M. Wada, K. Shimazaki, M. Iino (Eds.)
Light Sensing in Plants

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Preface

Plants utilize light not only for photosynthesis but also for monitoring changes in environmental conditions essential to their survival. Wavelength, intensity, direction, duration, and other attributes of light are used by plants to predict imminent seasonal change and to determine when to initiate physiological and developmental alterations. Most plants sense red/far-red light and blue light through photoreceptors: phytochromes detect red/far-red light, while there are several kinds of blue-light receptors, including cryptochromes, phototropins, and ZLP/FKF/LKP/ADO. The typical phytochrome responses known as red/far-red photoreversible phenomena were discovered in 1952 by Borthwick et al. and the phytochrome was characterized as a chromoprotein in 1959 by Butler et al. However, blue-light receptors were not identified until cryptochrome was found in 1993 by Cashmore's group. Now we are in an exceptional period of discovery of blue-light receptors such as phototropins, ZLP/FKF/LKP/ADO, and PAC in *Euglena*. Thus, it is very timely to publish this book on light sensing and signal transduction in plant photomorphogenesis written by leading scientists gathered at Okazaki from all over the world in June 2004. It was a great opportunity to discuss new discoveries in the field. It also marked the retirement of Prof. Masaki Furuya, who has contributed substantially to this field for many years.

This volume, published as part of the special-issue series of The Botanical Society of Japan, presents the advances made over the last 5 to 10 years in many of the related fields. Included are Prof. Furuya's "History and Insights" of plant photomorphogenesis, three overviews of the main photoreceptors, and Prof. Briggs' epilogue comparing the status of research in 1986 and 2004, when the XVI and the LVIII Yamada Conferences on plant photomorphogenesis were held at Okazaki. I believe that this book will prove indispensable and will contribute to the advancement of the study of photomorphogenesis.

I express my sincere gratitude to Yamada Science Foundation and to the executive members of the Foundation for their generosity, which made it possible for us to publish this book.

Masamitsu Wada

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Part I
Prologue

Chapter 1

History and Insights

Masaki Furuya[1,2]

Genesis (Legend to 1950s)

Human beings have always relied on plants to provide their staple foods and raw materials for diverse tools, and since prehistoric times must have known that sunlight greatly influences plant development and reproduction. From the Renaissance onwards, careful observations of nature led to a growing awareness that both higher and lower plants respond variously to light in terms of irradiation dosage for photosynthesis, direction for phototropism, timing and duration for photoperiodism, and wavelengths for photomorphogenesis. Joseph Priestley (1772) discovered that green plants utilize light as their source of energy for the production of complex organic substances. Julius Sachs (1864) demonstrated that only the blue region of visible light resulted in phototropic bending of plants. Charles Darwin and his son (1881) carried out a pioneering experiment on light-signal transduction of phototropism, in which they separated the photoreceptive site from the responding growth region in monocot seedlings. In 1910, Georg Klebs gathered a lot of evidence that the environmental light greatly influences growth and development of seed plants and ferns. However, the molecular basis of light perception and signal transduction in plants was not elucidated until quite recently.

The physiological capacity of plants to adjust processes throughout their life cycle to the seasonal change of environment is crucial for their survival. Julien Tournois (1914), a graduate student of the École Normale Supérieure in Paris, discovered that night length rather than day length was the determining factor for flowering time of his experimental material, Japanese hop. Wightman Garner and Harry Allard (1920) at the Arlington Farm of USDA carried out comprehensive experiments on flowering time in several plants by changing the night length using three dark houses. They discovered that most of the plants tested

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could be classified as "short-day" or "long-day" plants, and established the concept of photoperiodism. Karl Hamner and James Bonner (1938) made a decisive contribution to photoperiodism research by finding that a brief exposure of light in mid-night, given under normally inductive conditions for flowering, caused cocklebur, a short-day plant, to remain completely vegetative.

Recognition that many responses of plants to light have a common underlying cause came from the measurement of action spectra using a custom-built spectrograph (Parker et al 1949). The year 1952 was a momentous year in the history of plant photomorphogenesis, because Harry Borthwick and his colleagues of USDA in Beltsville discovered the red (R) and far-red (FR) photoreversible effect on seed germination in lettuce and night-break of photoperiodic floral induction in cocklebur (Borthwick et al 1952). They soon formulated the unique idea that reversible changes in the optical density of appropriate tissues might result from irradiating the sample alternately with actinic R and FR light. This hypothesis was proved by Warren Butler, Karl Norris, Bill Siegelman and Sterling Hendricks (1959), who showed repeatedly photoreversible absorption changes at 660 and 730 nm regions upon alternately given R and FR actinic light in etiolated maize tissues and a crude extract of the relevant proteinaceous pigment. Shortly after this discovery, the term "phytochrome" was half-jokingly used by Butler in their laboratory, then published by Borthwick and Hendricks (1960). It is remarkable that the members of the same institution discovered all key phenomena such as the photoperiodism, the R/FR reversible effect and the photoreceptor phytochrome (Sage 1992).

The Era of Spectrophotometry, Physiology, and Biochemistry (1960s–1980s)

Photoreversible Regulation and Molecular Properties of Phytochrome

The discoverers of phytochrome had proposed a simple hypothesis that phytochrome in its red light absorbing form (P_r) is physiologically inactive, and is only active in its far-red absorbing form (P_{fr}). In the following few years, they attempted to prove this hypothesis photometrically and biochemically (Siegelman and Butler 1965), but the puzzle did not prove to be simple. P_{fr} was found to undergo non-photochemical transformations in vivo such that both P_{fr} decay and P_{fr} reversion to P_r took place in the dark (Butler et al 1963). However, in crude extracts, P_{fr} showed neither decay nor reversion, and P_r and P_{fr} appeared quite stable in vitro (Furuya et al 1965). After a dual-wavelength difference spectrophotometer, Ratiospect R2, became commercially available in 1963, several laboratories began to measure phytochrome in vivo to examine the correlation of photoreversible responses of plants to R and FR light with photometrically measured phytochrome content, initial P_{fr} state and dark transformation of P_{fr} in

vivo. However, most of these attempts failed to find any correlation (Hillman 1967). This presented an obstacle, which persisted for some time, and is reflected in the fact that the number of publications on spectrophotometric measurements of phytochrome in vivo reached a plateau of ca. 20 papers/year by 1966.

In an alternative approach, workers were attempting to clarify the structure and molecular properties of phytochrome. The Beltsville group initially developed a procedure for the isolation and purification of phytochrome, finding its average molecular weight as a monomer to be ca. 40 kilodaltons (kDa). However, other larger forms of phytochrome, including degraded "small" (<60 kDa) and undegraded "large" (114–118 kDa) phytochromes were subsequently discovered (Briggs and Rice 1972, Pratt 1982), culminating in the isolation of full-length "native" (124 kDa) phytochrome by Vierstra and Quail (1982). In parallel with these efforts, Wolfhart Rüdiger and his colleagues spent two decades engaged in determining the nature of the phytochrome chromophore, and were finally able to describe the chemical structure of phytochromobilin in both P_r and P_{fr} forms (Rüdiger et al 1983). Lagarias and Rapoport (1980) discovered the structure of the A ring of phytochromobilin and demonstrated the manner of its linkage to the phytochrome peptide. Since the 1970s, Pill-Soon Song has developed his model of phytochrome molecules in terms of photoreversible change of the chromophore topography between P_r and P_{fr} and inter-domain crosstalk between the chromophore and the apoprotein (Park et al 2000, Chapter 6).

Although phytochrome was long believed to be easily extractable from plant tissues using a simple buffered solution, Rubinstein et al (1969) provided an evidence for bound phytochrome fraction in oat cells. Quail et al (1973) found that the pelletability of phytochrome from crude extracts was enhanced by a brief irradiation of etiolated tissues with R light. Using immunocytochemistry, Mackenzie et al (1975) observed a photoreversible redistribution of P_{fr} sequestering in the cytoplasm, but were not able to demonstrate the physiological significance of this process. In contrast, Wolfgang Haupt (1970) clearly demonstrated a role for membrane-bound phytochrome in chloroplast movement in *Mougeotia* using a microbeam irradiation technique.

During this era, evidence accumulated in support of the existence of two physiologically, photometrically, and immunochemically distinct phytochrome pools controlling R/FR reversible reactions in higher plants. Namely, "labile" type I phytochrome (phyI) is synthesized as P_r in the dark and P_{fr} is destroyed rapidly in the light, whereas "stable" type II phytochrome (phyII) is produced constitutively and stays in cells for longer time irrespective of the light conditions (Furuya 1993). In fact, the hottest issue in the Yamada Conference held at Okazaki in 1986 (Furuya 1987) was "green" phytochrome. At the enthusiastic request of the participants, an extra session was organized, in which Yukio Shimazaki from the Pratt laboratory, Jim Tokuhisa from the Quail laboratory, and Hiroshi Abe from my laboratory told their latest stories on biochemically and immunochemically distinguishable phytochromes from etiolated and "green" tissues. Further, during the past several decades, researchers in Wageningen genetically isolated many photomorphogenic mutants, including a cucumber long hypocotyl mutant (*lh*)

that was immunochemically determined to be a phyII-deficient mutant (López-Juez et al 1992).

A Period of Groping in Studies on Photomorphogenesis

From the 1960s to the 1980s, only phytochrome was the known photoreceptor for photomorphogenesis, and its action could only be recognized in R/FR photoreversible, low fluence (LF) responses. During this period, researchers had become aware that plants respond to light in a variety of other ways, but the corresponding photoreceptor pigments were not known.

In many early studies, we suffered from a significant effect on photomorphogenesis of the extremely dim "green safe light" used in dark rooms, which did not cause significant change of spectrophotometrically measured phytochrome in vivo. To avoid this effect and to prepare totally etiolated samples, we had to grow plants in lightproof aeration boxes. Blaauw et al (1968) found that red light of very low fluence (VLF) inhibited growth in Avena seedlings, and that this effect was not reversed by far-red light. Similar reports about VLF effects in etiolated plants increased time being, but further analysis was technically very difficult in those days.

Hans Mohr and his colleagues in Freiburg had extensively investigated the effect of blue and far-red light on photomorphogenesis in terms of sensor pigments, signal amplification, and gene expression, and established the concept of the High Energy Reaction (Mohr and Schäfer 1983), which was later renamed the high irradiance reaction (HIR). In a crucial experiment using bichromatic light, Karl Hartmann (1966) was able to show that although the HIR does not show R/FR reversibility and does not obey the reciprocity law, it is indubitably mediated by phytochrome.

Since the early report of Sachs (1864), blue and near-UV light effects on development and metabolism were widely documented in the plant kingdom and microbes (Senger 1980), but at this time we understood little about the photoreceptor pigments for these phenomena. One of the reasons for this frustrating situation was that plant cells contain a number of natural compounds that absorb light in the blue and/or near-UV spectral regions. Using only the conventional spectrophotometric, biological, and biochemical methods of the day, it was very difficult to identify any of them as photoreceptors for specific phenomena.

It is our good fortune that we can look back at the early history of phytochrome studies in the book by Linda Sage (1992) and of photomorphogenesis in the proceedings of symposia (Mitrakos and Shropshire 1972, Smith 1976 1983, De Greef 1980, Furuya 1987, Thomas and Johnson 1990), an encyclopedia (Shropshire and Mohr 1983), and other more advanced treatises (Kendrick and Kronenberg 1994).

The Era of Molecular Genetic Approaches (1990s)

Differential Photoperception by Phytochromes

The year 1989 was another turning point for phytochrome research, because of the discoveries of the phytochrome gene family by Bob Sharrock and Peter Quail (1989) and of the *det* mutant, which caused morphogenesis to follow the photomorphogenic path in complete darkness, by Joanne Chory and her collaborators (1989). These findings caused a great sensation among us and provided new questions about whether individual phytochrome family members have discrete physiological or photosensory functions, and whether each has a discrete primary mechanism of action and a unique signal transduction pathway.

To answer these questions, molecular genetic approaches using Arabidopsis mutants soon became a main highway in this field during the 1990s, while transgenic overexpression of each phytochrome gene (*PHY*) proved to be less fruitful. Individual phytochrome photoreceptor mutants were reported in 1993, and phytochrome A (phyA) null mutant (*phyA*) and phytochrome B (phyB) null mutant (*phyB*) were soon being extensively used. One of Maarteen Koornneef's Arabidopsis mutants, *hy3* (Koornneef et al 1980), was found to have mutations in the *PHYB* gene by Reed et al (1993), whereas *hy1* and *hy2* were shown to be chromophore-deficient mutants. Several different groups screened mutant seedlings under continuous FR light and identified *phyA* mutants, finding that *phyA*-null mutants of Arabidopsis display a WT phenotype in white light (Whitelam et al 1993), and that phyA and phyB showed overlapping functions in Arabidopsis development (Reed et al 1994). Despite the apparently unique photoperception of phyA and phyB under continuous irradiation with FR light (cFR) and R light (cR) respectively, evidence soon accumulated for redundancy between phyA and phyB effects and for mutual antagonism between the actions of these phytochromes (Whitelam and Devlin 1997). Fifteen *PHYA*-regulated genes identified by fluorescent differential display screen were expressed photoreversibly by R/FR exposures, suggesting redundancy among phyA, phyB, and other phyII type phytochromes (Kuno et al 2000).

Using the relevant Arabidopsis *phyA* and *phyB* mutants, Shinomura et al (1996) determined separate action spectra for phyA- and phyB-specific induction of seed germination at Okazaki large spectrograph. We discovered that phyA induces seed germination photo-irreversibly in response to VLF light in the range 300–780 nm, while phyB regulates germination in R/FR reversible manner of LF light, identical with the result by Borthwick et al (1952). The classic HIR is now known to include phyA-, phyB-, and blue-UV photoreceptor-mediated HIRs. Shinomura et al (2000) found that the phyA-HIR can in fact be replaced by intermittent irradiation with FR pulses if given at intervals of 3 min for 24 h, and that the action spectra for phyA-HIR determined by such intermittent treatment of 300–800 nm lights using Arabidopsis WT, *phyB*-, and *phyAphyB*-mutants had peaks at blue and FR regions and was very similar to the action spectra constructed for the HIR in *Sinapis* (Mohr and Schäfer 1983). Very similar differen-

tial photoperception by phytochromes was recently shown in rice using *phyA*-, *phyB*- and *phyC*-mutants (Chapter 12).

In addition to photoreceptor mutants, putative mutants for early steps in light signal transduction were isolated in Arabidopsis in the laboratories of Peter Quail (Chapter 2), Nam-Hai Chua (Bolle et al 2000) and several others. These mutants were characterized for their epistasis with *phyA* and *phyB* mutations, allowing some (FHY1, FHY3, FAR1, and PAT1) to be assigned to phyA signaling and others (PEF2, PEF3, and RED1) to phyB, while a third group (PIF3, PSI2, and PEF1) could be assigned to both (see review by Hudson 2000). However, it seems too early to assemble the entire phytochrome signaling pathway upon these mutant studies. The constitutively de-etiolate mutants, *cop/det/fus*, mimic the phenotype of light-grown seedlings when grown in the dark and appear to act at later stages of light signal transduction in association with the COP1/COP9 signalosome (Chapter 29).

Apart from the mutant analyses described above, a new field of phytochrome signaling studies was born in this era, based on the growing recognition that light-induced nuclear import of cytosolic phytochromes is a multi-step signaling process. The first evidence came from the demonstration by immunocytochemistry and *PHYB::GUS* transgenic techniques that phyB was translocated into the nucleus under cR (Sakamoto and Nagatani 1996). This observation has subsequently been extended to all five Arabidopsis phytochromes, using *PHYA-E::GFP* fusion proteins in transgenic plants (Nagy and Schäfer 2002), and indicates the importance of phytochromes in the control of gene expression. The intracellular distribution of native phytochromes has also been observed using cryosectioning and immunochemical staining techniques at the optical (Hisada et al 2000) and electron microscope (Hisada et al, 2001) levels. Another victory in this era was the successful chemical synthesis of phytochromobilin and its diverse derivatives by the group of Katsuhiko Inomata in Kanazawa, enabling us at long last to analyze the relationship between chromophore structure and phytochrome function in vitro and in vivo (Hanzawa et al 2001, 2002).

Thanks to recent genome projects, phytochrome-related proteins have been discovered in cyanobacteria and eubacteria, and this has opened new avenues for investigating biliprotein photosensory function and the evolution of phytochromes in the entire plant kingdom (Montgomery and Lagarias 2002, Chapter 3). The diversity of phytochrome gene families reflects the diverse evolutionary histories of plants, and it would be of interest to investigate a possible relationship between the most functionally advanced phytochrome, phyA, and the evolutionary emergence of seed plants.

Discovery of Blue Light Photoreceptor Pigments

Every meeting on plant photomorphogenesis during the 1970s and 1980s consisted of two major sessions, respectively dealing with phytochrome and blue-UV absorbing pigments. In the latter of these sessions we had long been frustrated with our inability to identify photoreceptor pigments. However, in 1993 Margaret

Ahmad and Tony Cashmore have opened this heavy door using one of Koornneef's Arabidopsis mutants, *hy4*, which was defective in blue light-dependent photomorphogenesis. They isolated a T-DNA tagged *hy4* allele, which allowed the cloning of the *HY4* gene (Ahmad and Cashmore 1993). The protein encoded by *HY4* was a member of the photolyase family and was named cryptochrome (cry). Chentao Lin and colleagues (1996) cloned and characterized a second member of the cry family containing a distinct C-terminal sequence, which named cry2, and the *HY4*-encoded cry renamed as cry1. Since that time, Arabidopsis cryptochromes have been shown to be nuclear proteins that mediate light control of stem elongation, leaf expansion, photoperiodic flowering, and the circadian clock (Chapters 13, 14, 38).

Jiten Khurana and Ken Poff (1989) isolated several Arabidopsis mutants specifically defective in phototropic responses. Winslow Briggs and his colleagues cloned and characterized genes (*NPH1–4*) of these mutants, and showed that the gene product of *NPH1* was a blue light receptor, which was renamed phototropin 1 (Chapter 15). Phototropin research is the most rapidly moving area of photomorphogenesis research at the moment (Chapters 15–22).

The most recently discovered blue photoreceptor, FKF1, is essential for photoperiodic-specific light signaling in Arabidopsis (Imaizumi et al 2003). Looking through the literature of blue light effects and pertinent pigments (Table 1), it is quite likely that we will find other blue light receptors in future.

Problems and Dreams

A Working Hypothesis of Phytochrome Actions

The recent rapid progress of molecular genetic approaches to the study of phytochrome has increased our knowledge enormously, but I feel that we are still sailing on a boat cast adrift on a dark ocean (Furuya 2004). To get out of this situation, we need to provide a marine chart for further sailing. Let us try to draw a chart using the accumulated evidence about the different modes of photoperception by phytochromes. Here I present a tentative chart (Figure 1) as a model for discussion, assuming that: (1) all phytochromes are synthesized as P_r in cytoplasm; (2) upon light irradiation, all phytochromes produce "functionally indistinguishable P_{fr}" as the active form, and differential functional activities among their gene family members arise from different kinetics of intracellular P_{fr} translocation; (3) phytochrome degradation occurs mainly in nucleus; (4) VLF light is sufficient for photoconversion of $phyI_r$ to $phyI_{fr}$, kI_1, whereas that of kII_1 requires LF; (5) $kI_3 > > > > kI_4$; most $phyI_{fr}$ binds to a hypothetical carrier protein(s) very soon after its photoconversion to P_{fr}, so that only a minimal amount of $phyI_{fr}$ remains in cytoplasm; (6) in contrast, $kII_3 < < < kII_4$; the binding affinity of $phyII_{fr}$ to the carrier is significantly low, so the majority of $phyII_{fr}$ stays in cytoplasm for a long time, and results in a slow escape reaction; (7) the affinity of the carrier proteins to phytochromes is speculated from physiological

Table 1. Identification of photoreceptors for blue and UV-A light-dependent phenomena in plants (after Table 2 in Wada and Kadota 1989, with additions)

Organism Phenomena	Photoreceptors	References
Anthophyta		
Stem elongation	cry1, cry2	Ahmad and Cashmore 1993, Folta and Spalding 2001, Chapter 13
	phyA	Shinomura et al 2000
	phot1	Folta and Spalding 2001
Leaf expansion	cry2	Lin et al 1998
	phot1, phot2	Sakai et al 2001, Sakamoto and Briggs 2002, Chapter 15
Phototropism	phot1, phot2	Huala et al 1997, Sakai et al 2001, Chapter 15
Chloroplast relocation		
Accumulation response	phot1, phot2	Sakai et al 2001, Chapter 22
Avoidance response	phot2	Kagawa et al 2001, Chapter 22
Stomata opening	phot1, phot2	Kinoshita et al 2001, Chapter 21
Circadian clock	cry1, cry2	Somers et al 1998, Devlin and Kay 2000, Chapters 38–41
Photoperiodic flowering	cry2	Guo et al 1998, Chapters 38–41
	FKF1	Imaizumi et al 2003
Cytosolic Ca^{2+} increase	phot1, phot2	Baum et al 2001, Harada et al 2003
Ca^{2+} current	phot1, phot2	Stoelzle et al 2003
Anthocyanin synthesis	cry1, cry2	Jackson and Jenkins 1995
Pteridophyta		
Spore germination		
Protonema elongation		
Phototropism	phot?, phy3	Kawai et al 2003
Polarotropism	phot?, phy3	Kawai et al 2003
Apical swelling		
Cell cycle regulation (G1 phase)		
Chloroplast relocation		
Accumulation response	phot?, phy3	Kawai et al 2003, Chapter 22
Avoidance response	phot2, phy3	Kagawa et al 2004, Kawai et al 2003, Chapter 22
Membrane potential		
Bryophyta		
Phototropism		
Polarotropism		
Chloroplast movement	photA, photB	Kasahara et al 2004, Chapter 22
Branching	cry1a, cry1b	Imaizumi et al 2002
Chlorophyta		
Hair whorl formation		
Cap formation		
Chloroplast movement		
Vaucheriophyta		
Growth promotion		
Phototropism		
Apical swelling		
Branching		
Chloroplast movement		
Cortical fiber reticulation		
Electric current		

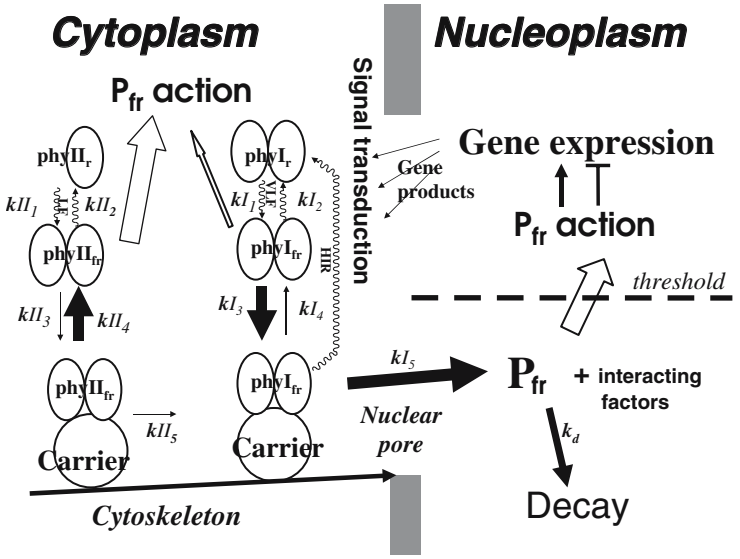

FIG. 1. A model for the P_{fr} action accommodates all differential photoperception modes, VLFR and HIR by type I (labile) and LFR by type II (stable) phytochromes. See text for details. *Wavy lines with arrows*, phototransformation of phytochrome; *Arrows*, Elementary process in cells. The size of arrow indicates speculated amounts of phyI- and phyII-flows, but does not mean faster or slower speed of each process

results to be $phyA_{fr} > > phyC_{fr} > > > phyB_{fr}$, and no P_r of any of the phytochromes binds to the carriers; and (8) $kI_5 = kII_5$, or similar rate; these P_{fr}-carrier complexes would transfer to nucleus at the same or similar speed along the cytoskeleton (Smith and Raikhel 1999).

The evidence that the peaks of action spectra for VLFR and LFR are essentially the same as those of the absorption spectrum of P_r strongly suggests that the both reaction would initiate from the phototransformation of P_r to P_{fr}, and that the difference between VLFR and LFR is the required amount of P_{fr}. The model (Figure 1) explains why only a small amount of $phyI_{fr}$ is enough to exceed the threshold level in the nucleus, while a higher level of $phyII_{fr}$ in the cytoplasm to support the required level of nuclear import. As discussed for a long time by Freiburg workers and others (Kendrick and Kronenberg 1994), real HIR processes would probably be more complicated than the scheme in Figure 1. If, however, phyA-HIR occurs anyway in this cycle, this model not only can account for all three modes of phytochrome photoperception, VLF, LF, and HIR, but also can explain why type I phytochrome is labile while type II stable. This model also explains why no major overall differences have been observed between *PHYA*- and *PHYB*-overproducers in Arabidopsis.

In this model, we expect photoreversible effects of all phytochromes, though VLFR was reported as photo-irreversible (Shinomura et al 1996). However, VLFR could be photoreversible if plants are exposed to extremely short R and FR pulses, and we have indirect evidence to support this idea. The reciprocity law holds when Arabidopsis seed germination is induced by exposure to 760 nm light of 5 $\mu mol\, m^{-2}$ for 3 s or longer, but not if exposure times are less than 3 s (Shinomura, unpublished), indicating an involvement of some slow rate-limiting process such as the interaction with carriers.

The NH_2-terminal chromophoric domain (N-domain) of phyA alone is light stable in transgenic Arabidopsis (Wagner et al 1996), probably because it cannot bind as monomer to the carriers. In contrast, the COOH-terminal domain (C-domain) of phyB exists as dimer in vivo and when fused with *GUS* (Sakamoto and Nagatani 1996) or *GFP* (Chapter 7) translocates into nucleus irrespective of the light conditions. Both $phyA_{fr}$ (Wagner et al 1996) and $phyB_{fr}$ (Chapter 7) can only induce their biological effects as dimers.This evidence, together with the fact that the N-domain contains the determinants for the differences in photosensory specificity and photolability between phyA and phyB (Quail 1997) suggests a possibility that differential nuclear import of phytochromes could result from the N-domain dependent change of surface properties of C-domain in terms of hydrophobicity and reactability. In such a case, the C-domains of all phytochromes in P_r form would be so hydrophilic that they stay in cytosol, whereas the C-domain of $phyI_{fr}$ is most hydrophobic and that of $phyII_{fr}$ is less hydrophobic, so they interact with other proteins accordingly. However, we have no idea at present whether only P_{fr}–P_{fr} homodimer can bind with the carrier, or whether P_r–P_{fr} heterodimer is also translocatable to nucleus (Furuya and Schäfer 1996).

Phytochrome effects clearly show a great variation in the lag period between light exposure and the onset of detectable responses in plants, from 2.5 s (Chapter 9) to several hours, and even days (Table 4 in Furuya 1968) and in the escape rate in photoreversible reactions, from a few minutes to many hours (Table 5 in Furuya 1968). From these observations, I assume that there are two essentially different sites of phytochrome primary action; the cytoplasm and the nucleoplasm (Figure 1). Phytochrome action in the cytoplasm rapidly regulates cytoplasmic properties (Chapter 9), while its action in the nucleus occurs more slowly through up- or down-regulation of gene expression (Chapter 2). In this respect, it would be interesting to know where, when and how each phytochrome interacts with PIF3 (Chapter 30), NDPK2 (Im et al 2004), and other interacting factors (Chapter 29).

Despite many attempts since its discovery, none has yet succeeded to develop an in vitro assay system for the primary action of phytochrome molecules. The model (Figure 1) suggests it may not be so easy to find such an assay system, but it could be achieved if it would allow us to identify the hypothetical carrier protein(s) chemically, and to carry out binding assays of the identified carrier protein(s) with $phyA_{fr}$, $phyB_{fr}$, or any others by an affinity sensor.

Crosstalk of Light-, Clock-, and Hormone-Dependent Signaling

The overlapping effects among phytochrome family members are widely observed in plants, and the model in Figure 1 will give a hint of candidate sites for their crosstalk. Cryptochromes also may act by interacting with phytochromes, COP1, and clock proteins (Chapters 13, 33 and 38). Interaction between signal transduction pathways from phytochrome and phototropins is evident (Figure 1 in Chapter 22). Besides light, plants respond to other physical stimuli like gravity for which signaling pathways are also likely to involve crosstalk with light signaling (Chapter 32). Light signaling pathways interact widely and diversely with the circadian clock in not only eukaryotes but also prokaryotes. Several models for crosstalk between downstream phytochrome signaling and the clock are proposed in other chapters of this book (Chapters 38–41).

During the last century, plant physiologists spent enormous time and energy to understand the action of plant hormones, starting from auxins in 1920s, gibberellins in 1930s, cytokines in 1950s, abscisic acid and ethylene in 1960s, and more recently expanding to brassinolides and jasmonic acid. They encountered very complicated interactions among these hormones, and could find no clear molecular mechanism for their crosstalk. It seems that it is now our turn as photomorphogenesis researchers to struggle with this old but fundamental problem in plant development, as crosstalk between light- and hormone signaling has now been widely discovered in plants (Chapter 31). Again, it is not yet clear where and how the above-mentioned crosstalk occur in plant cells. The reality of interactions among light-, clock-, and hormonal signaling pathways appears too complicated to allow the analysis of each separate interaction down to its to elementary processes by conventional methods and equipment, so we need a totally new approach to address the extremely complex system of a cell in its entirety.

Application of Photobiology to Plant Industry

We all now know that a wide range of growth and developmental processes in plants are controllable by environmental light, and it follows that the efficiency of productivity in agriculture, horticulture, forestry, and animal husbandry could be improved through manipulation of relevant photoregulatory systems in target plants. However, I know only two examples of applied photobiology in plants; namely, the production of chrysanthemum flowers and a spinach-like vegetable (*Salsola komarori*, Amaranthaceae) become possible throughout the year using the classic night-break of photoperiodism. The fact that our knowledge of photoregulation in plants has been not applied widely to these industries results from the wide gap between the basic photobiology and the industrial application. For example, the shade avoidance syndrome (Smith and Whitelam 1997) may be a good candidate for application in plant industries, but appropriate methods and inexpensive devices for large-scale irradiation with lights of specifically designed wavelength and timing in industrial fields have not been developed. To bridge

this gap, new investment to support collaborations between photobiologists and diverse types of engineers will be required. With growing awareness of the need to avoid chemical pollution and other environmental damage, an increased emphasis on applied photobiology and the development of new technology is warranted in the near future.

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