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Beyond Light Perception: The Function of Photoreceptors in Darkness and Environmental Signalling

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Light influences nearly all facets of plant growth, including seed germination, growth and development, flowering, and responses to stress. Plants perceive light mainly through photoreceptors, including phytochromes, cryptochromes (CRYs), phototropins (PHOTs) and UV RESISTANCE LOCUS 8 (UVR8). These proteins have traditionally been assumed to be inactive in the dark and activated only after photon absorption. But recent results contradict this, showing that some photoreceptors can perform biological functions in their non-photoexcited state, particularly in tissues that develop in darkness. An important example is Arabidopsis CRY2, which can suppress primary root elongation in darkness by regulating cell-division-promoting factors. Other studies suggest possible roles for photoreceptors in lateral root formation, root elongation and nodulation. Photoreceptors can also respond to signals other than light, including temperature, ATP, metabolites and salt stress. These studies suggest that photoreceptors are not simply light switches but dynamic signalling proteins capable of existing in different functional states. However, proving genuine dark state activity remains challenging because of residual light signalling, light transmission through plant tissues, shoot-to-root communication and the slow thermal reversion of photoexcited receptors. This article discusses the emerging functions of non- photoexcited photoreceptors and their significance for plant development.

Introduction

Light is one of the most important environmental signals perceived by plants. Besides providing energy for photosynthesis, light provides information about the surrounding environment and controls major developmental processes. Plants use different photoreceptors to detect different wavelengths, including UVR8 for UV-B, cryptochromes, phototropins and ZEITLUPLE (ZTL)-family proteins for Blue, and phytochromes for red and far-red light. For many years, the basic concept of photoreceptor function was relatively simple. Photoreceptors in darkness were considered to be in an inactive ground state. After absorbing the appropriate wavelength of light, it changes its structure and becomes biologically active. This active state then interacted with downstream signalling proteins to alter gene expression, growth and development. Recent research has shown that this model is incomplete. Photoreceptors do not necessarily become completely inactive in darkness. Instead, some can retain biological activity in their non-photoexcited states. The discovery that CRY2 can regulate root growth in darkness is particularly important because it provides direct evidence

that plant photoreceptors can have specific physiological functions without photon activation (Zheng and Liu, 2026). This discovery changes how darkness should be viewed in plant physiology. Darkness is not simply the absence of light. Plants normally spend part of every day in darkness, while roots develop largely underground. Therefore, understanding what photoreceptors do when they are not photoexcited could reveal important aspects of plant development. The emerging evidence also suggests that photoreceptors can interact with signals other than photons. Temperature, ATP, metabolites and salt stress can influence photoreceptor behaviour (Qi et al., 2025; Jung et al., 2016; Legris et al., 2016; Burney et al., 2009). These observations raise an important possibility: photoreceptors may act as broader environmental sensors rather than functioning only as light receptors.

Photoreceptor states: From light activation to thermal reversion

Photoreceptors contain chromophores that absorb particular wavelengths of light. Photon absorption causes molecular changes within the receptor and can alter its conformation, oligomerisation, localisation, and interaction with signalling proteins (Zheng and Liu, 2026). For example, blue light promotes oligomerisation of CRY2, whereas UV-B causes UVR8 to change from a dimeric to a monomeric state. Phytochromes undergo photoconversion between their red- and far-red-light-absorbing forms, while phototropins undergo light-induced structural changes in their LOV domains (Shao et al., 2020; Salomon et al., 2004). This process is particularly important when studying photoreceptor functions in darkness. A plant transferred from light into darkness does not necessarily contain photoreceptors that are immediately in their ground state. Some photoexcited receptors may remain active for considerable periods. CRY2 illustrates this clearly. Blue light can induce CRY2 oligomerisation rapidly, whereas its return to the monomeric state in darkness occurs much more slowly. Under the conditions examined, 50% saturation of CRY2 oligomerisation occurred in approximately 0.8 minutes, whereas half reversion took approximately 17 minutes (Liu et al., 2020). Thermal reversion is also influenced by environmental conditions. Temperature can strongly affect phytochrome reversion and therefore phytochrome signalling. Proteins such as PCH1 and PCHL can also regulate phyB thermal reversion (Jung et al., 2016). Therefore, a photoreceptor should not be considered simply ‘on’ or ‘off’. It can exist in several molecular states; each potentially associated with different biological functions.

CRY2: A Clear example of dark-state photoreceptor function

The strongest current evidence for a specific function of a non-photoexcited plant photoreceptor comes from Arabidopsis CRY2. CRY2 is best known as a signalling pathway involved in plant development. However, recent work has demonstrated that CRY2 also functions in darkness. In dark-grown Arabidopsis seedlings, non-photoexcited CRY2 suppresses primary root elongation by inhibiting the activity of the cell-division-promoting factor FORKED-LIKE1 (FL1) and FL3 (14). This mechanism is important because it demonstrates that CRY2 is not simply inactive in darkness. The basic relationship can be represented as

Darkness → non-photoexcited CRY2 → inhibition of FL1/FL3 → reduced cell division → reduced root elongation.

Blue light changes CRY2 into a different molecular state and modifies this regulatory activity (Liu et al., 2020). The finding provides a useful example of how one photoreceptor can perform different functions depending on its molecular state. It also raises a broader question: Could other plant photoreceptors possess similar dark state functions? Evidence from roots and other developmental processes suggests that this possibility deserves serious investigation.

Photoreceptors in roots: More than light sensors

Roots are particularly interesting for studying non-photoexcited photoreceptors because most roots grow underground. Although roots generally experience very little direct light, they

express several photoreceptor families, including phytochromes, CRYs, phototropins and UVR8. This creates the apparent paradox. Why should a tissue that develops in darkness contain proteins specialised for light perception? One hypothesis is that these photoreceptors still have biological functions in the absence of photon absorption. Using Arabidopsis mutants, there is evidence that photoreceptors regulate root growth under dark conditions. For instance, the phyB-1 mutant exhibited shorter roots in darkness, and the phyA-201 phyB-1 double mutant showed a stronger phenotype. Under dark conditions, phyA-211 and phyB-9 mutants showed shorter primary roots, whereas the phot1phot2 double mutant had longer primary roots compared with the wild types.

Photoreceptors may also regulate lateral root development. PhyB promotes lateral root formation, while CRY1 and CRY2 have inhibitory effects. This possibility is further extended by evidence from other plants. In tomato, cry1a mutants exhibit longer roots, suggesting a role for CRY1 in root growth. In soybean, CRY proteins have also been associated with nodule formation under dark conditions; the Gmcry1s-qm mutant produced fewer nodules than wild type. However, these observations must be interpreted carefully. The CRY2-FL1/FL3 mechanism is currently the strongest mechanistic demonstration of a darkness-specific photoreceptor function. Other proposed functions in root elongation, lateral-root development and nodulation remain emerging and require further experimental confirmation (Zheng et al., 2026).

Direct and indirect effects of photoreceptors in roots

A major challenge in understanding root photoreceptor biology is to separate direct receptor activity in roots from signals that originate in shoots. Light received by leaves can influence roots through hormones, sugars and mobile proteins. Phytochromes, for example, regulate auxin transport from shoots and influence root development. They also affect the distribution of photosynthetically produced sugars. The transcription factor HY5 can move from shoots to roots and regulate root growth and nitrate acquisition. Light can even reach roots indirectly. Light transmitted through plant tissues can activate phytochrome in roots and influence the root circadian system. Therefore, a root phenotype observed after a light treatment does not necessarily mean that the root photoreceptor itself was directly activated. This distinction becomes even more important when studying darkness. If the aim is to demonstrate a non-photoexcited function, researchers must establish that the receptor was not activated by light either directly or indirectly. Spatially controlled experiments, grafting approaches and improved dark-growth systems can help separate local photoreceptor function from shoot-derived signals (Motte et al., 2019)

Photoreceptors can respond to signals other than light

Temperature

Temperature can affect photoreceptor behaviour. Phytochrome thermal reversion is strongly influenced by temperature, leading to the proposal that phytochromes can act as thermosensors. CRYs also participate in temperature responses. CRY1 interacts with PFI4 to regulate high-temperature hypocotyl elongation, while temperature can influence CRY2 abundance. However, these experiments were conducted under light, so they do not, by themselves, demonstrate a temperature-sensing function of the non-photoexcited state (Zeng et al., 2026).

ATP and CRY1

ATP provides an example of a metabolic signal that can influence a photoreceptor. Even in darkness, ATP binding can alter the conformation of CRY1 and increase its responsiveness to subsequent illumination. This finding suggests that the metabolic status of the cell can influence photoreceptor behaviour. Although it does not establish a complete ATP-driven CRY1 signalling pathway in darkness, it demonstrates that CRY1 is capable of responding to a molecule other than light (Burney et al., 2009).

Naringenin Chalcone and UVR8

UVR8 is classically known as a UV-B receptor. However, recent evidence suggests that it can also respond to naringenin chalcone (NGC), a flavonoid pathway intermediate. NGC stabilises UVR8 in its monomeric state and promotes expression of stress- and immunity-associated genes (Jian et al., 2025). This finding provides an important connection between plant metabolism and environmental signalling. It suggests that a plant's metabolic state could influence a protein traditionally regarded as a photoreceptor.

Salt stress and PhyB

Salt stress can also influence photoreceptor signalling. Under salt stress, non-photoexcited PhyB undergoes stabilisation and phosphorylation, including phosphorylation at Ser86, and contributes to hypocotyl regulation in darkness (Qi et al., 2025).

Together, the effects of temperature, ATP, NGC, and salt stress suggest that photoreceptors can function within broader cellular signalling networks; however, these mechanisms should not automatically be classified as intrinsic dark-state photoreceptor functions. The molecular mechanisms differ, and more evidence is required to establish exactly how non-photonic signals alter receptor activity.

Light-Repressed and Light-Enhanced Photoreceptor Functions

The emerging picture becomes even more interesting when light is considered not only as an activating signal but also as a signal that can suppress or enhance existing receptor activity. The CRY2-FL1/FL3 system provides an example of a light-repressed dark state function. In darkness, CRY2 inhibits FL1/FL3 association with genes involved in cell division. Blue light changes CRY2 activity and releases this repression. Thus, light does not simply turn CRY2 'on'. Instead, it changes which molecular function of CRY2 predominates. PhyA provides another example. Evidence suggests that non-photoexcited phyA can interact with COP1-SPA proteins and produce a modest photomorphogenic response even in darkness. This suggests that some photoreceptors may possess basal activity in darkness, which can then be enhanced or modified by light.

Experimental challenges in studying dark state functions

The study of non-photoexcited photoreceptors presents several methodological challenges.

True darkness

The first challenge is proving that the experimental material has not received biologically relevant light. Roots may receive light transmitted through stems or other tissues. Therefore, physical isolation from the lamp does not necessarily mean that roots are completely dark.

Residual photoexcitation

Photoreceptors can remain in photoexcited states after light exposure because thermal reversion may take considerable time. Consequently, plants transferred from light to darkness may still show responses caused by earlier illumination.

Shoot-to-root signalling

Hormones, sugars and proteins can move between shoots and roots. Therefore, root phenotypes may result from light perception in the shoot rather than direct photoreceptor activity in roots.

The 'pseudo-dark' effect

Previous light exposure can establish developmental signals that persist after plants are subsequently grown in darkness. Pre-germinative phyB activation can influence later seedling development, a phenomenon associated with the "pseudo-dark" effect. Therefore, the history of the plant before the dark treatment is extremely important.

Maternal effects

The light environment experienced by the mother plant may also influence offspring development. Such effects must be considered when interpreting dark-grown photoreceptor mutants.

These issues explain why the study of non-photoexcited photoreceptors requires much stricter experimental controls than conventional light response experiments.

Future Directions

The field is still developing, and several important questions remain unanswered. First, it is not yet clear whether dark-state activity is a widespread feature of plant photoreceptors or a specialized property of particular proteins. Second, researchers need to determine the structural basis of dark-state activity. Advanced structural and biochemical approaches may reveal how different receptor conformations produce different outputs. Third, more work is needed to distinguish photoreceptor activity from indirect signalling. Root-specific experiments, grafting systems and carefully controlled illumination will be particularly useful. Fourth, multiomics approaches may help identify the full range of biological processes regulated by non-photoexcited receptors. For example, transcriptomic, epitranscriptomic and translational analyses have revealed broad changes associated with CRY activity in dark-grown plants. Finally, the development of photoreceptor variants that remain constitutively in defined molecular states could provide powerful tools for studying dark state signalling. The field therefore requires a combination of molecular biology, structural biology, plant physiology, imaging and quantitative photobiology.

Conclusion

The traditional view of plant photoreceptors as simple light-activated switches is being replaced by a more complex model. Photoreceptors can exist in several molecular states, and some of these states can remain biologically active without photon absorption. The best-established example is CRY2, which regulates root growth in darkness by controlling FL1 and FL3. Additional studies suggest that photoreceptors influence root development, lateral root formation and nodulation under conditions in which direct light perception is limited. Photoreceptors can also interact with non-photonic signals, including temperature, ATP, metabolites and salt stress. At the same time, researchers must distinguish genuine dark state activity from residual photoexcitation, light transmitted through plant tissues and shoot-derived signals. Overall, the emerging evidence suggests that photoreceptors should be viewed as dynamic environmental signalling proteins rather than simple light switches (Fig 1). Their functions may be dependent on molecular state, environmental conditions and interactions with other cellular pathways. Understanding these hidden functions of photoreceptors could provide new insights into root development, plant stress adaptation and sensing of the environment, while also opening possibilities to manipulate photoreceptor signalling in future crop improvement.

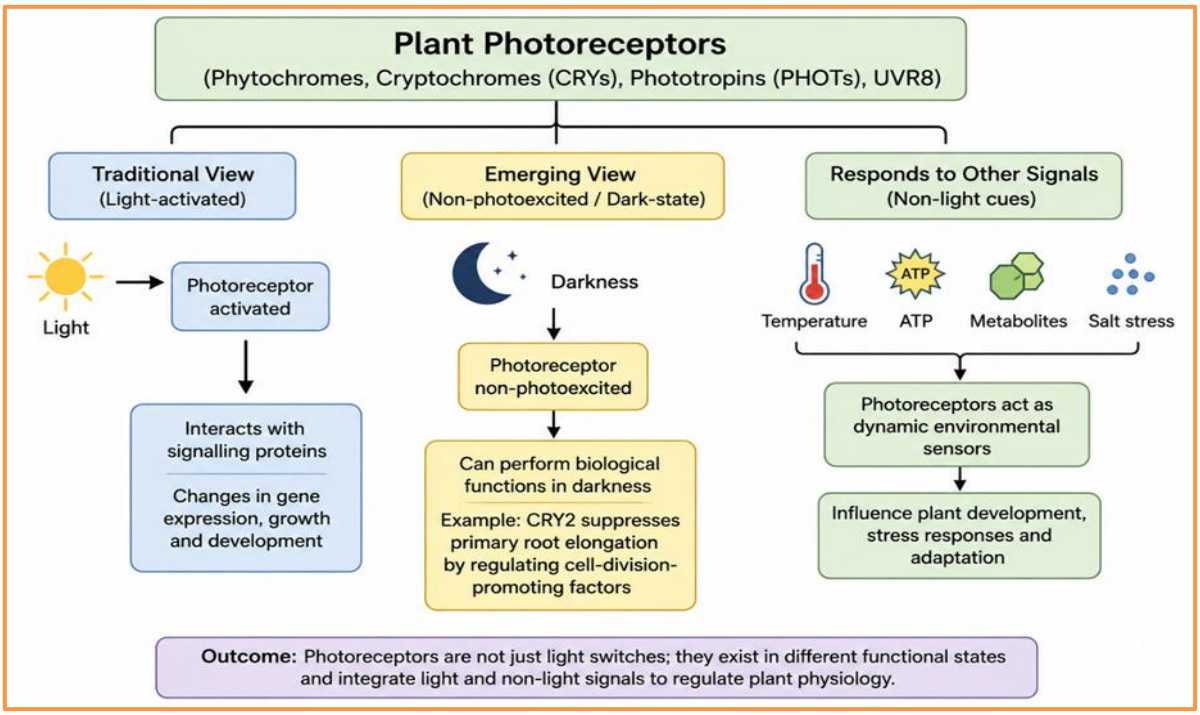

Fig 1: Role of plant photoreceptors beyond light sensing

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