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The Cutting Edge of Photoresponse Mechanisms: Photoreceptor and Signaling Mechanism

Evolutionary aspects of plant photoreceptors

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Abstract Plant photoreceptors link environmental light cues with physiological responses, determining how individual plants complete their life cycles. Structural and functional evolution of photoreceptors has co-occurred as plants diversified and faced the challenge of new light environments, during the transition of plants to land and as substantial plant canopies evolved. Large-scale comparative sequencing projects allow us for the first time to document photoreceptor evolution in understudied clades, revealing some surprises. Here we review recent progress in evolutionary studies of three photoreceptor families: phytochromes, phototropins and neochromes.

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Introduction

Light exerts a powerful influence on most vegetable tissues, and there can be no doubt that it generally tends to check their growth—Charles Darwin, 1880 (in The Power of Movement in Plants)

Light provides the energy for plant growth but it also is one of the most important informational cues for plants. Light influences the direction in which plants grow, how they array their leaves and reproductive structures in space (Galvão and Fankhauser 2015), and the nature of their response to pathogens and herbivores (Ballaré 2009). Light signals also interact with gravity- and temperature-sensing pathways (Kami et al. 2010) and thus influence plant responses to gravity and temperature. At the interface between light and plant responses are the photoreceptors, which measure the intensity and wavelength of light, and use the information to modulate physiological responses.

Photoreceptors not only govern plant survival on the short term, but also influence long-term evolutionary trajectories and have a role in species diversification. When plants colonized the land, bringing their photoreceptors with them, it was largely bare. With respect to light, surface environments were uniformly well lit during the day. It is likely that plants at this time used photoreceptors to control the synthesis of beneficial biochemicals such as anti-oxidants and UV-protectants that would help them adapt to harsh environments, as well as to control reproductive timing and chloroplast movement (Mathews 2006). When wood and the arborescent habit later evolved, contrasting light environments came to exist in open and shaded habitats. Light gradients developed under canopies, and absorption by plant pigments drastically altered the light spectrum. From that time forward, plants diversified to occupy

both shaded and open habitats, and they needed an array of photoreceptors that would enhance their success in a greater variety of environments (Mathews 2006). Indeed, ferns and bryophytes diversified under the canopy of seed plants (Laenen et al. 2014; Schneider et al. 2004; Schuettpelz and Pryer 2009), and photoreceptor families also have diversified. In particular, the phototropin and phytochrome families have evolved through gene duplication, resulting in divergent paralogs that require different amounts and/or quality of light to trigger a physiological response (Galvão and Fankhauser 2015; Li et al. 2015a, b).

Plants use diverse photoreceptors to monitor the light environment. Phytochromes (phy) measure the ratio of red to far-red light; phototropins (phot), cryptochromes (cry) and ZEITLUPE/FLAVIN-BINDING, KELCH REPEAT, F-BOX 1/LOV KELCH PROTEIN 2 (ZTL/FKF1/LKP2) measure blue/UV-A; UV RESISTANCE LOCUS 8 (UVR8) measures UV-B (Galvão and Fankhauser 2015); neochrome (neo) is a fusion of PHY and PHOT and measures both blue and red light (Kawai et al. 2003; Kanegae et al. 2006; Nozue et al. 1998; Suetsugu et al. 2005). The biochemistry, structure, and function of these photoreceptors have been characterized in considerable detail (Chaves et al. 2011; Christie 2007; Kami et al. 2010; Mathews 2010; Möglich et al. 2010; Rockwell et al. 2006; Suetsugu and Wada 2013), with the advances coming largely from studies of *Arabidopsis thaliana* and a handful of additional model systems. Only limited data have existed to address the molecular evolution of photoreceptors in land plants, except for seed plant *PHY* (Mathews et al. 2003; Mathews 2010), and thus a solid foundation for understanding their functional evolution has not been available.

The recent surge of genome and transcriptome sequencing projects on non-model organisms (e.g., the 1KP transcriptomes; Matasci et al. 2014) has opened an unprecedented opportunity to systemically survey photoreceptors from across all algal and land plant lineages. Data from these and from more focused projects are revealing fascinating evolutionary aspects of photoreceptors (Duanmu et al. 2014; Li et al. 2014, 2015a, b; Rockwell et al. 2014). We provide in this review updates on the evolution of three photoreceptor families, phytochromes, phototropins and neochromes, summarizing new insights into their origin, diversity, and evolution. We then highlight questions that should be priorities for future research projects.

The origin and diversity of phytochromes

Phytochromes are red/far-red photoreceptors that regulate seed germination, seedling de-etiolation, shade avoidance, and flowering time, and that modulate responses to pathogens, herbivores, gravity, and temperature (Franklin and Quail 2010; Kami et al. 2010). Phytochromes are present in all land plant and most green algal lineages, except in the chlorophytes (Fig. 1b). Phytochromes also have been detected in a brown algae, diatoms, fungi, but not in red algae (Rhodophytes) (Li et al. 2015a); bacteriophytochromes are widespread in prokaryotes (Karniol et al. 2005). Phytochromes comprise two modules—the photosensory module at the N-terminus, and the regulatory module at the C-terminus. The domain composition of the photosensory module is largely conserved across the phytochrome superfamily as PAS-GAF-PHY, whereas the regulatory module is much more variable (Auldridge and Forest 2011; Li et al. 2015a) (Fig. 1b)

Land plants and charophyte algae (together called streptophytes) have the canonical plant phytochrome structure, characterized by having a PAS–PAS repeat and a histidine-kinase related domain (HKRD) in the C-terminal regulatory module (Li et al. 2015a) (Fig. 1b). HKRD has high sequence similarity to histidine kinase, but it lacks the conserved histidine residue that is necessary for kinase activity (Yeh and Lagarias 1998). The origin of this canonical structure has until recently remained obscure. Herdman et al. (2000) sought to understand relationships of the different *PHY* being discovered in cyanobacteria at the time and used PCR to obtain *PHY* from a greater diversity of cyanobacterial species. Their data established that *CPH1* from *Synechocystis* to its homologs in other cyanobacteria had N-terminal modules more closely related to canonical plant *PHY* than did other *PHY*-like sequences in cyanobacterial genomes. Lamparter and colleagues (Buchberger and Lamparter 2015; Lamparter 2004) revisited the question as more data became available. Buchberger and Lamparter (2015) separately analyzed sequences from the N- and C-terminal modules and established that they had different evolutionary origins. They further suggested that the photosensory module was inherited from cyanobacteria (likely through endosymbiotic transfer), and the regulatory module from proteobacteria. Their data, however, could not rule out other explanations for the origins of these modules because key taxa had not been sampled.

It is possible that the ancestor of the archaeplastid lineage (Fig. 1b) obtained a phytochrome during or after the primary endosymbiosis that gave rise to plastids (Gould et al. 2008), as has often been suggested (e.g., Herdman et al. 2000; Karniol et al. 2005; Buchberger and Lamparter 2015). This would be supported if cyanobacterial phytochromes were paraphyletic to, or formed the sister clade of, archaeplastid phytochromes in trees from analyses of sequences from all the additional phytochrome-bearing lineages: bacteriophytochromes, fungi, stramenopiles (diatoms and brown algae), glaucophytes, cryptophytes. The first study to include all the relevant lineages found
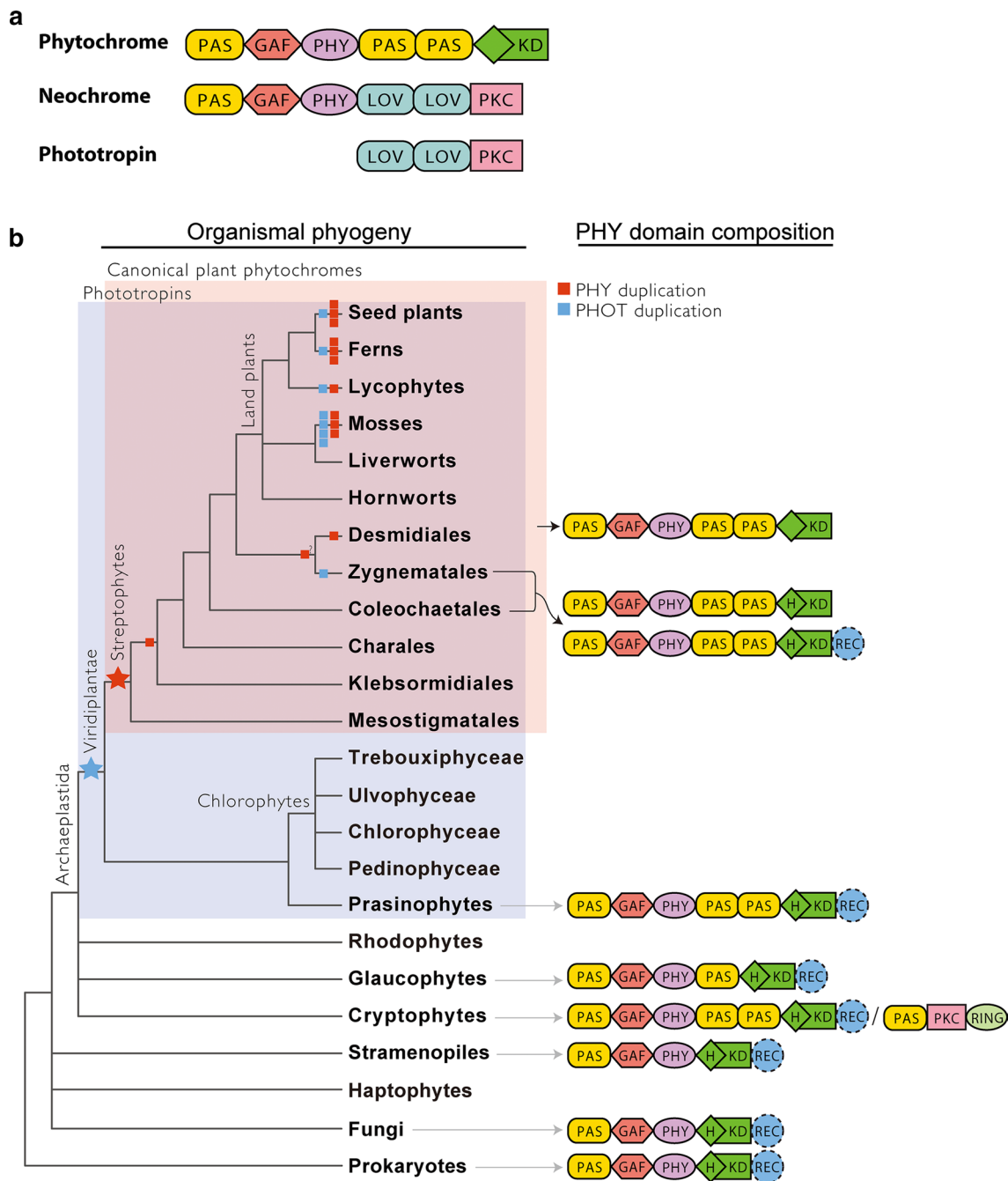
Fig. 1 a Domain composition of the canonical plant phytochromes, neochromes and phototropins. The length of the photoreceptors and domains are not to scale. **b** The origin and evolution of plant phytochromes and phototropins. *Blue* and *red* backgrounds mark the distribution of phototropins and canonical plant phytochromes, respectively. Phytochrome domain diversity is shown on the *right*. Zygnematales and Coleochaetales have both canonical and non-canonical plant phytochromes, although the origin of the latter is unclear. Cryptophytes have two types of phytochromes, with different C-terminal regulatory modules (marked by "/"). Domains that are not always present are indicated by *dashed outlines*. The *blue* and *red stars* mark the origin of phototropins and canonical plant phytochromes, respectively. *GAF* cGMP phosphodiesterase/adenylate cyclase/FhlA, *H/KD* histidine phosphorylation site (H) in the histidine kinase domain (KD), *LOV* Light/Oxygen/Voltage, *PAS* Per/Arnt/Sim, *PHY* phytochrome, *PKC* Protein Kinase C, *REC* response regulator, *RING* really interesting new gene (color figure online)

that cyanobacterial sequences were nested within bacteriophytochromes rather than on the branch leading to the Archaeplastida (Duanmu et al. 2014) (Fig. 1b). A later study including fewer bacterial sequences but a much more extensive sampling of phytochromes from the green algal lineages obtained a similar result (Li et al. 2015a).

Although the trees are unrooted, they cannot be rooted in a way that would place cyanobacterial and archaeplastidal sequences together. This suggests Archaeplastida could as easily have acquired a phytochrome from a bacterial donor via horizontal gene transfer (HGT) as from a cyanobacterium via endosymbiotic gene transfer. Regardless of the prokaryotic source of an ancestral archaeplastidal phytochrome, the additional data obtained from Viridiplantae by Li et al. (2015a) provided compelling confirmation of the origin of canonical phytochrome from within the green algae, and allowed them to reconstruct the steps by which its structure evolved, through assembly of modules and the loss of a conserved histidine.

Canonical plant phytochromes are present in all streptophyte lineages, including the earliest-diverging mesostigmatalean algae (Fig. 1a; Li et al. 2015a). These phytochromes have experienced multiple rounds of gene duplications, both in the charophyte algae and in land plants (Fig. 1b). The earliest one appeared to take place after Mesostigmatales diverged, resulting in charophyte *PHY1* and *PHY2* (Li et al. 2015a); the latter includes the previously known *Mougeotia* and *Mesotaenium* phytochromes (Lagarias et al. 1995; Winands and Wagner 1996). Land plant phytochromes were derived from the charophyte *PHY2* lineage, and then independently duplicated in mosses, homosporous lycophytes, ferns and seed plants, while remaining single-copy in heterosporous lycophytes, liverworts and hornworts (Li et al. 2015a). Comparison of gene and species trees, allows one to establish the orthology and the timing of gene duplications for land plant phytochromes. At least ten phytochrome duplications occurred on the major branches of the land plant species tree (Fig. 1; Li et al. 2015a).

The origin and diversity of phototropins

Phototropins are blue-light photoreceptors that regulate shoot phototropism, chloroplast movement, stomatal opening, and leaf expansion; they also contribute to rapid de-etiolation (Christie 2007; Fankhauser and Christie 2015). Phototropins comprise two Light/Oxygen/Voltage (LOV) domains (LOV1 and LOV2), and a Serine/Threonine Kinase domain (STK; Fig. 1a). Much less was known about the evolutionary history of phototropins than phytochromes, since even for flowering plants and other seed plants, detailed gene phylogenies did not exist. In a second study, Li et al. (2015b) found that phototropins were ubiquitous in Viridiplantae (land plants + green algae; Li et al. 2015b), but no phototropin homologs were found in glaucophytes or in red algae, suggesting that phototropins originated in an ancestor of Viridiplantae (Li et al. 2015b) (Fig. 1b). The use of LOV domains in blue light sensing is found in structurally diverse proteins from plants, animals, fungi, and bacteria (Crosson et al. 2003; Krauss et al. 2009; Suetsugu and Wada 2013). The uniqueness of phototropins to plants is thus not surprising.

In contrast to the phytochrome diversity observed in algae, algal phototropin apparently exists as a single-copy gene, except in Zygnematales where two copies are present (*PHOTA* and *PHOTB*). Previous studies indicated that phototropins are multi-copy in angiosperms, ferns, and mosses, although relationships among these phototropin homologs remained unclear. Based on limited taxonomic samplings, Lariguet and Dunand (2005) and Galván-Ampudia and Offringa (2007) both found that angiosperm phototropins fell into two groups, *PHOT1* and *PHOT2*, and that fern phototropins clustered with *PHOT2*. This relationship, if true, would suggest that the known fern phototropins are orthologous to *Arabidopsis PHOT2*.

As in the studies of phytochrome evolution, greatly expanding the taxonomic sampling in a study of phototropins provided clear insights into the question of homology of *PHOT* genes. Li et al. (2015b) found that phototropins independently duplicated in mosses, ferns, and seed plants (Li et al. 2015b) (Fig. 1b). The independence of the duplications was strongly supported in bootstrapping analyses. Thus, contra (Lariguet and Dunand 2005) and (Galván-Ampudia and Offringa 2007), seed plant *PHOT1* and *PHOT2* do not have orthologs outside of seed plants. Rather, separate duplications have resulted in three distinct pairs of paralogous *PHOT1* and *PHOT2* in land plants. Phototropins likely are single-copy in hornworts and liverworts, based on genomic and transcriptomic evidence (Komatsu et al. 2014; Li et al. 2015b). Interestingly, all the hornwort phototropins known to date lack introns, and were likely derived from a retrotransposition event (Li et al. 2014). These intronless phototropins are the close relative of the phototropin module of neochromes (see below).

Neochromes

Neochromes are unique chimeric photoreceptors, having a phytochrome photosensory module at the N-terminus and a full set of phototropin domains at the C-terminus (Nozue et al. 1998; Suetsugu et al. 2005) (Fig. 1a). They are found in zygnematalean algae, hornworts, and ferns (Li et al. 2015b). All algal neochromes known to date lack the conserved cysteine residue in LOV2 domain, which is essential for flavin mononucleotide (FMN) adduct formation and blue light perception (Christie 2007). It is thus possible that algal neochromes function only as a red light photoreceptor. Kanegae and Kimura (2015) recently showed, however, that in *Adiantum capillus-veneris* (a fern) neochromes, FMN-cysteinyl adduct formation is not required

for blue light-induced phototropism, suggesting that algal neochromes might still be able to relay both blue and red/far-red signals (Suetsugu et al. 2005; Kagawa and Suetsugu 2007).

Neochromes have a remarkable evolutionary history, having originated twice, once in zygnematalean algae and once in hornworts (Li et al. 2014). Furthermore, after their origin, hornwort neochromes apparently were transferred horizontally to ferns (Li et al. 2014). Hornwort and fern neochromes completely lack introns, and the fern sequences are nested within the hornwort neochrome clade. Algal neochromes, in contrast, have introns in both the *PHY* and *PHOT* modules, and their *PHOT* module is not closely related to those in land plants. These data, together with the apparent lack of neochromes from all other land plant clades and from early-diverging ferns, suggest that fern neochromes were derived from hornworts via horizontal transfer. Molecular dating placed the divergence time between fern and hornwort neochromes to be around 178 million years ago, much later than the separation of ferns and hornworts (at least 400 million years ago), further supporting the HGT scenario.

In ferns, neochromes can sense both blue and red/far-red light to regulate chloroplast movement and phototropism (Kanegae et al. 2006; Kanegae and Kimura 2015; Kawai et al. 2003), and confer a significantly higher sensitivity to light. Consequently, neochromes may have played a critical role in facilitating the diversification under low-light angiosperm canopies (Kawai et al. 2003; Schneider et al. 2004; Schuettpelz and Pryer 2009). The vehicle and mechanism of neochrome HGT is unknown, but the sequencing of whole fern genomes will likely help address this question (Li and Pryer 2014; Sessa et al. 2014).

Interplay of phytochromes and phototropins

The integration of blue and red/far-red light sensory systems is widespread in land plants and it may be particularly useful for plants facing light environments under canopies. Integration occurs in diverse ways: these include merging the receptors (i.e. neochromes), forming protein complexes (Purschwitz et al. 2008; Kasahara et al. 2004; Jaedicke et al. 2012), and sharing signaling pathways (Hughes 2013; Galvão and Fankhauser 2015). We found that phytochromes and phototropins exhibit a similar pattern of gene family expansion and stasis (Fig. 1b). They both duplicated in seed plants, ferns and mosses, while remaining single-copy in liverworts and hornworts. A shared whole genome duplication history may explain this pattern in part, but the exact branches where duplication took place differ in some cases. For example, in ferns, phototropin duplicated once after Ophioglossales diverged (Li et al. 2015b), whereas

phytochromes duplicated three times, once in an ancestor of all extant ferns, once after Gleicheniales diverged and the other after Schizaeales diverged (Li et al. 2015a).

Li et al. (2015b) hypothesized that phytochromes and phototropins might have been co-evolving. This is consistent with their physical interaction (Jaedicke et al. 2012). It may be also likely, however, that coincidence or near coincidence of duplications in the *PHY* and *PHOT* families indicates that in both red and blue light signaling systems, having separate copies for responses in high and low light environments was adaptive. For example, lineages in which there has been functional diversification in both phytochrome and phototropin families appear to be more species rich. The highest diversity in the fern and moss lineages is in Polypodiales and Bryopsida, both of which experienced the most phytochrome and phototropin gene duplication events compared to other fern and moss clades. The extent to which these extra duplications are due to whole genome duplication remains to be thoroughly tested, and future studies should also examine the adaptive effect of many other genes that have duplicated on the branches to these clades.

Future directions

The recent findings on photoreceptor origin, diversity and orthology suggest many interesting research questions, and below we highlight some that we believe are feasible and worthwhile to pursue in the future.

What happens when both canonical and non-canonical phytochromes are present in the same organism?

Some streptophyte algae (Zygnematales and Coleochaetales) possess both canonical and non-canonical phytochromes (Fig. 1). The non-canonical ones (*PHYX1* and *PHYX2*) have the PAS-PAS repeat, but the histidine residue is conserved in the C-terminal kinase domain and sometimes a response regulator is also present (Li et al. 2015a) (Fig. 1b). It would be of particular interests to examine the functions and interactions between the canonical and non-canonical phytochromes within the same organism. Do they form heterodimers, have different spectral properties, modulate different functions, and/or use different signaling transduction pathways?

Which photoreceptors control hornwort chloroplast contraction and rotation?

One of the key functions of phototropin is to regulate chloroplast movement, which has been shown in seed plants (Kagawa et al. 2001), ferns (Kagawa et al. 2004), mosses

(Kasahara et al. 2004) and liverworts (Komatsu et al. 2014). In hornworts (a bryophyte lineage), chloroplasts are usually large and occupy most of the cellular space. It is unknown if such chloroplasts move (if there is much space to move), but an early study found that they can significantly contract/expand, or rotate according to light intensity (Burr 1968). We recently found that the contraction response can be elicited by high intensity blue light (Li et al. 2014), which suggests phototropins and/or neochromes might be involved. With *Anthoceros agrestis* being developed as a model hornwort (Szövényi et al. 2015), it will be possible in the near future to carry out genetic studies dissecting the roles of phototropins and neochromes in chloroplast contraction and rotation.

What are the functions of phytochromes and phototropins in algae?

Algae have markedly different body plans and habitats compared to land plants; therefore, their photoreceptors likely modulate different physiological responses than those that have been characterized in land plants (Hegemann 2008). A recent study found a fascinating spectral diversity in algal phytochromes—in addition to the conventional red/far-red light absorption spectrum, some of them have shifted to blue, green, or orange light (Rockwell et al. 2014). This very diverse spectral sensitivity likely results from adaption to aquatic environments. Red and far-red light does not penetrate far into water, although red light signals may be generated in marine environments by processes such as Raman scattering and chlorophyll *a* fluorescence (Ragni and d'Alcalá, 2004). Relying on other regions of the light spectrum would therefore have adaptive advantages (Rockwell et al. 2014). To date, only a fraction of algal phytochromes have been characterized, and further exploration will likely find additional spectral and biochemical variants.

Similarly, only a few studies have examined phototropin functions in algae. In *Chlamydomonas reinhardtii* (a chlorophyte alga), phototropin (Crphot) regulates sex determination, eyespot size, phototactic behavior, and expression of photosynthesis genes (Huang and Beck 2003; Im et al. 2006; Trippens et al. 2012), and it can restore most of the phototropin functions in the *Arabidopsis phot1 phot2* double mutant (Onodera and Kong 2005). Sullivan et al. (2015) recently characterized the phototropin from *Ostreococcus tauri* (Otphot), a prasinophyte alga that diverged earlier than *C. reinhardtii*. Otphot exhibits several typical phototropin properties. For example, Otphot is plasma membrane-bound, and partially internalized upon blue-light irradiation. On the other hand, it cannot rescue chloroplast avoidance or phototropic responses in the *Arabidopsis phot1 phot2* double mutant. The function of Otphot within

O. tauri, however, was not examined. More studies focusing on phototropins in algal lineages will be essential to understand not only the early events in phototropin functional evolution, but also how phototropins were later co-opted to modulate multi-cellular (e.g., shoot phototropism) and cell-autonomous (e.g., stomatal opening; Doi et al. 2015) physiological responses in land plants.

Conclusion

Past research on model organisms has greatly advanced our understanding of photoreceptor functions and their molecular underpinnings. These studies can now be augmented with data from all of plant biodiversity. The great diversity of phytochromes and phototropins from across the plant kingdom that has recently been revealed (Duanmu et al. 2014; Li et al. 2015a, b; Rockwell et al. 2014), and the resolution of relationships among them sets the stage for studies that take advantage of such diversity to gain a holistic view on photoreceptor molecular biology and its role in plant evolution.

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