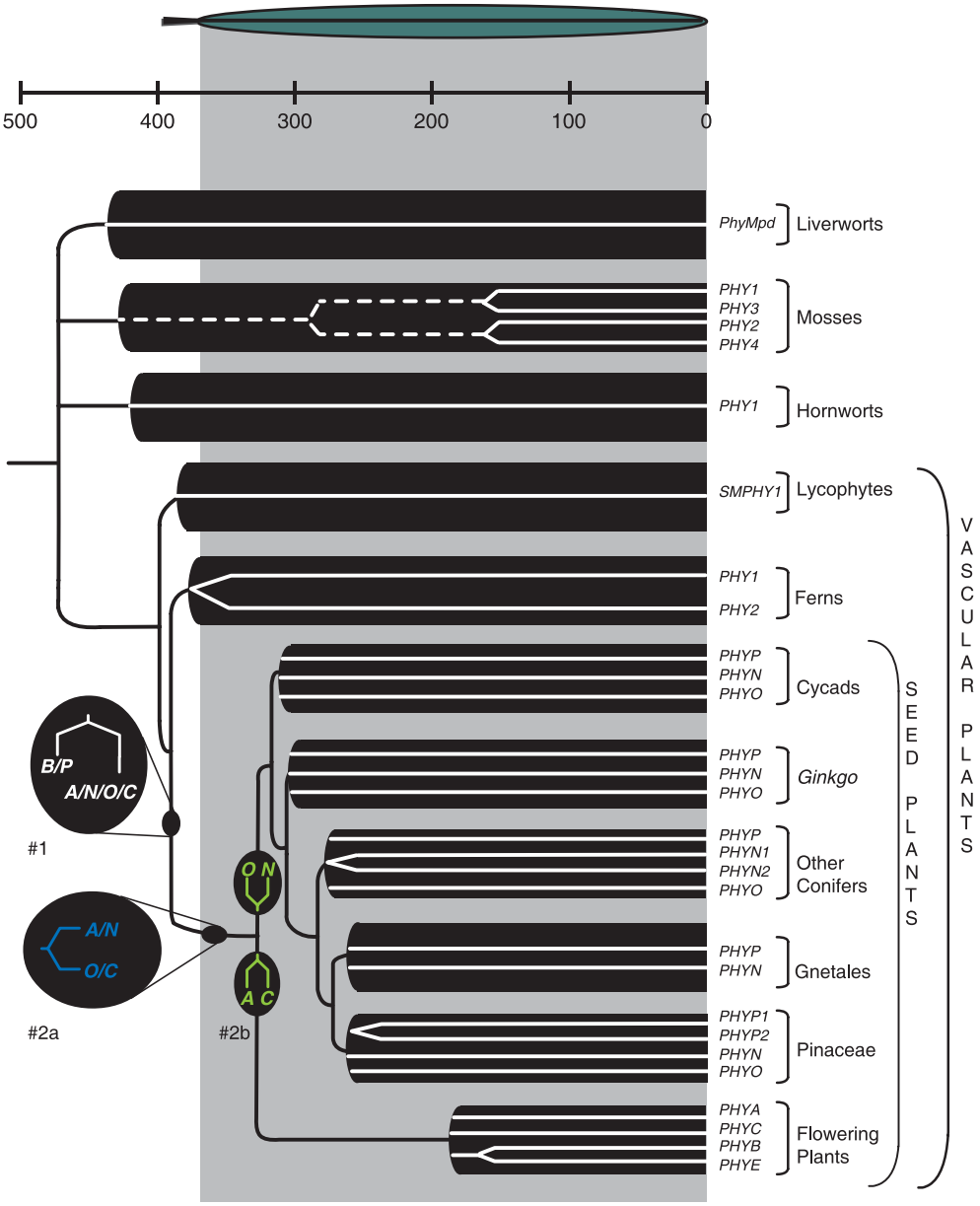

Fig. 2 Relationships among major clades of land plants (Burleigh & Mathews 2004; Pryer *et al*. 2004) shown in solid black lines, widened for each clade to show gene lineages occurring within them based on data in GenBank. Duplications in flowering plants, Pinaceae, other conifers, and ferns are inferred based on the phylogenetic distribution of the genes and on results from phylogenetic analyses (e.g. Mathews *et al*. 1995; Schmidt & Schneider-Poetsch 2002; S. Mathews, unpublished data). For example, the first evidence of *PHYE* in angiosperms is in Austrobaileyes, which diverged from other angiosperms prior to the origin of monocots (S. Mathews, unpublished data) about 134 Ma. All genera of Pinaceae appear to have two copies of *PHYP*, while all other conifers appear to have two copies of *PHYN* suggesting that these duplications occurred early in the history of these lineages (Schmidt & Schneider-Poetsch 2002; S. Mathews, unpublished data). A duplication early in the radiation of ferns is evidenced by the position of the longest and most informative phytochrome sequence from *Psilotum nudum* (GenBank Accession X74930) in a clade with *Adiantum PHY2* (GenBank Accession AB016232; S. Mathews, unpublished data). Lycophytes appear to have more than one phytochrome, but the fragmentary data in GenBank do not allow estimation of the number of discrete lineages, so only one is shown. The positions of the duplications in mosses remain unknown (dashed lines) because data from only a single moss clade are available. A major split in the land plant phytochrome lineage occurred near the origin of seed plants (#1). A single subsequent duplication occurred before the divergence of angiosperms and extant gymnosperms (#2a), or separate duplications occurred in angiosperms and gymnosperms (#2b). Timeline indicates million years ago. The origin of canopy shade occurred between 360 and 380 Ma. Widened lines for each clade extend to the earliest date for which reliable evidence of the lineage occurs in the stratigraphic record. Divergences in the species tree are positioned according to molecular estimates of divergence times. Stratigraphic data and divergence times are from Kenrick & Crane (1997), Pryer *et al*. (2004), Sanderson (2003), Sanderson *et al*. (2004), Stewart & Rothwell (1993), and Wellman *et al*. (2003).

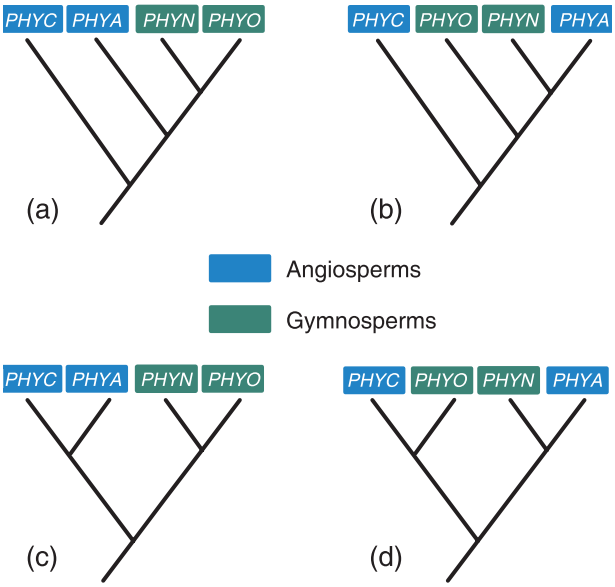

Fig. 3 Gene trees depicting possible relationships among *PHYA*, *PHYC*, *PHYN*, and *PHYO*. The trees in Fig. 3(a, b) were inferred in unweighted and weighted parsimony analyses of partial gene sequences, respectively, where weighting consisted of exclusion of the fastest evolving sites that had been inferred using maximum likelihood. The trees in Fig. 3(c, d) are rerooted versions of 3a and 3b, respectively, such that each is compatible with species relationships.

our understanding of organismal phylogeny (Fig. 3c, d), and it is possible that one of these trees more accurately represents the gene phylogeny. Tree 3c is consistent with two later duplications (e.g. Fig. 2, 2b), whereas Tree 3d is consistent with a single duplication early in seed plants (e.g. Fig. 2a). The trees in Fig. 3(a, b) were inferred in unweighted and weighted parsimony analyses of partial gene sequences (S. Mathews, unpublished data), respectively, where weighting consisted of exclusion of the fastest evolving sites that had been inferred using maximum likelihood. Preliminary results from parsimony-based hypothesis tests to determine if either of the trees can be rejected show that the data set with all sites strongly rejects tree 3d and that the data set with fastest evolving sites excluded strongly rejects tree 3c (S. Mathews, unpublished data). Phylogenetic conflict within seed plant data sets, among classes of nucleotide sites estimated to be evolving at different rates, has been noted previously and it contributes to the difficulty of resolving branching orders among both genes and taxa (Sanderson *et al*. 2000; Magallón & Sanderson 2002; Rydin *et al*. 2002; Burleigh & Mathews 2004). Tree 3d is congruent with trees inferred from smaller data sets using maximum likelihood as the optimality criterion, which may be more robust to analytical errors caused by long-branch effects and variable rates of evolution across sites (Felsenstein 2004). For this reason, tree 3d may be the best hypothesis of the gene phylogeny, but it should be tested with additional data and further rigorous analyses.

Within angiosperms, the evolutionary history of homologues of the five phytochrome genes (*PHYA-PHYE*) of *Arabidopsis thaliana* has been investigated in a series of phylogenetic analyses that have allowed inference of some of the angiosperm-specific events of gene duplication and loss (Sharrock & Quail 1989; Mathews *et al*. 1995; Mathews & Sharrock 1996, 1997). In some cases, hybridization experiments and genome sequences have confirmed the patterns inferred from polymerase chain reaction (PCR) surveys (e.g. Mathews & Sharrock 1996; Howe *et al*. 1998; Goff *et al*. 2002; Yu *et al*. 2002; Li & Chinnappa 2003). Consistent with a duplication prior to the origin of angiosperms (Fig. 2), *PHYA* appears to be ubiquitous in flowering plants and its sister gene, *PHYC*, is nearly so; the loss of *PHYA* has not been detected in any species and the loss of *PHYC* has been documented in a single taxon, *Populus trichocarpa* (Howe *et al*. 1998). Both genes occur in the extant remnants of the earliest diverging angiosperm lineages (Mathews & Donoghue 1999). Independent duplications in the *PHYA* lineage have led to multiple copies in *Stellaria* (Caryophyllaceae; Li & Chinnappa 2003), legumes (Fabaceae; Lavin *et al*. 1998), and parasitic figworts (Orobanchaceae; Bennett & Mathews in press). *PHYE* originated as a duplicate of *PHYB* very early in the history of angiosperms (Fig. 2; S. Mathews, unpublished data). Like *PHYA*, *PHYB* has been detected in all flowering plants that have been sampled, but *PHYE* is missing from some plant lineages, including monocots, Piperales (Mathews & Sharrock 1996, 1997; Goff *et al*. 2002; Yu *et al*. 2002), and possibly Caryophyllales (Li & Chinnappa 2003; S. Mathews, unpublished data). *PHYD* is a more recent duplicate of *PHYB*, resulting from a duplication that occurred along the branch leading to the Brassicaceae (mustard family; K. McBreen & S. Mathews, unpublished data). Independent duplications in the *PHYB* lineage have led to multiple copies in *Solanum* (Solanaceae; Hauser *et al*. 1995; Mathews *et al*. 1995), *Populus* (Salicaceae; Howe *et al*. 1998), and *Daucus* (Apiaceae; Mathews *et al*. 1995).

Similarly, within gymnosperms, independent duplications have led to two copies of *PHYP* in Pinaceae and two copies of *PHYN* in all other conifer families (Fig. 2; Mathews & Donoghue 2002; Schmidt & Schneider-Poetsch 2002). In ferns, it is clear that *Adiantum* has at least two distinct phytochrome lineages, and that other ferns have orthologues of these genes. The duplication giving rise to these two genes apparently occurred very early in the history of ferns (Fig. 2), since the copy detected in the early diverging fern *Psilotum* is most closely related to *Adiantum PHY2* (data not shown). Analysis of unpublished data from *Ceratopteris richardii* shows that it has homologues of both *PHY1* and *PHY2* (T. Bissoondial and T. Short, personal communication). The genome of *Ceratopteris* also has a homologue of *Adiantum PHY4*, which is interrupted by gypsy-like retrotransposon,

suggesting that there was a gene duplication in polypod ferns prior to the divergence of these closely related genera. Additional copies detected in *Ceratopteris* result from more recent gene duplications, possibly involving retrotransposition and gene conversion (T. Bissoondial and T. Short, personal communication). Additional copies in other ferns also may result from relatively recent gene or genome duplications (polyploidy is widespread in ferns and chromosome numbers are among the highest in land plants). In lycophytes, just a single full-length sequence is available from *Selaginella martensii* and the fragments in GenBank that suggest there are multiple copies are not informative enough to determine whether they represent distinct phytochrome lineages. In mosses, *Physcomitrella patens* has two well-defined phytochrome lineages, each of which is duplicated, perhaps as a result of a past polyploidization event (Reski 1998). Orthologues of each of the major types also occur in *Ceratodon purpureus*, but their broader distribution in mosses remains to be determined, and thus the timing of the duplication is uncertain (dashed lines, Fig. 2). All of the genes from mosses are more closely related to each other than to any gene from other land plant groups, including the single genes that have been detected in the hornwort, *Anthoceros punctatus* and the liverwort *Marchantia polymorpha*. In charophytes, an assemblage of green algal families that includes Charophyceae, the sister group of land plants (Lewis & McCourt 2004), gene diversification may be limited. *Mesotaenium caldariorum* has two highly similar genes (99.25% identity; Wu & Lagarias 1997). Noncanonical phytochromes, which have a canonical photosensory core fused to novel C-termini, have been detected in some ferns, in the moss *C. purpureus*, and in the alga *Mougeotia scalaris* (Thümmler *et al*. 1992; Suetsugu *et al*. 2005).

One important implication of the pattern of independent gene diversification events in major clades of land plants (Fig. 2) is that it increases the likelihood that similar functions found in different clades have independent origins and evolutionary histories. Within angiosperms, there is a much firmer basis for the inference of phytochrome function based on sequence homology because angiosperm *PHY* gene lineages are highly conserved, with gene duplication and loss being relatively infrequent (Mathews & Sharrock 1997) compared with many nuclear gene families (Clegg *et al*. 1997). Nonetheless, gene duplication and loss, although limited, mean that different species may have slightly different complements of *PHY* loci and thus, differences in patterns of functional divergence may be expected. The larger question is the one of how the function of a single ancestral phytochrome has changed, been conserved, or subdivided as new clades of both genes and plants have originated and diversified. Are any of the functions seen in angiosperms uniquely derived? Are patterns of functional divergence similar in different clades? How have changes in function impacted the evolution of species and vice versa? Comparison of phytochrome-mediated development in *Arabidopsis* and rice, representing divergent angiosperm clades, suggests that the functional divergence of phytochromes in these species has followed different patterns. A survey of phytochrome-mediated developmental pathways in other clades of land plants suggests that phytochromes play similar, but perhaps independently evolved, roles in linking development with environmental signals across divergent clades of land plants.

Phytochrome-mediated development in green plants

Germination in Arabidopsis *and rice*

Appropriate positioning and timing in germination are critical for seedling establishment, and phytochromes predominate over blue light (B) receptors in the control of germination of light-sensitive seeds, perhaps because longer wavelengths of light more readily penetrate the seed coats and the initial few millimeters of soil (Smith 1982; Frankland & Taylorson 1983). The fact that phytochromes have such a prominent role in mediating germination suggests that neighbour proximity, sensed via variation in the R:FR ratio of ambient light, is a critical factor in the control of germination of photoblastic seeds. R/FR reversible germination, that is, LFR germination that is induced by R and inhibited by FR, is found in a taxonomically diverse set of angiosperm lineages, and may be widespread in species with light-sensitive germination. In at least some species, the roles of R and FR are reversed, with FR inducing and R inhibiting germination; in species in which R is inductive, shade light also inhibits germination (Frankland & Taylorson 1983), suggesting that outputs can be modified in a way that is ecologically significant. In *Arabidopsis*, phyB is the mediator of R/FR reversible germination, whereas phyA mediates FR-HIR germination, with phyE playing a secondary role (Fig. 4; Botto *et al*. 1996; Shinomura *et al*. 1996; Hennig *et al*. 2002). Additionally, phyA uniquely mediates VLFR germination, which allows dark-imbibed seeds to germinate in response to millisecond pulses of light, irrespective of wavelength (Fig. 4; Botto *et al*. 1996; Shinomura *et al*. 1996). Photoblastic rice seeds germinate in the same three modes, but the roles of specific phy in the responses have not been determined because photoblastic seeds are rare in rice and the lines in which *phy* mutants have been isolated do not require light for germination (Fig. 4; Chung & Paek 2003). However, the roles of rice phytochromes in de-etiolation and flowering (see below) suggest that as in *Arabidopsis*, phyB may mediate R/FR-reversible germination while phyA mediates VLFR and FR-HIR germination. The relative importance of these three different modes of germination in natural populations has not been investigated. Such data are needed to determine the ecological significance of this

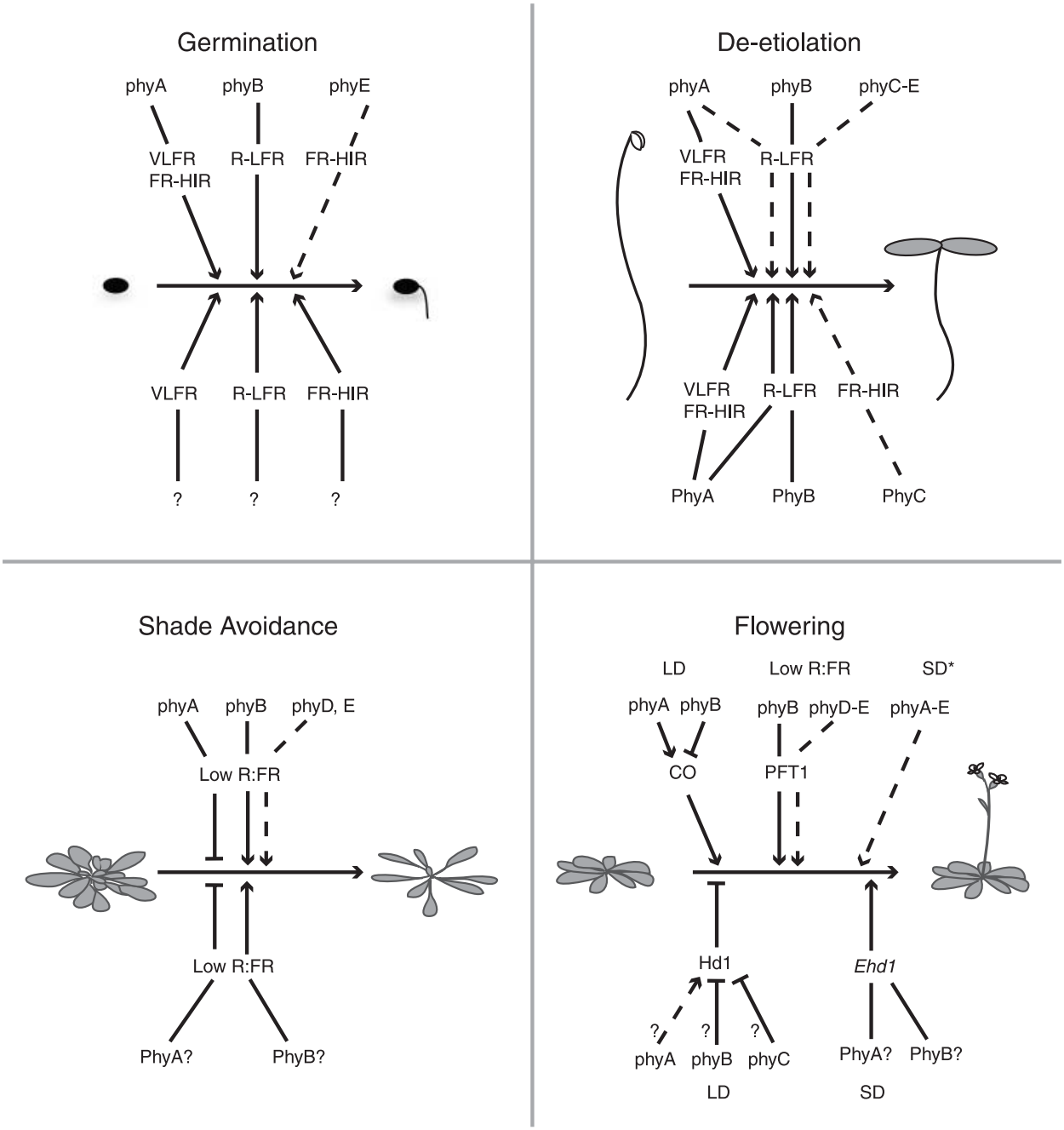

Fig. 4 The roles of individual phytochromes in germination, de-etiolation, shade avoidance, and flowering as described in the text. Solid lines or arrows indicate a phytochrome that has a prominent role in the depicted transition; dashed lines or arrows indicate a phytochrome that has a lesser role in the depicted transition. *Arabidopsis* phytochromes (phyA-phyE) are above and rice phytochromes (PhyA-PhyC) are below the transition arrow. *The prominence of various phytochromes in SD flowering is temperature-dependent.

multiplicity of responses. It is possible that in different environments different responses predominate, suggesting that phytochrome diversification has contributed to increased ecological amplitude of species. However, it also is possible that a subset of the responses is rare in natural populations, despite our ability to detect them in laboratory settings, and that maintenance of variation is more important for long-term evolutionary potential than for short-term ecological flexibility.

Germination outside of angiosperms

The very long history of LFR reversible germination in the green plant lineage suggests that this is one of the most

basic of phytochrome functions in plants that colonized the land, first influencing germination of spores, then of seeds. While spores and seeds are not equivalent structures, dormancy requires the synthesis and accumulation of similar proteins in each case, and metabolism during germination also is similar (Banks 1999). R/FR reversible germination has been documented outside of land plants, in the green alga *Chara* (Charophyceae; Takatori & Imahori 1971), in the nonvascular plants, liverworts and mosses (Cove *et al*. 1978; Bopp 1983; Hartmann & Jenkins 1984), in ferns (Miller 1968; Cooke *et al*. 1993), and in pines (Toole *et al*. 1961; Frankland & Taylorson 1983). In ferns, as in angiosperms (Frankland & Taylorson 1983), there is variability among species respecting the light quality that induces reversible germination, with R or FR being effective in different cases (Miller 1968; Raghavan 1973), and as in angiosperm seed development (Frankland & Taylorson 1983; Shinomura 1997), the light requirement for germination in some species is determined by light conditions during sporogenesis (Wada & Kadota 1989). The fern *Ceratopteris richardii* has high germination rates in continuous FR, typical of the HIR, as well as in response to brief light pulses, typical of VLFR (Cooke *et al*. 1993). Thus, phytochrome-mediated germination in ferns is similar in several respects to that of angiosperm seeds. More surprisingly, there is evidence that previously buried spores of *Nitella* (a green algal species in Charophyceae) are extremely light sensitive and germinate at an activation energy similar to that which induces the VLFR germination of angiosperm seeds (Sokol & Stross 1986).

De-etiolation in Arabidopsis *and rice*

De-etiolation is a syndrome of several responses, including inhibition of extension growth, unfolding of cotyledons, development of the photosynthetic apparatus, expression of anthocyanins, and leaf development, all of which are critical for seedling establishment. In *Arabidopsis*, the repressive function of *COP*/*DET*/*FUS* loci on photomorphogenetic development, or de-etiolation, is abolished by light sensed through phytochromes and blue light sensing cryptochromes (Wei *et al*. 1994). Phytochromes also influence the activity of PIF1, which may protect emerging etiolated seedlings by regulating chlorophyll biosynthesis in a way that reduces photo-oxidative damage (Huq *et al*. 2004). Until a light signal is received, seedlings are etiolated and negatively gravitropic. This allows seedlings buried beneath soil and/or leaf litter to devote the limited resources in the seed to rapidly reaching the light necessary for them to switch from heterotrophic to autotrophic growth. As in germination, phyA and phyB are the principal mediators of R and FR-induced de-etiolation in *Arabidopsis thaliana* (Fig. 4; Reed *et al*. 1994), and it is likely that phyB-mediated LFR predominate in open habitats while phyA-mediated FR-HIR predominate in shaded habitats. In *Arabidopsis*, phyC, phyD, and phyE also contribute to R-induced de-etiolation (Franklin & Whitelam 2005). In the de-etiolation of rice seedlings, phyA and phyB may act more redundantly than in *Arabidopsis* (Fig. 4; Takano *et al*. 2005). In both species, phyA induces VLFR and FR-HIR de-etiolation and phyB induces R-LFR de-etiolation. However, in rice, phyA also can mediate R-induced de-etiolation and phyC can mediate FR-HIR.

De-etiolation outside of angiosperms

As with germination, etiolated development, along with R-induced de-etiolation, has a long history in land plants, suggestive of a very early origin of both etiolation and phytochrome-mediated de-etiolation. It has been postulated, based on the observation that some gymnosperms and most algae form chloroplasts in the dark (e.g. Bogorad 1950; Kirk & Tilney-Bassett 1967), that photomorphogenetic development is the default pathway in green plants and that skotomorphogenetic (or etiolated) development is a specialized pathway that evolved in higher plants as a response to terrestrial conditions such as soil and dense vegetation canopies (Wei *et al*. 1994; McNellis & Deng 1995; Jiao *et al*. 2005). However, even very early diverging nonvascular plants such as mosses etiolate in the dark. For example, dark-grown gametophores of *Physcomitrella patens* are strongly negatively gravitropic, etiolated, and the leaves are reduced to scales (Cove *et al*. 1978). Conversely, if exposed to R, gametophores are agravitropic, de-etiolated, and have large leaves and the effects of R are inhibited if FR is given after R and while chlorophyll synthesis in moss spores does not require light (Valanne 1971), the study of a chromophore deficient mutant, *ptr116*, of *Ceratadon purpureus* demonstrated a role for phytochrome in chlorophyll accumulation, an important aspect of de-etiolation, during protonemal development (Lamparter *et al*. 1997a).

In free-sporing vascular plants, etiolation has been noted in ferns and in the lycophyte, *Lycopodium lucidulum* (MacDougal 1903). In ferns, etiolation occurs during the development of both gametophytes, which have greatly elongated cells in the dark (Miller 1968), and sporophytes, which may display drastic frond elongation (Conway 1948; Tavares & Sussex 1968; Harvey & Caponetti 1972), spore-ling internode elongation (Laetsch & Briggs 1962), failure of the crozier to uncoil (Harvey & Caponetti 1972), and inhibition of leaf development (Steeves & Sussex 1957). In some cases, chlorophyll is synthesized in the dark (Laetsch & Briggs 1962) while in other cases, including in *Equisetum*, it is not (Kirk & Tilney-Bassett 1967; Tavares & Sussex 1968); and in at least one species, dark-grown fronds of the same individual are either green or not (Conway 1948). When etiolated, strap-shaped gametophytes of *Ceratopteris richardii* are irradiated with R, rhizoids are initiated behind the apical meristem and the meristem begins to broaden prior to developing the heart-shaped form typical of

light-grown plants; induction by R is reversible by FR (Murata & Sugai 2000). As in angiosperms, cytokinins have a role in mediating R-induced de-etiolation (Spiro *et al*. 2004).

The observation that gymnosperms are green in the dark apparently is based on the observation that some conifers synthesize chlorophyll in the dark (e.g. Bogorad 1950). However, conifers are a derived lineage within gymnosperms (e.g. Burleigh & Mathews 2004), and not all conifers are de-etiolated in the dark (Burgerstein 1900; Mukai *et al*. 1992). In fact, etiolation is very pronounced in the more anciently derived gymnosperm groups, cycads and *Ginkgo*, as well as in some gnetophytes (Burgerstein 1900). Phytochromes mediate de-etiolation in *Ginkgo* (Chinn & Silverthorne 1993; Christensen *et al*. 2002; Christensen *et al*. 2002; S. Mathews & D. Tremonte, unpublished data), in cycads, gnetophytes, and in those conifers that etiolate (S. Mathews & D. Tremonte, unpublished data).

Together these observations suggest that etiolated development is important in all vascular plant groups and that it also occurs in nonvascular plants such as mosses. Perhaps more surprising, critical elements of etiolated development also occur outside land plants. While many algae do synthesize chlorophpyll in the dark, the condition is variable, and R-FR reversible chlorophyll synthesis has been noted in brown, red, and green algae (Rüdiger & López-Figueroa 1992). Dark-grown filaments of the green alga *Spirogyra* also show aspects of etiolated development, and the inhibition of filament elongation and the induction of rhizoids are controlled by R in a FR-reversible manner (Nagata 1973; Virgin 1978).

Shade avoidance in Arabidopsis *and rice*

As noted above, phytochromes are uniquely suited to neighbour detection, arguably one of their most ecologically important capacities. In response to neighbour detection shade-intolerant plants increase extension growth, suppress branches, make thinner leaves with less chlorophyll, flower early, and decrease allocation to storage organs, a set of responses collectively known as shade avoidance. In addition to altering the R:FR ratio, canopies create horizontal gradients of blue light, which can lead to phototropic bending toward canopy gaps, mediated by blue light sensing phototropin (Ballaré 1999). Furthermore, a decrease in blue light perceived by one or both cryptochromes in stems of mustard (*Brassica*), and of reduced photon fluences perceived by phytochromes in mustard, tobacco, and tomato, also stimulate stem elongation when canopies close (Ballaré 1999). These data from different angiosperm species hint at the true complexity underlying shade avoidance in natural environments and in flowering plants in general.

Experiments with *Arabidopsis* and *Brassica* mutants in the field have defined a clear role for phyB in detection of reflected FR (Schmitt *et al*. 1995; Ballaré 1999). While phyA may enhance the sensitivity to subtle changes in the R:FR ratio caused by reflected light from nonshading neighbours (Ballaré 1999), the role of phyA in promoting de-etiolation under dense canopies may be antagonistic to some shade avoidance responses (Fig. 4; Smith *et al*. 1997). Moreover, analyses of mutants under canopies indicate a primary role for phyB in mediating shade avoidance under canopies of low density, with lesser roles attributed to the phyB-related photoreceptors, phyD and phyE (Fig. 4; Ballaré 1999). Under denser canopies, *phyB* mutants have measurable responses to shade, perhaps indicating a greater role for phyD and phyE, and/or for other perception systems, in shade avoidance in deep shade (Ballaré 1999). Phenotypes of the *phyB* mutants of rice, maize, and sorghum (Childs *et al*. 1997; Sheehan *et al*. 2004; Takano *et al*. 2005) are consistent with the hypothesis that phyB controls shade avoidance in rice and other grasses as it does in *Arabidopsis* (Maddonni *et al*. 2002), but the roles of individual rice phytochromes in shade avoidance have not been determined.

Shade avoidance outside of angiosperms

The adaptive benefits of plastic responses to shade were demonstrated in a study that showed reduced fitness of *phyB*-deficient *Brassica rapa* mutants grown in dense stands (Schmitt *et al*. 1995). This led to speculation that shade avoidance was an innovation that played a role in the diversification and ascendancy of flowering plants (Smith & Whitelam 1997; Smith 2000). If shade avoidance gave a particular advantage to angiosperms, we might expect it to be absent from other groups of land plants (e.g. Donoghue 2005), an expectation that is not confirmed by the available data. As with phytochrome-mediated de-etiolation, elements of shade avoidance have been observed in other land plant groups, and even outside of land plants. Sporelings of *Chara* show increased elongation, reduced development of branchlets, and reduced chlorophyll content in response to end-of-day FR treatments (EOD-FR; Rethy 1968). The practice of giving an FR pulse at the end of a light period is commonly used in studies of photomorphogenesis because it mimics the effects of shade (e.g. Fankhauser & Casal 2004). Also notable is a study of the liverwort, *Marchantia polymorpha*, which documents shade avoidance responses in a nonvascular plant (Fredericq 1964). In this study, it was shown that EOD-FR induced prostrate gametophores with wide lobes to grow erect, to have narrow lobes, reduced chlorophyll content, and higher numbers of gemmae (vegetative propagules). In mosses, FR induces extreme elongation of filaments, inhibits chloroplast development and branching of chloronema, and changes in the R:FR ratio influence leaf size (Hartmann & Jenkins 1984), all elements of the shade avoidance syndrome of angiosperms. Fern sporophytes also show evidence of shade avoidance responses induced by changes in the R/FR ratio. For example, the tree fern *Cyathea caracasana*, commonly an open-habitat

species, produces nearly vertical fronds (hyponasty) with long stipes and blades when overtopped by regenerating angiosperm forests, and there is a positive relationship between stipe length and the distance of the fern apical meristem below the canopy (Arens & Baracaldo 2000). In gymnosperms, phytochrome-mediated shade avoidance occurs in conifers (Morgan *et al*. 1983; Warrington *et al*. 1988), and while the growth habit of cycads, without nodes and internodes, restricts their shade responsiveness to brief periods of rapid leaf development, either sun leaves or shade leaves are produced at these times, the latter showing greater elongation and wider spacing between leaflets (Norstog & Nicholls 1997). It seems likely that gnetophytes, which are related to conifers (Burleigh & Mathews 2004), and *Ginkgo*, also are capable of shade avoidance, and that in gymnosperms shade avoidance is mediated by phyP, the gymnosperm orthologue of phyB (Fig. 2). That elements of shade avoidance are found in ferns, nonvascular plants, and even outside of land plants suggests that responses to changes in the R:FR ratio of ambient light has long been an important phytochrome function. However, it seems likely that the adaptive significance of shade avoiding responses increased with the evolution of vascular plants and canopy shade, and it is possible that when coupled with the rapid growth rates that evolved in angiosperms, shade avoidance has played a critical role in their spectacular success.

Flowering in Arabidopsis *and rice*

Plants use both seasonal cues (daylength and temperature) and light quality cues to control flowering time. LD promote flowering in *Arabidopsis* (Fig. 4). FR is the most effective light for the acceleration of flowering in daylength extension experiments (Johnson *et al*. 1994), and it has a direct role in the control of flowering through the activation of *FT* (*FLOWERING LOCUS T*) expression by CONSTANS (CO) protein (Yanovsky & Kay 2002; Valverde *et al*. 2004). LD promotion of flowering by phyA in *Arabidopsis* fits the external coincidence model of photoperiodic time measurement (see Yanovsky & Kay 2003 for a description of this and other models), in which there is overlap between a photoinducible phase of a regulator and an external light signal that has a promotive effect. First, the levels of *CO* mRNA are under clock control such that they are high during the daytime only in long days (Suárez-López *et al*. 2001), with phyA, phyB and cry1 all contributing to entrainment of the clock (Somers *et al*. 1998). Second, light signals coinciding with the peak of *CO* mRNA and CO protein function to balance the abundance of CO to promote flowering through *FT*, with phyA and cry2 serving to stabilize and phyB serving to destabilize CO (Fig. 4; Valverde *et al*. 2004).

Key elements of this model are conserved in rice, which flowers under short days (SD). Homologues of both *CO* and *FT* have been identified, and *FT* homologues promote flowering (Hayama & Coupland 2004). In rice, the expression of *Hd1*, the *CO* homologue, is rhythmic, and as in *Arabidopsis*, mRNA levels are high in the daytime only under LD (Izawa *et al*. 2002). However, in LD, the coincidence of light signals with the peak in *Hd1* expression does not promote expression of *FT* homologues such as *Hd3a* (*heading date 3a*). The early flowering phenotype of rice *phyB* mutants under both LD and SD is consistent with a conserved role for phyB in the destabilization of Hd1 protein under LD, and since the loss of phyC also leads to early flowering in LD (Takano *et al*. 2005), it could function similarly (Fig. 4). However, rice *phyA* mutants flower at the same time as wild type plants, suggesting that phyA may not stabilize Hd1 to the degree that it stabilizes CO in *Arabidopsis*. This might result from a more rapid attenuation of *PHYA* gene expression by light in rice relative to *Arabidopsis* (Kay *et al*. 1989; Quail 1994), which could contribute to a greater decrease of phyA protein levels. A different balance between the stabilizing and destabilizing effects of phytochromes on Hd1 than occurs in *Arabidopsis* is one mechanism whereby Hd1 could fail to promote flowering under LD.

Under SD, phytochromes may regulate levels of Hd3a and flowering both dependently and independently of Hd1 (Ishikawa *et al*. 2005). Independent of Hd1, SD flowering in rice is induced by expression of *Ehd1*, a response regulator gene (Fig. 4; Doi *et al*. 2004). Expression peaks during the day, inducing *Hd3a* activity and flowering in a manner that is consistent with the external coincidence model (Doi *et al*. 2004). The roles of phytochromes in the *Ehd1* photoperiodic pathway remain to be determined, but *phyA* mutants flower late while *phyB* mutants flower early (Takano *et al*. 2005), consistent with stabilizing and destabilizing activities, respectively, for these phytochromes on proteins in the *Ehd1*-dependent flowering pathway.

The photoperiodic flowering pathway converges on the same targets of downstream signalling as do other flowering pathways, including the autonomous and vernalization, pathways, which also induce flowering by promoting the expression of *FT* (Boss *et al*. 2004). Additionally, the presence of a light-quality flowering pathway has been postulated (e.g. Halliday *et al*. 1994, 2003). Recent characterization of a nuclear protein from *Arabidopsis*, PFT1 (PHYTOCHROME and FLOWERING TIME), confirmed that this is the case. PFT1 functions downstream of phyB to regulate levels of *FT* in a pathway that does not involve CO (Cerdán & Chory 2003). phyD and phyE also contribute to early flowering in reduced R:FR conditions (Aukerman *et al*. 1997; Devlin *et al*. 1998) and may also act through PFT1 pathway. The activities of rice homologues of PFT1 have not been determined.

Reproduction outside of angiosperms

The influence of photoperiod on reproduction is observed widely in green plants and is apparent in algal groups, where

phytochromes mediate short-day induction of sporulation in the red and green algae, *Porphyra tenera* and *Monostroma grevillei*, and of short-day induction of erect thalli in the brown alga *Scytosiphon lomentaria* (Dring & Lüning 1983). Phytochrome also mediates R/FR reversible aplanospore formation in *Trebouxia*, the green algal partner of the lichen *Cladonia cristatella* (Giles 1970). In early land plants, mosses require light for induction of antheridia and archegonia (Knoop 1984), but photoperiodic effects appear to be limited. However, some natural populations of *Funaria hygrometrica* form gametangia under LD while others require SD for sporophyte development (Hartmann & Jenkins 1984). In liverworts, *Marchantia* and *Lunularia* form antheridia and archegonia under LD and asexual gemmae under SD (Wann 1925; Voth & Hamner 1940; Hartmann & Jenkins 1984), and Mediterranean strains of *Lunularia cruciata* become dormant and dessication tolerant under LD in an R/FR reversible manner; under SD growth resumes (Wilson & Schwabe 1964). In ferns, the role of photoperiod, if any, in the induction of antheridia and archegonia is not well understood (Furuya 1983; Raghavan 1989). R inhibits induction of antheridia in *Pteris vittata* and R-induced inhibition is FR-reversible in *Polypodium crassifolium* (Wada & Kadota 1989). In *Pteridium aquilinum*, archegonia form under long days, but the photoreceptor for this response was not investigated (Conway 1948). Similarly, long- and short-day behaviours were established in several species of ferns, sometimes dependent on thermoperiodicity, but the effective light qualities were not determined (Labouriau 1958). In gymnosperms, cycads show a marked and regular periodicity in coning (Norstog & Nicholls 1997), irrespective of temperature (Vorster 1993), but the roles of daylength and photoreceptors remain to be investigated. Conversely, the role of photoperiod in reproduction, bud set, and dormancy in species from two of the five conifer families has been documented (e.g. Pharis *et al*. 1970; Dormling 1993), and the role of phytochromes in mediating dormancy has been established in three species of spruce (Young & Hanover 1977; D'Aoust & Hubac 1986; Clapham *et al*. 1998). These observations suggest that phytochrome control of photoperiodic effects may occur widely in green plants.

Phytochrome functional divergence differs in *Arabidopsis* and rice

Arabidopsis, a eudicot, and rice, a monocot, last shared a common ancestor approximately 134 million years ago (Ma) (Sanderson *et al*. 2004), and each species belongs to a family of relatively recent origin. Brassicaceae (mustards) and Poaceae (grasses) diverged from their closest relatives approximately 40 and 83 Ma, respectively (Koch *et al*. 2001; Janssen & Bremer 2004). In *Arabidopsis*, phyA and phyB are the principal mediators of photomorphogenesis induced by FR and R cues, respectively. The fact that no flowering plant has been found to lack homologues of *PHYA* or *PHYB* suggests that their prominence is a widespread feature in angiosperms. Notably, *Populus trichocarpa* has homologues of just *PHYA* (one copy) and *PHYB* (two copies; Howe *et al*. 1998). The contrasting photosensory specificities of these two photoreceptors place them in complementary roles, with phyB taking on prominence in open habitats, where ambient light has a higher ratio of R:FR (1.05–1.25, Smith 1982), and with phyA taking on prominence in shady environments, where the ratio is reduced (0.05–1.15, Smith 1982). At the same time, in conditions of reduced R:FR, the roles of phyA and phyB may be antagonistic, promoting opposing responses in processes such as elongation and leaf development (McCormac *et al*. 1992; Johnson *et al*. 1994; Smith *et al*. 1997; Folta & Spalding 2001; Devlin *et al*. 2003). The failure of *Arabidopsis* mutants lacking phyA to establish under canopy shade (Yanovsky *et al*. 1995) suggests that phyA may counteract the potentially counterproductive effects of phyB-induced shade avoidance during seedling establishment (Smith *et al*. 1997). The down-regulation and degradation of phyA in light, which occurs both in eudicots and the grasses (Quail 1991, 1994), would reduce its opposition of shade-avoidance responses occurring later in development.

Data from analyses of tomato and pea mutants indicate a similar division of labour between phyA and phyB (Weller *et al*. 2001; Platten *et al*. 2005). However, in rice, phyA and phyB act redundantly in de-etiolation under R and *phyA* mutants are only partially impaired in responses to FR, with phyC also inducing responses to FR (Fig. 4; Takano *et al*. 2005). In contrast, *phyC* mutants of *Arabidopsis* suggest it has no role in mediating responses to FR (Franklin *et al*. 2003; Monte *et al*. 2003). Thus, the photosensory functions of rice phyA and phyB appear to be more redundant than are those of *Arabidopsis* phyA and phyB, as are those of rice phyA and phyC. Very recent evidence suggests that allelic variation at *PHYC* among *Arabidopsis* ecotypes contributes to variation in flowering time in a latitude-dependent manner (Balasubramanian *et al*. 2006), providing insight into a novel role of phyC that complements insights from forward and reverse genetic screens, and defining an additional potentially adaptive role for phyC. It would be interesting to determine if phyC functions similarly in other species, thus helping to explain its wide conservation in angiosperms.

In the absence of comparable data from nongrass monocots and from several additional dicot clades, it is impossible to determine what were the ancestral photosensory specificities and functions of phyA, phyB, and phyC, or to determine if the rice, *Arabidopsis*, or some other model might be more representative of angiosperms as a whole. Sequence analyses of *PHYA* and *PHYC* photosensory domain sequences from basal angiosperms provided evidence that positive selection and a high number of replacement substitutions influenced the evolution of phyA during the origin of flowering plants

(Mathews *et al*. 2003; Mathews 2005), suggesting that functional change in phyA occurred at that time. The data from rice indicate that despite this burst of innovation, the distinct functional identities of *Arabidopsis* phyA and phyC may not have evolved before the monocots diverged from other angiosperms. Alternatively, more recent changes in grasses might have lessened the functional distinctions of rice phyA and phyC. Future functional studies should target other lineages that may have only phyA, phyB, phyC, such as Piperales and Caryophyllales, as well as early diverging monocots and basal angiosperms. While the lack of genetic tools presents an obstacle, model organisms are being developed in some of the relevant clades, and virally induced gene silencing systems are proving effective in others (Hileman *et al*. 2005; E. Kramer, personal communication). Data from *Populus* will continue to be instructive. While it does have two phyB, it lacks both phyC and phyE (Howe *et al*. 1998). Recent data demonstrate that CO and *FT* control both photoperiodic flowering and growth cessation and bud set in this woody species (Böhlenius *et al*. 2006), highlighting the utility of multiple models with diverse life histories.

Unlike in monocots that have been investigated, phytochrome evolution in eudicots is marked by diversification in the *PHYB* lineage, and in *Arabidopsis*, both phyD and phyE mediate shade avoidance and responses to R (Aukerman *et al*. 1997; Devlin *et al*. 1998, 1999). Overall, the relatively mild phenotypes of the *phyD* and *phyE* null mutants of *Arabidopsis* have suggested lesser roles in photomorphogenesis for these loci (Aukerman *et al*. 1997; Devlin *et al*. 1998, 1999), and their absence from some species or plant groups is consistent with this suggestion. Moreover, the *phyD* mutant is a naturally occurring deletion allele (Aukerman *et al*. 1997), and alleles without the deletion are evolving under relaxed constraints (K. McBreen & S. Mathews, unpublished data). Nonetheless, both phyD and phyE have been retained much longer that the estimated half-life of duplicated genes (3–7 million years; Lynch & Conery 2000). This suggests that they are important, perhaps playing more significant roles in some plant groups or in some environments than in others. Data from rice support the possibility that functional relationships among phytochromes vary across plant groups. In tomato, there is more functional overlap between phyB1 and phyB2 (Weller *et al*. 2000, 2001) than between *Arabidopsis* phyB and phyD, also suggesting that patterns of functional divergence are clade-specific. In *Nicotiana plumbaginifolia*, it appears that R-induction of seedling development and detection of photoperiod are under the control of a different phyB than controls shade avoidance, although just one copy has been detected and characterized (Hudson *et al*. 1997; Hudson & Smith 1998). A well-defined case of subfunctionalization of phyB in seedling development and shade avoidance responses is found in the *PhyB* homologues of maize, *PhyB1* and *PhyB2*, which diverged approximately 11–16 Ma (M. J. Sheehan and T. P. Brutnell, personal communication), suggesting that such subfunctionalization can occur relatively quickly. Support for the idea that functional relationships among phytochromes vary across environments comes from the growing body of evidence showing that the relative prominence of the different *Arabidopsis* phytochromes changes with temperature. For example, phyD, and especially phyE, take on a more prominent role in the control of flowering time at 16 °C than at higher temperatures (Halliday & Whitelam 2003; Halliday *et al*. 2003) and phyE plays a critical role in germination at temperatures from 7 °C to 19 °C (S. Heschel and K. Donohue, personal communication). Additionally, there is evidence that the prominence of *Arabidopsis* phytochromes in germination is influenced by maternal temperature (S. Heschel & K. Donohue, personal communication). Nevertheless, despite the apparent advantages associated with diversification of phyB-type phytochromes, several angiosperms have been quite successful with an apparently simpler gene family. Monocots comprise about 60 000 of the 260 000 species of extant angiosperms. Caryophyllales also may have just phyA, phyB, and phyC and they comprise approximately 9000 species that have been highly successful in arid and or halophytic environments, and contain about 6.3% of eudicot diversity (Magallón *et al*. 1999).

Origins of phytochrome-mediated development

As described above, phytochrome control of growth and development outside of angiosperms, even in the earliest diverging extant land plants, is strikingly similar in several respects to that in angiosperms. Many of the regulatory functions that have been characterized in eudicots and grasses, including control of germination, de-etiolation, shade avoidance, and reproduction occur widely in land plants, suggesting that they originated early in the history of the group. Despite this general conclusion, the limited data on the distribution of responses, the lack of more detailed gene trees for several clades, and the limited understanding of the function of individual phy outside of angiosperms make it difficult to test the homology of responses and to infer ancestral functions and patterns of divergence. In lieu of robust homology tests, the collected observations suggest a series of tentative conclusions. First, phytochrome-mediated germination is likely to have been important early in the history of land plants. The presence of R/FR-reversible germination in all the major clades and in green algae suggests that phytochromes functioned early to promote development via LFR when light conditions were perceived to be adequate. Evidence of VLFR germination is much more limited, but its occurrence outside of land plants, in *Nitella*, suggests that the capacity to tell darkness from light via VLFR also was established very early. Second, while the importance of etiolation may well

have increased as land plants established and diversified, the separate elements of light-mediated de-etiolation occur even in marine and freshwater organisms, where phytochrome control of chlorophyll synthesis occurs in green algae, but also in the more distantly related red and brown algae. Inhibition by R of cell or filament elongation also occurs outside of land plants. Control of such processes by light could be viewed as a preadaptation for life on land, where the chances of burial would increase, first under soil and ultimately under leaf litter. Third, phytochrome-mediated shade avoidance responses are likely to have evolved with shade, as early as the Devonian (~360 Ma). The evolution of a vascular system allowed plants to achieve great size and ultimately to form dense canopies, creating a more complex light environment. The differential effects of R and FR on elongation, greening, and reproduction, all of which are observed in nonvascular plants, might have facilitated rudimentary shade avoidance as canopy shade evolved, with the sophisticated coordination of responses that is characteristic of angiosperm shade avoidance evolving later. Fourth, phytochrome control of photoperiodic responses also is likely to have been important early in the history of land plants. It is observed in all clades of green plants and also in red and brown algae. Finally, it is notable that all three physiological response modes, VLFR, LFR, and HIR, characterize responses outside of angiosperms. Reports of LFR predominate, but VLFR may be more widespread than is apparent since they can only be detected in tissues kept in complete darkness. There are few reports of FR-HIR, perhaps none outside of vascular plants. Their ecological relevance may be greater in shaded environments, and this mode of phytochrome control of development may have become more prominent after the origin of vascular plants that were capable of forming canopies.

Patterns of functional divergence outside of angiosperms

Together with the inferred gene phylogeny, these observations indicate that developmental pathways controlled by three to four distinct phytochrome paralogues in angiosperms and other seed plants may be controlled by fewer distinct paralogues in earlier diverging land plants. This implies that subfunctionalization has played a prominent role during the evolution of the gene family. One of the most important avenues of subfunctionalization may have been the subdivision of photosensory specificity between duplicate genes. Until about 400 Ma, there was little plant cover of any height (DiMichele *et al*. 1992). Beginning about this time, the early radiation of vascular plants produced low canopies, up to about two meters (DiMichele *et al*. 1992). It appears that the structure of plant communities in the Lower to Middle Devonian (~375–400 Ma) was controlled largely by the ability of plants to locate patches opened for colonization by disturbance (DiMichele *et al*. 1992), suggesting that R-induced LFR may have predominated in the ecology of these communities. By about 360 Ma, arborescent lycopods, progymnosperms, seed ferns, and ferns had appeared (Stewart & Rothwell 1993). Environments were characterized by increased spatial heterogeneity, by large trees (achieving heights comparable with those of extant conifers), and by the first significant production of leaf litter by progymnosperms such as *Archaeopteris*, which produced many flattened deciduous branchlets with laminar leaves; forests dominated by species of *Archaeopteris* also were likely to have been shaded as a result of these features (DiMichele *et al*. 1992).

With the origin of forest canopies and the increased heterogeneity of the light environment, responses that are inherently antagonistic may have become equally important. This is an issue that is particularly relevant to our understanding of phytochrome diversification and its potential benefits. For example, a phytochrome that induces germination under high R:FR ratios in a R/FR reversible manner will not induce germination under the low R:FR ratios of shaded environments, or it will induce germination at reduced levels. This is unlikely to have been a problem for early land plants, which existed in open environments, but it would potentially limit the ecological amplitude of taxa that either persisted or originated after the evolution of vascular plants that could produce substantial amounts of shade. One possible solution would be the possession of separate photoreceptors for R- and FR-induced germination. Thus, a potentially important benefit of phytochrome diversification was that it allowed species to partition opposing responses between separate photoreceptors. In species of open habitats, R-induced responses may predominate, but populations would always retain the option of relying more heavily on FR-induced responses, giving them more flexibility in the selection of habitats. Notably, each of the major clades of vascular plants has at least two divergent phytochrome gene lineages and species in each clade display distinct responses to both R and FR. Conversely, the condition is not readily apparent outside of vascular plants, where R-induced, reversible LFR appear to predominate. It is interesting that in *Agrobacterium tumefaciens*, a bacterial species that invades plant stems, and in a strain of *Bradyrhizobium* that is a legume symbiont, there are phytochromes in which Pfr is the thermal ground state and which may promote responses primarily dependent on conversion of Pfr to Pr (Giraud *et al*. 2002; Karniol & Vierstra 2003). In *Agrobacterium*, a second phytochrome occurs, in which Pr is the ground state, as is typical in plant phy (Karniol & Vierstra 2003). Depending on the location of the bacteria within stems, they may be exposed to higher fluences of FR than are found in incident light (Vogelmann 1994), suggesting that there has been parallel phytochrome diversification in bacteria and plants exposed to FR-rich environments. A more subtle form of photosensory diversification

is exemplified by the slight blue shifts in the absorption maxima of *Arabidopsis* phyC and phyE (Eichenberg *et al*. 2000). The ecological significance of these shifts is unknown. It would be interesting to determine if this mode of diversification has occurred in other plant groups with multiple phytochromes.

Gene duplication also has allowed the evolution of light labile and light stable phytochromes. This may be important in groups such as mosses, particularly if they lack a distinct FR-responsive function. Light labile and light stable phytochromes have been detected in mosses, ferns and conifers (Maucher *et al*. 1992; Burgin *et al*. 1999; Mittman *et al*. 2004). The activity of a light labile phytochrome pool in the fern, *Anemia phyllitidis*, appears to be very phyA-like, with transcripts accumulating in dark-imbibed spores and decreasing when spores are transferred to the light (Maucher *et al*. 1992). The blue-light sensing cryptochromes are similarly partitioned into light labile and stable forms in *Arabidopsis* (Briggs & Huala 1999). The division of light lability and stability into different loci may provide a mechanism for restricting opposing functions, such as seedling de-etiolation in the shade and shade avoidance, to discrete periods of development. Since both transcript levels and protein stability may be light regulated, both coding sequence evolution and patterns of regulatory mutations that fit the complementary and degenerative mutation model of duplicate gene preservation (Force *et al*. 1999) may have been important in the divergence between light stable and light labile phytochromes. The activities of the five *Arabidopsis PHY* promoters fused to a reporter gene peak at four different times during the light phase of 12-h days (Tóth *et al*. 2001). Thus, further fine-tuning to coordinate the function of paralogous phytochromes might occur through temporal differences in their peak expression levels.

Concluding remarks

The ecological implications of phytochrome persistence and evolution are profound. Red and far-red sensing has unparalleled utility in plants, and as more recently realized, is widespread in prokaryotes. In prokaryotes and single-celled or simple filamentous eukaryotes, phytochromes are crucial for adaptation to physical surroundings and to the presence of other organisms. Bacteriophytochromes control such responses as the synthesis of protective pigments in response to light intensity (e.g. Davis *et al*. 1999) and the synthesis and composition of photosystem II in response to light quality, specifically to the ratio of R:FR (Giraud *et al*. 2002, 2005). Additionally, the presence in bacteria of phytochromes with Pfr thermal ground states (Giraud *et al*. 2002; Karniol & Vierstra 2003) may facilitate the colonization of plant stems, where the R:FR ratio may be reduced. In the green algae, *Mesotaenium* and *Mouteotia*, phytochromes control movement of the single ribbon-like chloroplast in an R/FR reversible manner such that either exposure to, or protection from, light is maximized (Haupt & Häder 1994). A role for phytochromes in phototaxis has not been demonstrated, but the action spectra for phototaxis in the dinoflagellate *Peridinium gatunense* (Haupt & Häder 1994) leave open this possibility. Our understanding of phytochrome evolution in prokaryotes and during the radiation of eukaryotes is extremely limited at this time, but it is clear that the persistence of phytochromes in green plants has led to their control of very similar responses. Additionally, phytochrome signalling in sessile plants is linked with the ability to forage for light through growth responses (e.g. photo- and polarotropism in moss and fern gametophytes, shade avoidance, interaction with the gravity sensing system). And in multicellular plants, the linking of phytochrome signalling with developmental transitions is critical to the ability of plants to synchronize their growth and development with environmental cues.

Further investigations are needed to address the question of how phytochrome evolution and function might have affected the establishment, radiation, and persistence of species. Patterns of molecular evolution following gene duplication and during morphological transitions remain poorly characterized and this limits our ability to understand the impacts of evolution in light sensing during major evolutionary transitions. Episodic sequence innovation in phyA occurred early in the history of angiosperms, and this may have been linked with functional innovation that was critical to their establishment (Mathews *et al*. 2003). It is intriguing that this episode of molecular adaptation coincided with the origin of the angiosperms, and may not have closely followed the duplication leading to *PHYA* and *PHYC*, for example, if #2a in Fig. 2 is correct. This suggests that the tempo of functional innovation following gene duplications may be modulated by patterns of morphological change as well as by environmental pressures. Within species, patterns of natural variation in light responses and/or phytochrome signalling have been characterized for *Arabidopsis* (Maloof *et al*. 2000, 2001), Scots pine (Clapham *et al*. 1998; García-Gil *et al*. 2003), and poplar (Howe *et al*. 1996). Additional investigations capitalizing on natural variation will lead to models that explain the plasticity of phytochrome responses within a species, and they will reveal specific genetic changes that are linked with increased fitness. It would be very interesting in these studies to better characterize the influence of environmental parameters such as temperature, and to characterize variation in endogenous parameters such as circadian patterns of gene expression and protein abundance.

In this review, two scales of evolution in phytochrome-mediated development have been considered in order to investigate how similar phytochrome function and functional divergence might be across major clades of land plants. First, from the survey of phytochrome-mediated developmental pathways in green plants it appears that

phytochromes play similar roles in development in divergent clades of land plants. This suggests that some of these roles originated much earlier in the history of land plants than previously has been recognized. In the context of the gene phylogeny, it also indicates that gene subfunctionalization has been important. Although a number of duplications cannot be pinpointed in time without additional data, it appears that diversification events in the gene family may have coincided with the evolution of canopy shade, creating conditions under which inherently antagonistic pathways such as de-etiolation and shade avoidance would be equally important. The maintenance of two forms of phytochrome to control opposing responses may have become advantageous at this time. A test of this hypothesis will require that phytochrome-mediated responses be systematically characterized in multiple exemplars in the major clades of bryophytes (mosses, liverworts, hornworts), lycopods (club mosses, spike mosses, quill worts), ferns (including *Psilotum* and horsetails), and gymnosperms (cycads, *Ginkgo*, gnetophytes, conifers), and for these responses to be linked with specific phytochromes in a strategic subset of these exemplars such as is proceeding in *Physcomitrella patens* (Mittman *et al*. 2004). Additionally, phytochrome gene phylogenies for each of the major clades are needed in order to more precisely infer the positions of gene duplications. Second, from the comparison of rice and *Arabidopsis*, it appears that patterns of functional divergence in angiosperms are clade-specific. Together with the evidence that the relative functional prominence of individual phytochromes changes across environments, this attests to the evolutionary lability and contemporaneous plasticity of phytochrome function, characteristics that are likely to have ensured this photoreceptor system an important role in diversification and species longevity.

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References

Aravind L, Ponting CP (1997) The GAF domain: an evolutionary link between diverse phototransducing proteins. *Trends in Biochemistry*, **22**, 458–459.

Arens NC, Baracaldo PS (2000) Variation in tree fern stipe length with canopy height: tracking preferred habitat through morphological change. *American Fern Journal*, **90**, 1–15.

Aukerman MJ, Hirschfeld M, Wester L *et al.* (1997) A deletion in the *PHYD* gene of the *Arabidopsis Wassilewskija* ecotype defines a role for phytochrome D in red/far-red light sensing. *Plant Cell*, **9**, 1317–1326.

Balasubramanian S, Sureshkumar S, Agrawal M *et al.* (2006) The PHYTOCHROME C photoreceptor gene mediates natural variation in flowering and growth responses of *Arabidopsis thaliana*. *Nature Genetics*, **38**, 711–715.

Ballaré CL (1999) Keeping up with the neighbours: phytochrome sensing and other signalling mechanisms. *Trends in Plant Science*, **4**, 97–102.

Ballaré C, Scopel AL, Sanchez R (1990) Far-red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science*, **247**, 329–332.

Banks JA (1999) Gametophyte development in ferns. *Annual Review of Plant Physiology and Plant Molecular Biology*, **50**, 163–186.

Bennett JR, Mathews S (2006) Phylogeny of the parasitic family Orobanchaceae inferred from phytochrome A. *American Journal of Botany*, in press.

Blumenstein A, Vienken K, Tasler R *et al.* (2005) The *Aspergillus nidulans* phytochrome FphA represses sexual development in red light. *Current Biology*, **15**, 1833–1838.

Bogorad L (1950) Factors associated with the synthesis of chlorophyll in the dark in seedlings of *Pinus jeffreyi*. *Botanical Gazette*, **111**, 221–241.

Böhlenius H, Huang T, Charbonnel-Campaa L *et al.* (2006) CO/FT Regulatory module controls timing of flowering and seasonal growth cessation in trees. *Science*, **312**, 1040–1043.

Bopp M (1983) Developmental physiology of bryophytes. In: *New Manual of Bryology* (ed. Schuster RM), pp. 276–324. Hattori Botanical Laboratory, Nichinan, Miyazaki, Japan.

Borthwick HA, Hendricks SB, Parker MW, Toole EH, Toole VK (1952) A reversible photoreaction controlling seed germination. *Proceedings of the National Academy of Sciences, USA*, **38**, 662–666.

Boss PK, Bastow RM, Mylne JS, Dean C (2004) Multiple pathways in the decision to flower: enabling, promoting, and resetting. *Plant Cell*, **16**, S18–S31.

Botto JF, Sanchez RA, Whitelam GC, Casal JJ (1996) Phytochrome A mediates the promotion of seed germination by very low fluences of light and canopy shade light in *Arabidopsis*. *Plant Physiology*, **110**, 439–444.

Briggs WR, Huala E (1999) Blue-light receptors in higher plants. *Annual Review of Cell and Developmental Biology*, **15**, 33–62.

Burgerstein A (1900) Ueber das Verhalten der Gymnospermen-Keimlinge im Licht und im Dunkeln. *Berichte Der Deutschen Botanischen Gesellschaft*, **18**, 168–184.

Burgin M, Casal J, Whitelam G, Sanchez R (1999) A light-regulated pool of phytochrome and rudimentary high-irradiance responses under far-red light in *Pinus elliottii* and *Pseudotsuga menziesii*. *Journal of Experimental Botany*, **50**, 831–836.

Burleigh JG, Mathews S (2004) Phylogenetic signal in nucleotide data from seed plants: implications for resolving the seed plant tree of life. *American Journal of Botany*, **91**, 1599–1613.

Butler WL, Norris KH, Seigelman HW, Hendricks SB (1959) Detection, assay, and preliminary purification of the pigment controlling photoresponsive development of plants. *Proceedings of the National Academy of Sciences, USA*, **45**, 1703–1708.

Casal JJ, Sanchez RA, Yanovsky MJ (1997) The function of phytochrome A. *Plant, Cell & Environment*, **20**, 813–819.

Cerdán PD, Chory J (2003) Regulation of flowering time by light quality. *Nature*, **423**, 881–885.

Childs KL, Miller FR, Cordonnier-Pratt MM *et al.* (1997) The sorghum photoperiod sensitivity gene, *Ma3*, encodes a phytochrome B. *Plant Physiology*, **113**, 611–619.

Chinn E, Silverthorne J (1993) Light-dependent chloroplast development and expression of a light-harvesting chlorophyll a/b-binding protein gene in the gymnosperm *Ginkgo biloba*. *Plant Physiology*, **103**, 727–732.

Christensen S, LaVerne E, Boyd G, Silverthorne J (2002) *Ginkgo biloba* retains functions of both type I and type II flowering plant phytochrome. *Plant & Cell Physiology*, **43**, 768–777.

Chung N-J, Paek N-C (2003) Photoblastism and ecophysiology of seed germination in weedy rice. *Agronomy Journal*, **95**, 184–190.

Clapham DH, Dormling I, Ekberg I *et al.* (1998) Latitudinal cline of requirement for far-red light for the photoperiodic control of budset and extension growth in *Picea abies* (Norway spruce). *Physiologia Plantarum*, **102**, 71–78.

Clegg MT, Cummings MP, Durbin ML (1997) The evolution of plant nuclear genes. *Proceedings of the National Academy of Sciences, USA*, **94**, 7791–7798.

Conway E (1948) The autecology of bracken [*Pteridium aquilinum* (L.) Kuhn]: the germination of the spore, and the development of the prothallus and the young sporophyte. *Proceedings of the Royal Society of Edinburgh. Section B, Biology*, **63**, 325–342.

Cooke TJ, Hickok LG, VanDer Woude WJ, Banks JA, Scott RJ (1993) Photobiological characterization of a spore germination mutant dkg1 with reversed photoregulation in the fern *Ceratopteris richardii*. *Photochemistry and Photobiology*, **57**, 1032–1041.

Cove DJ, Schild A, Ashton NW, Hartmann E (1978) Genetic and physiological studies of the effect of light on the development of the moss, *Physcomitrella patens*. *Photochemistry and Photobiology*, **27**, 249–254.

D'Aoust AL, Hubac C (1986) Phytochrome action and frost hardening in black spruce seedlings. *Physiologia Plantarum*, **67**, 141–144.

Davis SJ, Vener AV, Vierstra RD (1999) Bacteriophytochromes: phytochrome-like photoreceptors from nonphotosynthetic eubacteria. *Science*, **286**, 2517–2520.

Devlin PF, Patel SR, Whitelam GC (1998) Phytochrome E influences internode elongation and flowering time in *Arabidopsis*. *Plant Cell*, **10**, 1479–1487.

Devlin PF, Robson PR, Patel SR *et al.* (1999) Phytochrome D acts in the shade–avoidance syndrome in *Arabidopsis* by controlling elongation growth and flowering time. *Plant Physiology*, **119**, 909–915.

Devlin PF, Yanovsky MJ, Kay SA (2003) A genomic analysis of the shade avoidance response in *Arabidopsis*. *Plant Physiology*, **133**, 1617–1629.

DiMichele WA, Hook RW, Beerbower R *et al.* (1992) Paleozoic terrestrial ecosystems. In: *Terrestrial Ecosystems Through Time* (eds Behrensmeyer AK Damuth JD DiMichele WA *et al.*), pp. 205–325. University of Chicago Press, Chicago.

Doi K, Izawa T, Fuse T *et al.* (2004) *Edh1*, a B-type response regulator in rice, confers short-day promotion of flowering and controls *FT-like* gene expression independently of *Hd1*. *Genes & Development*, **18**, 926–936.

Donoghue MJ (2005) Key innovations, convergence, and success: macroevolutionary lessons from plant phylogeny. *Paleobiology*, **31**, 77–93.

Dormling I (1993) Bud dormancy, frost hardiness, and frost drought in seedlings of *Pinus sylvestris* and *Picea abies*. In: *Advances in Plant Cold Hardiness* (eds PH Christersson L), pp. 285–298. CRC Press, London.

Dring MJ, Lüning K (1983) Photomorphogenesis of marine macroalgae. In: *Encyclopedia of Plant Physiology: Photomorphogenesis* (eds Shropshire W Jr, Mohr H), pp. 545–568. Springer-Verlag, Berlin.

Eichenberg K, Baurle I, Paulo N *et al.* (2000) *Arabidopsis* phytochromes C and E have different spectral characteristics from those of phytochromes A and B. *FEBS Letters*, **470**, 107–112.

Fankhauser C (2001) The phytochromes, a family of red/far-red absorbing photoreceptors. *Journal of Biological Chemistry*, **276**, 11453–11456.

Fankhauser C, Casal JJ (2004) Phenotypic characterization of a photomorphogenic mutant. *Plant Journal*, **39**, 747–760.

Felsenstein J (2004) *Inferring Phylogenies*. Sinauer Associates, Sunderland, Massachusetts.

Flint LH, McAlister ED (1935) Wavelengths of radiation in the visible spectrum inhibiting the germination of light-sensitive lettuce seed. *Smithsonian Miscellaneous Collections*, **94**, 1–11.

Flint LH, McAlister ED (1937) Wavelengths of radiation in the visible spectrum promoting the germination of light-sensitive lettuce seed. *Smithsonian Miscellaneous Collections*, **96**, 1–8.

Folta KM, Spalding EP (2001) Opposing roles of phytochrome A and phytochrome B in early cryptochrome-mediated growth inhibition. *Plant Journal*, **28**, 333–340.

Force A, Lynch M, Pickett FB *et al.* (1999) Preservation of duplicate genes by complementary, degenerative mutations. *Genetics*, **151**, 1531–1545.

Frankland B, Taylorson R (1983) Light control of seed germination. In: *Photomorphogenesis* (eds Shropshire W, Mohr H), pp. 428–456. Springer-Verlag, Berlin.

Franklin KA, Whitelam GC (2005) Phytochromes and shade-avoidance responses in plants. *Annals of Botany*, **96**, 169–175.

Franklin KA, Davis SJ, Stoddart WM, Vierstra RD, Whitelam GC (2003) Mutant analyses define multiple roles for phytochrome C in *Arabidopsis* photomorphogenesis. *Plant Cell*, **15**, 1981–1989.

Fredericq H (1964) Influence formatrice de la lumière rouge-foncé sur le développement des thalles de *Marchantia polymorpha* L. *Bulletin de la Societe royal de Botanique de Belgique*, **98**, 67–76.

Furuya M (1983) Photomorphogenesis in ferns. In: *Encyclopedia of Plant Physiology: Photomorphogenesis* (eds Shropshire W, Mohr H), pp. 569–600. Springer-Verlag, Berlin.

Furuya M, Schäfer E (1996) Photoperception and signalling of induction reactions by different phytochromes. *Trends in Plant Science*, **1**, 301–307.

García-Gil MR, Mikkonen M, Savolainen O (2003) Nucleotide diversity at two phytochrome loci along a latitudinal cline in *Pinus sylvestris*. *Molecular Ecology*, **12**, 1195–1206.

Garner WW, Allard HA (1920) Effect of the relative length of the day and night and other factors of the environment on growth and reproduction in plants. *Journal of Agricultural Research*, **18**, 553–606.

Gendreau E, Hofte H, Grandjean O, Brown S, Traas J (1998) Phytochrome controls the number of endoreduplication cycles in the *Arabidopsis thaliana* hypocotyl. *Plant Journal*, **13**, 221–230.

Giles KL (1970) The phytochrome system, phenolic compounds, and aplanospore formation in a lichenized strain of *Trebouxia*. *Canadian Journal of Botany*, **48**, 1343–1346.

Giraud E, Fardoux J, Fourrier N *et al.* (2002) Bacteriophytochrome controls photosystem synthesis in anoxygenic bacteria. *Nature*, **417**, 202–205.

Giraud E, Zappa S, Vuillet L *et al.* (2005) A new type of bacteriophytochrome acts in tandem with a classical bacteriophytochrome to control the antennae synthesis in *Rhodopseudomonas palustris*. *Journal of Biological Chemistry*, **280**, 32389–32397.

Goff SA, Ricke D, Lan TH *et al.* (2002) A draft sequence of the rice genome (*Oryza sativa* L. ssp. *japonica*). *Science*, **296**, 92–100.

Halliday KJ, Whitelam GC (2003) Changes in photoperiod or temperature alter the functional relationships between phytochromes and reveal roles for phyD and phyE. *Plant Physiology*, **131**, 1913–1920.

Halliday KJ, Koornneef M, Whitelam GC (1994) Phytochrome B and at least one other phytochrome mediate the accelerated flowering response of *Arabidopsis thaliana* L. to low red/far-red ratio. *Plant Physiology*, **104**, 1311–1315.

Halliday KJ, Salter MG, Thingnaes E, Whitelam GC (2003) Phytochrome control of flowering is temperature sensitive and correlates with expression of the floral integrator FT. *Plant Journal*, **33**, 875–885.

Hangarter RP (1997) Gravity, light and plant form. *Plant, Cell & Environment*, **20**, 796–800.

Hartmann E, Jenkins GI (1984) Photomorphogenesis of mosses and liverworts. In: *The Experimental Biology of Bryophytes* (eds Dyer AF, Duckett JG), pp. 203–228. Academic Press, London.

Harvey WH, Caponetti JD (1972) In vitro studies on the induction of sporogenous tissue on leaves of cinnamon fern. I. Environmental factors. *Canadian Journal of Botany*, **50**, 2673–2682.

Haupt W, Häder D-P (1994) Photomovement. In: *Photomorphogenesis in Plants* (eds Kendrick RE, Kronenberg GHM), pp. 707–732. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Hauser BA, Cordonnier-Pratt MM, Daniel-Vedele F, Pratt LH (1995) The phytochrome gene family in tomato includes a novel subfamily. *Plant Molecular Biology*, **29**, 1143–1155.

Hayama R, Coupland G (2004) The molecular basis of diversity in the photoperiodic flowering responses of *Arabidopsis* and rice. *Plant Physiology*, **135**, 677–684.

Hennig L, Stoddart WM, Dieterle M, Whitelam GC, Schafer E (2002) Phytochrome E controls light-induced germination of *Arabidopsis*. *Plant Physiology*, **128**, 194–200.

Hileman L, Drea S, de Martino G, Litt A, Irish VF (2005) Virus-induced gene silencing is an effective tool for assaying gene function in the basal eudicot species *Papaver somniferum* (opium poppy). *Plant Journal*, **44**, 334–341.

Howe GT, Gardner G, Hackett WP, Furnier GR (1996) Phytochrome control of short-day-induced bud set in black cottonwood. *Physiologia Plantarum*, **97**, 95–103.

Howe GT, Bucciaglia PA, Hackett WP *et al.* (1998) Evidence that the phytochrome gene family in black cottonwood has one *PHYA* locus and two *PHYB* loci but lacks members of the *PHYC/F* and *PHYE* subfamilies. *Molecular Biology and Evolution*, **15**, 160–175.

Hudson M, Smith H (1998) The phytochrome B encoded by the *HLG* locus of *Nicotiana plumbaginifolia* is required for detection of photoperiod: *hlg* mutants show altered regulation of flowering and circadian movement. *Plant Journal*, **15**, 281–287.

Hudson M, Robson PR, Kraepiel Y, Caboche M, Smith H (1997) *Nicotiana plumbaginifolia hlg* mutants have a mutation in a *PHYB*-type phytochrome gene: they have elongated hypocotyls in red light, but are not elongated as adult plants. *Plant Journal*, **12**, 1091–1101.

Hughes J, Lamparter T, Mittmann F, Hartmann E (1997) A prokaryotic phytochrome. *Nature*, **386**, 663.

Huq E, Al-Sady B, Hudson M *et al.* (2004) PHYTOCHROME-INTERACTING FACTOR 1 is a critical bHLH regulator of chlorophyll biosynthesis. *Science*, **305**, 1937–1941.

Ishikawa R, Tamaki S, Yokoi S *et al.* (2005) Suppression of the floral activator Hd3a is the principal cause of the night break effect in rice. *Plant Cell*, **17**, 3326–3336.

Izawa T, Oikawa T, Sugiyama N *et al.* (2002) Phytochrome mediates the external light signal to repress *FT* orthologues in photoperiodic flowering of rice. *Genes & Development*, **16**, 2006–2020.

Janssen T, Bremer K (2004) The age of major monocot groups inferred from 800+ *rbcL* sequences. *Botanical Journal of the Linnean Society*, **146**, 385–398.

Jiao Y, Ma L, Strickland E, Deng XW (2005) Conservation and divergence of light-regulated genome expression patterns during seedling development in rice and *Arabidopsis*. *Plant Cell*, **17**, 3239–3256.

Johnson E, Bradley M, Harberd NP, Whitelam GC (1994) Photoresponses of light-grown *phyA* mutants of *Arabidopsis* (phytochrome A Is required for the perception of daylength extensions). *Plant Physiology*, **105**, 141–149.

Karniol B, Vierstra RD (2003) The pair of bacteriophytochromes from *Agrobacterium tumefaciens* are histidine kinases with opposing photobiological properties. *Proceedings of the National Academy of Sciences, USA*, **100**, 2807–2812.

Karniol B, Wagner JR, Walker JM, Vierstra RD (2005) Phylogenetic analysis of the phytochrome superfamily reveals distinct microbial subfamilies of photoreceptors. *Biochemical Journal*, **392**, 103–116.

Kay SA, Keith B, Shinozaki K, Chye ML, Chua NH (1989) The rice phytochrome gene: structure, autoregulated expression, and binding of GT-1 to a conserved site in the 5′ upstream region. *Plant Cell*, **1**, 351–360.

Kenrick P, Crane PR (1997) *The Origin and Early Diversification of Land Plants: a Cladistic Study*. Smithsonian Institution, Washington, DC.

Kim HY, Coté GG, Crain RC (1993) Potassium channels in *Samanea saman* protoplasts controlled by phytochrome and the biological clock. *Science*, **260**, 960–962.

Kirk JTO, Tilney-Bassett RAE (1967) *The Plastids*. W.H. Freeman, London.

Knoop B (1984) Development in bryophytes. In: *The Experimental Biology of Bryophytes* (eds Dyer AF, Duckett JG), pp. 143–176. Academic Press, London.

Koch M, Haubold B, Mitchell-Olds T (2001) Molecular systematics of the Brassicaceae: evidence from coding plastidic *matK and* nuclear *Chs* sequences. *American Journal of Botany*, **88**, 534–544.

Krall L, Reed JW (2000) The histidine kinase-related domain participates in phytochrome B function but is dispensable. *Proceedings of the National Academy of Sciences, USA*, **97**, 8169–8174.

Labouriau LG (1958) Studies on the initiation of sporangia in ferns. *Arquivos do Museo Nacional*, **46**, 119–202.

Laetsch WM, Briggs WR (1962) Photomorphogenetic responses of sporelings of *Marsilea vestita*. *Plant Physiology*, **37**, 142–148.

Lamparter T (2004) Evolution of cyanobacterial and plant phytochromes. *FEBS Letters*, **273**, 1–5.

Lamparter T, Esch H, Cove D, Hartmann E (1997a) Phytochrome control of photoperiodism and chlorophyll accumulation in the apical cells of protonemal filaments of wildtype and an aphototropic mutant of the moss *Ceratodon purpureus*. *Plant & Cell Physiology*, **38**, 51–58.

Lamparter T, Mittmann F, Gärtner W *et al.* (1997b) Characterization of recombinant phytochrome from the cyanobacterium *Synechocystis*. *Proceedings of the National Academy of Sciences, USA*, **94**, 11792–11797.

Lavin M, Eshbaugh E, Hu J, Mathews S, Sharrock R (1998) Monophyletic subgroups of the tribe Millettieae (Leguminosae) as revealed by phytochrome nucleotide sequence data. *American Journal of Botany*, **85**, 412–.

Lewis LA, McCourt RM (2004) Green algae and the origin of land plants. *American Journal of Botany*, **91**, 1535–1556.

Li WZ, Chinnappa CC (2003) The phytochrome gene family in the *Stellaria longipes* complex. *International Journal of Plant Sciences*, **164**, 657–673.

Lynch M, Conery JS (2000) The evolutionary fate and consequences of duplicate genes. *Science*, **290**, 1151–1155.

MacDougal D (1903) The influence of light and darkness upon growth and development. *Memoirs of the New York Botanical Garden*, **2**, 1–319.

Maddonni GA, Otegui ME, Andrieu B, Chelle M, Casal JJ (2002) Maize leaves turn away from neighbors. *Plant Physiology*, **130**, 1181–1189.

Magallón S, Sanderson MJ (2002) Relationships among seed plants inferred from highly conserved genes: sorting conflicting phylogenetic signals among ancient lineages. *American Journal of Botany*, **89**, 1991–2006.

Magallón SA, Crane PR, Herendeen PS (1999) Phylogenetic pattern, diversity, and diversification of eudicots. *Annals of the Missouri Botanical Garden*, **86**, 297–372.

Maloof JN, Borevitz JO, Weigel D, Chory J (2000) Natural variation in phytochrome signaling. *Seminars in Cell and Developmental Biology*, **11**, 523–530.

Maloof JN, Borevitz JO, Dabi T, *et al.* (2001) Natural variation light sensitivity in Arabidopsis. *Nature Genetics*, **29**, 441–446.

Mancinelli AL (1994) The physiology of phytochrome action. In: *Photomorphogenesis in Plants* (eds Kendrick RE, Kronenberg GHM), pp. 211–269. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Mathews S (2005) Phytochrome evolution in green and nongreen plants. *Journal of Heredity*, **96**, 1–8.

Mathews S, Sharrock RA (1996) The phytochrome gene family in grasses (Poaceae): a phylogeny and evidence that grasses have a subset of the loci found in dicot angiosperms. *Molecular Biology and Evolution*, **13**, 1141–1150.

Mathews S, Sharrock RA (1997) Phytochrome gene diversity. *Plant, Cell & Environment*, **20**, 666–671.

Mathews S, Donoghue MJ (1999) The root of angiosperm phylogeny inferred from duplicate phytochrome genes. *Science*, **286**, 947–950.

Mathews S, Donoghue MJ (2002) Analyses of phytochrome data from seed plants: exploration of conflicting results from parsimony and Bayesian approaches. http://www.2002.botanyconference.org/section12/abstracts/238.shtml.

Mathews S, Lavin M, Sharrock RA (1995) Evolution of the phytochrome gene family and its utility for phylogenetic analyses of angiosperms. *Annals of the Missouri Botanical Garden*, **82**, 296–321.

Mathews S, Burleigh JG, Donoghue MJ (2003) Adaptive evolution in the photosensory domain of phytochrome A in early angiosperms. *Molecular Biology and Evolution*, **20**, 1087–1097.

Matsushita T, Mochizuki N, Nagatani A (2003) Dimers of the N-terminal domain of phytochrome B are functional in the nucleus. *Nature*, **424**, 571–574.

Maucher HP, Scheuerlein R, Schraudolf H (1992) Detection and partial sequence of phytochrome genes in the ferns *Anemia phyllitidis* (L.) Sw (Schizaeaceae) and *Dryopteris filix-mas* L. (Polypodiaceae) by using polymerase-chain reaction technology. *Photochemistry and Photobiology*, **56**, 759–763.

Mazzella MA, Arana MV, Staneloni RJ *et al.* (2005) Phytochrome control of the *Arabidopsis* transcriptome anticipates seedling exposure to light. *Plant Cell*, **17**, 2507–2516.

McCormac AC, Whitelam GC, Boylan MT, Quail PH, Smith H (1992) Contrasting responses of etiolated and light-adapted seedlings to red: far-red ratio: a comparison of wild type, mutant and transgenic plants has revealed differential functions of members of the phytochrome family. *Journal of Plant Physiology*, **140**, 707–714.

McNellis TW, Deng XW (1995) Light control of seedling morphogenetic pattern. *Plant Cell*, **7**, 1749–1761.

Miller JH (1968) Fern gametophytes as experimental material. *Botanical Review*, **34**, 360–441.

Mittmann F, Brucker G, Zeidler M *et al.* (2004) Targeted knockout in *Physcomitrella* reveals direct actions of phytochrome in the cytoplasm. *Proceedings of the National Academy of Sciences, USA*, **101**, 13939–13944.

Monte E, Alonso JM, Ecker JR *et al.* (2003) Isolation and characterization of *phyC* mutants in *Arabidopsis* reveals complex crosstalk between phytochrome signaling pathways. *Plant Cell*, **15**, 1962–1980.

Montgomery BL, Lagarias JC (2002) Phytochrome ancestry: sensors of bilins and light. *Trends in Plant Science*, **7**, 357–366.

Morgan DC, Rook DA, Warrington IJ, Turnbull HL (1983) Growth and development of *Pinus radiata* D. Don: the effect of light quality. *Plant, Cell & Environment*, **6**, 691–701.

Mukai Y, Tazaki K, Fuji T, Yamamoto N (1992) Light-independent expression of three photosynthetic genes, *cab*, *rbcS*, and *rbcL*, in coniferous plants. *Plant & Cell Physiology*, **33**, 859–866.

Murata T, Sugai M (2000) Photoregulation of asymmetric cell division followed by rhizoid development in the fern *Ceratopteris prothalli*. *Plant & Cell Physiology*, **41**, 1313–1320.

Nagata Y (1973) Rhizoid differentiation in *Spirogyra* II. Photoreversibility of rhizoid induction by red and far-red light. *Plant & Cell Physiology*, **14**, 543–554.

Norstog KJ, Nicholls TJ (1997) *The Biology of the Cycads*. Cornell University Press.

Oka Y, Matsushita T, Mochizuki N *et al.* (2004) Functional analysis of a 450-amino acid N-terminal fragment of phytochrome B in Arabidopsis. *Plant Cell*, **16**, 2104–2116.

Parker MW, Hendricks SB, Borthwick HA, Scully NJ (1946) Action spectrum for the photoperiodic control of floral initiation of a short day plant. *Botanical Gazette*, **108**, 1–26.

Pharis RP, Ruddat MDE, Glenn JL, Morf W (1970) A quantitative requirement for long day in the induction of staminate strobili by gibberellin in the conifer *Cupressus arizonica*. *Canadian Journal of Botany*, **48**, 653–658.

Platten JD, Foo E, Elliott RC *et al.* (2005) Cryptochrome 1 contributes to blue-light sensing in pea. *Plant Physiology*, **139**, 1472–1482.

Ponting CP, Aravind L (1997) PAS: a multifunctional domain family comes to light. *Current Biology*, **7**, R674–R677.

Pryer KM, Scheuttpelz E, Wolf PG *et al.* (2004) Phylogeny and evolution of ferns (Monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany*, **91**, 1582–1598.

Quail PH (1991) Phytochrome: a light-activated molecular switch that regulates plant gene expression. *Annual Review of Genetics*, **25**, 389–409.

Quail PH (1994) Phytochrome genes and their expression. In: *Photomorphogenesis in Plants* (eds Kendrick RE, Kronenberg GHM), pp. 71–104. Kluwer Academic Publishers, Dordrecht.

Raghavan V (1973) Photomorphogenesis of the gametophytes of *Lygodium japonicum*. *American Journal of Botany*, **60**, 313–321.

Raghavan V (1989) *Developmental Biology of Fern Gametophytes*. Cambridge University Press, Cambridge, UK.

Reed JW, Nagatani A, Elich TD, Fagan M, Chory J (1994) Phytochrome A and phytochrome B have overlapping but distinct functions in *Arabidopsis* development. *Plant Physiology*, **104**, 1139–1149.

Reski R (1998) Development, genetics and molecular biology of mosses. *Botanica Acta*, **111**, 1–15.

Rethy R (1968) Red (R), far-red (FR) photoreversible effects on the growth of *Chara* sporelings. *Zeitschrift fuer Pflanzenphysiologie*, **59S**, 100–102.

Rockwell NC, Lagarias JC (2005) The structure of phytochrome: a picture is worth a thousand spectra. *Plant Cell*, **18**, 4–14.

Rockwell NC, Su Y-S, Lagarias JC (2006) Phytochrome structure and signaling mechanisms. *Annual Review of Plant Biology*, **57**, 837–858.

Rüdiger W, López-Figueroa F (1992) Photoreceptors in algae. *Photochemistry and Photobiology*, **55**, 949–954.

Rydin C, Källersjö M, Friis EM (2002) Seed plant relationships and the systematic position of Gnetales based on nuclear and chloroplast DNA: Conflicting data, rooting problems, and the monophyly of conifers. *International Journal of Plant Sciences*, **163**, 197–214.

Sanderson MJ (2003) Molecular data from 27 proteins do not support a Precambrian origin of land plants. *American Journal of Botany*, **90**, 954–956.

Sanderson MJ, Wojciechowski MF, Hu JM, Khan TS, Brady SG (2000) Error, bias, and long-branch attraction in data for two chloroplast photosystem genes in seed plants. *Molecular Biology and Evolution*, **17**, 782–797.

Sanderson MJ, Thorne JL, Wikstrom N, Bremer K (2004) Molecular evidence on plant divergence times. *American Journal of Botany*, **91**, 1656–1665.

Schmidt M, Schneider-Poetsch HA (2002) The evolution of gymnosperms redrawn by phytochrome genes: the Gnetatae appear at the base of the gymnosperms. *Journal of Molecular Evolution*, **54**, 715–724.

Schmitt J, McCormac AC, Smith H (1995) A test of the adaptive plasticity hypothesis using transgenic and mutant plants disabled in phytochrome-mediated elongation responses to neighbors. *American Naturalist*, **146**, 937–953.

Sharrock R, Clack T (2004) Heterodimerization of type II phytochromes in *Arabidopsis*. *Proceedings of the National Academy of Sciences, USA*, **101**, 11500–11505.

Sharrock RA, Mathews S (2006) Phytochrome genes in higher plants: structure, expression, and evolution. In: *Photomorphogenesis in Plants and Bacteria* (eds Schäfer E Nagy F), pp. 99–129. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Sharrock RA, Quail PH (1989) Novel phytochrome sequences in *Arabidopsis thaliana*: Structure, evolution, and differential expression of a plant regulatory photoreceptor family. *Genes & Development*, **3**, 1745–1757.

Sheehan MJ, Farmer PR, Brutnell TP (2004) Structure and expression of maize phytochrome family homologs. *Genetics*, **167**, 1395–1405.

Shinomura T (1997) Phytochrome regulation of seed germination. *Journal of Plant Research*, **110**, 151–161.

Shinomura T, Nagatani A, Hanzawa H *et al.* (1996) Action spectra for phytochrome A- and B-specific photoinduction of seed germination in Arabidopsis thaliana. *Proceedings of the National Academy of Sciences, USA*, **93**, 8129–8133.

Shinomura T, Uchida K, Furuya M (2000) Elementary processes of photoperception by phytochrome A for high-irradiance response of hypocotyl elongation in *Arabidopsis*. *Plant Physiology*, **122**, 147–156.

Smith H (1982) Light quality, photoperception, and plant strategy. *Annual Review of Plant Physiology*, **33**, 481–518.

Smith H (1995) Physiological and ecological function within the phytochrome family. *Annual Review of Plant Physiology and Plant Molecular Biology*, **46**, 289–315.

Smith H (2000) Phytochromes and light signal perception by plants — an emerging synthesis. *Nature*, **407**, 585–591.

Smith H, Whitelam GC (1990) Phytochrome, a family of photoreceptors with multiple physiological roles. *Plant, Cell & Environment*, **13**, 695–707.

Smith H, Whitelam GC (1997) The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant, Cell & Environment*, **20**, 840–844.

Smith H, Xu Y, Quail PH (1997) Antagonistic but complementary actions of phytochromes A and B allow optimum seedling de-etiolation. *Plant Physiology*, **114**, 637–641.

Sokol RC, Stross RG (1986) Annual germination window in oospores of *Nitella furcata* (Charophyaceae). *Journal of Phycology*, **22**, 403–406.

Somers DE, Sharrock RA, Tepperman JM, Quail PH (1991) The *hy3* long hypocotyl mutant of *Arabidopsis* is deficient in phytochrome B. *Plant Cell*, **3**, 1263–1274.

Somers DE, Devlin PF, Kay SA (1998) Phytochromes and cryptochromes in the entrainment of the *Arabidopsis* circadian clock. *Science*, **282**, 1488–1490.

Spiro MD, Torabi B, Cornell CN (2004) Cytokinins induce photomorphogenic development in dark-grown gametophytes of *Ceratopteris richardii*. *Plant Cell Physiology*, **45**, 1252–1260.

Steeves TA, Sussex IM (1957) Studies on the development of excised leaves in sterile culture. *American Journal of Botany*, **44**, 665–673.

Stewart WN, Rothwell GW (1993) *Paleobotany and the Evolution of Plants*, 2nd edn. Cambridge University Press, Cambridge, UK.

Suárez-López P, Wheatley K, Robson F *et al.* (2001) CONSTANS mediates between the circadian clock and the control of flowering in Arabidopsis. *Nature*, **410**, 1116–1120.

Suetsugu N, Mittmann F, Wagner G, Hughes J, Wada M (2005) A chimeric photoreceptor gene, NEOCHROME, has arisen twice during plant evolution. *Proceedings of the National Academy of Sciences, USA*, **102**, 13705–13709.

Takagi S, Kong SG, Mineyuki Y, Furuya M (2003) Regulation of actin-dependent cytoplasmic motility by type II phytochrome occurs within seconds in *Vallisneria gigantea* epidermal cells. *Plant Cell*, **15**, 331–345.

Takano M, Inagaki N, Xie X *et al.* (2005) Distinct and cooperative functions of phytochromes A, B, and C in the control of deetiolation and flowering in rice. *Plant Cell*, **17**, 3311–3325.

Takatori S, Imahori K (1971) Light reactions in the control of oospore germination of *Chara delicatula*. *Phycologia*, **10** (2/3), 221–228.

Tavares JE, Sussex IM (1968) Expansion growth of isolated leaf blades of *Todea barbara*. *Planta*, **80**, 113–128.

Thümmler F, Dufner M, Kreisl P, Dittrich P (1992) Molecular cloning of a novel phytochrome gene of the moss *Ceratodon purpureus* which encodes a putative light-regulated protein kinase. *Plant Molecular Biology*, **20**, 1003–1017.

Toole VK, Toole EH, Hendricks SB, Borthwick HA, Snow AG (1961) Responses of seeds of *Pinus virginiana* to light. *Plant Physiology*, **36**, 285–290.

Tóth R, Kevei É, Hall A *et al.* (2001) Circadian clock-regulated expression of phytochrome and cryptochrome genes in *Arabidopsis*. *Plant Physiology*, **127**, 1607–1616.

Uenaka H, Wada M, Kadota A (2005) Four distinct photoreceptors contribute to light-induced side branch formation in the moss *Physcomitrella patens*. *Planta*, **222**, 623–631.

Valanne N (1971) The effects of prolonged darkness and light on the fine structure of *Ceratodon purpureus*. *Canadian Journal of Botany*, **49**, 547–554.

Valverde F, Mouradov A, Soppe W *et al.* (2004) Photoreceptor regulation of CONSTANS protein in photperiodic flowering. *Science*, **303**, 1003–1006.

Virgin HI (1978) Inhibition of etiolation in *Spirogyra* by phytochrome. *Physiologia Plantarum*, **44**, 241–245.

Vogelmann TC (1994) LIght within the plant. In: *Photomorphogenesis in Plants* (eds Kendrick RE Kronenberg GHM), pp. 491–535. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Vorster P (1993) Aspects of the reproduction of cycads. 2. An annotated review of known information. In: *Proceedings of the Third International Conference on Cycad Biology* (ed. Vorster P), pp. 379–389. Cycad Society of South Africa, Pretoria.

Voth PD, Hamner KC (1940) Responses of *Marchantia polymorpha* to nutrient supply and photoperiod. *Botanical Gazette*, **102**, 169–205.

Wada M, Kadota A (1989) Photomorphogenesis in lower green plants. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 169–191.

Wagner JR, Brunzelle JS, Forest KT, Vierstra RD (2005) A light-sensing knot revealed by the structure of the chromophore-binding domain of teh phytochrome. *Nature*, **438**, 325–331.

Wann FB (1925) Some of the factors involved in the sexual reproduction of *Marchantia polymorpha*. *American Journal of Botany*, **12**, 307–318, plus plates.

Warrington IJ, Rook DA, Morgan DC, Turnbull HL (1988) The influence of simulated shadelight and daylight on growth, development and photosynthesis of *Pinus radiata*, *Agathis australis*, and *Dacrydium cupressinum*. *Plant, Cell & Environment*, **11**, 343–356.

Wei N, Kwok SF, von Arnim AG *et al.* (1994) Arabidopsis COP8, COP10, and COP11 genes are involved in repression of photomorphogenic development in darkness. *Plant Cell*, **6**, 629–643.

Weller JL, Schreuder ME, Smith H, Koornneef M, Kendrick RE (2000) Physiological interactions of phytochromes A, B1 and B2 in the control of development in tomato. *Plant Journal*, **24**, 345–356.

Weller JL, Perrotta G, Schreuder ME *et al.* (2001) Genetic dissection of blue-light sensing in tomato using mutants deficient in cryptochrome 1 and phytochromes A, B1 and B2. *Plant Journal*, **25**, 427–440.

Wellman CH, Osterloff PL, Mohiuddin U (2003) Fragments of the earliest land plants. *Nature*, **425**, 282–285.

Wilson JR, Schwabe WW (1964) Growth and dormancy in *Lunularia cruciata* (L.) Dum. III. The wavelengths of light effective in photoperiodic control. *Journal of Experimental Botany*, **15**, 368–380.

Wu S-H, Lagarias JC (1997) The phytochrome photoreceptor in the green alga *Mesotaenium caldariorum*: implication for a conserved mechanism of phytochrome action. *Plant, Cell & Environment*, **20**, 691–699.

Wu S-H, Lagarias JC (2000) Defining the bilin lyase domain: lessons from the extended phytochrome superfamily. *Biochemistry*, **39**, 13487–13495.

Yanovsky MJ, Kay SA (2002) Molecular basis of seasonal time measurement in *Arabidopsis*. *Nature*, **419**, 308–312.

Yanovsky MJ, Kay SA (2003) Living by the calendar: how plants know when to flower. *Nature Genetics*, **4**, 265–275.

Yanovsky MJ, Casal JJ, Whitelam GC (1995) Phytochrome A, phytochrome B and *HY4* are involved in hypocotyl growth responses to natural radiation in *Arabidopsis*: weak de-etiolation of the *phyA* mutant under dense canopies. *Plant, Cell &Environment*, **18**, 788–794.

Yeh K-C, Wu S-H, Murphy JT, Lagarias JC (1997) A cyanobacterial phytochrome two-component light sensory system. *Science*, **277**, 1505–1508.

Young E, Hanover JW (1977) Effects on quality, intensity, and duration of light breaks during a long night on dormancy in blue spruce (*Picea pungens* Engelm.) seedlings. *Plant Physiology*, **60**, 271–273.

Yu J, Hu S, Wang J *et al.* (2002) A draft sequence of the rice genome (*Oryza sativa* L. ssp. *indica*). *Science*, **296**, 79–92.

The author is interested in the question of how changes in light-sensing systems have influenced the ability of plants to survive and diversify. Specifically, she uses phylogenetic, genetic, and comparative physiological approaches to explore the links between molecular and functional evolution in the phytochrome photoreceptor family. The author is a Sargent Fellow at the Arnold Arboretum of Harvard University where she is supported by funding from the US National Science Foundation and the Arnold Arboretum.
