

Receptors

1. Introduction:

Though eukaryotes, both plant and animals have had separate evolutionary histories for more than a billion years. Their last common ancestor was a unicellular eukaryote that had mitochondria but no chloroplasts.

In plants, as in animals, cells are in constant communication with one another. Plant cells communicate to coordinate their activities in response to the changing conditions of light and temperature that guide the plant's cycle of growth, flowering, and fruiting. Plant cells also communicate to coordinate what goes on in their roots, stems, and leaves. [1]

The cascade of signal on a cell surface that gets converted into a specific cellular response is called a signal transduction pathway. The process involves three stages: reception, transduction and response. In reception, a chemical signal binds to a cellular protein at the cell surface or inside the cell. In transduction, binding leads to a change in the receptor that triggers a series of changes in various relay molecules. In response, a specific cellular activity is triggered [2].

Successful adaptation to changing ecological conditions is a common challenge faces by all organisms. Multicellular life forms has to face one more level of challenge that is to develop egg or seed into a mature organisms which requires spatially and temporally regulated cell-cell signaling.

Though mutational approach has been a powerful technique for identification of genes encoding components of signal transduction pathways, classical biochemical approaches along with latest technological advances being made in proteomics and genomics are going to have a radical impact upon our understanding of how plants perceive and respond to signals.

It is natural; if multicellularity has evolved independently in plants and animals then the mechanisms for cell communication will also have evolved separately and would be expected to be different. *Arabidopsis thaliana*, a model system has completely sequenced genome, suggests that there are no homologs of Wnt, Notch, Jak/STAT, TGF-beta, Ras, or the nuclear receptor family in plants. Also cAMP has not been implicated in intracellular signaling. There is some resemblance between plant and animal signaling in the form of Nitric oxide and Ca²⁺.

Most cell surface receptors in animals are G-protein-linked which are very rare in plants. Plants prefer mostly enzyme-linked receptors which are transmembrane receptor serine/threonine kinases as against receptor tyrosine kinases in animals.

Various plant hormones / growth regulators help to coordinate plant development. These are small molecules which diffuse readily through cell walls and may act locally or away. Most common examples include ethylene, auxin, gibberellins and abscisic

acid. Each growth regulator may have multiple effects. The specific effect depends on which other growth regulators are acting, on environmental conditions, on the nutritional state of the plant, and on the responsiveness of the target cell.

In plants, there are various light responsive proteins to sense light of different wavelengths which are referred as photoreceptors / photoprotein. All photoproteins sense light by means of a covalently attached light-absorbing chromophore, which changes its shape in response to light and then induces a change in the protein's conformation. Signal transduction pathway from light absorption by photoreceptors to the light-dependent developmental changes that prepare a plant for photosynthetic activity / photomorphogenesis [3].

2 Plant receptors:

Unlike animal systems, where organs and glands are discrete, plant development is a continuum of growth and differentiation in which cells and tissues both produce and respond to many hormones. Biochemical analysis is further compromised by the cell wall and the plethora of secondary chemical products that plants synthesize. Fortunately, with the arrival of modern *Arabidopsis* genetics, mutations were identified that increased or decreased the response of a whole plant to a particular hormone

2.1 Two-component-based hormone receptors

Two-component regulators derive their name from the transfer of phosphates between a collection of signature proteins. This starts when the first component perceives an input signal to cause an autophosphorylation of a conserved histidine in the transmitter domain. The fungal and plant two-component systems are more complicated than the canonical prokaryotic system in that the input histidine kinase domain itself often carries a receiver domain. In *Arabidopsis*, eight two-component input regulators genes have been functionally identified as hormone receptors. Three are involved in cytokinin perception, and five encode ethylene receptors[4].

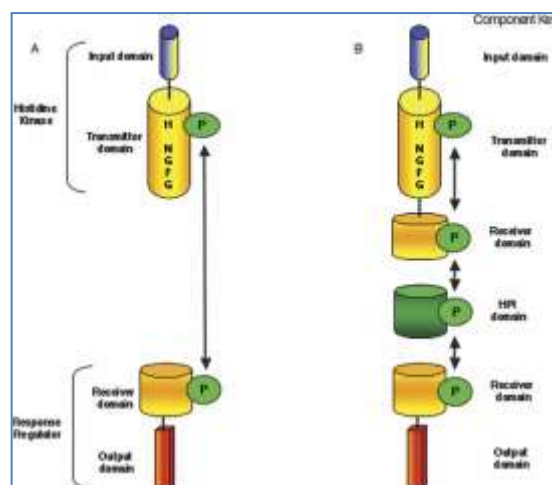
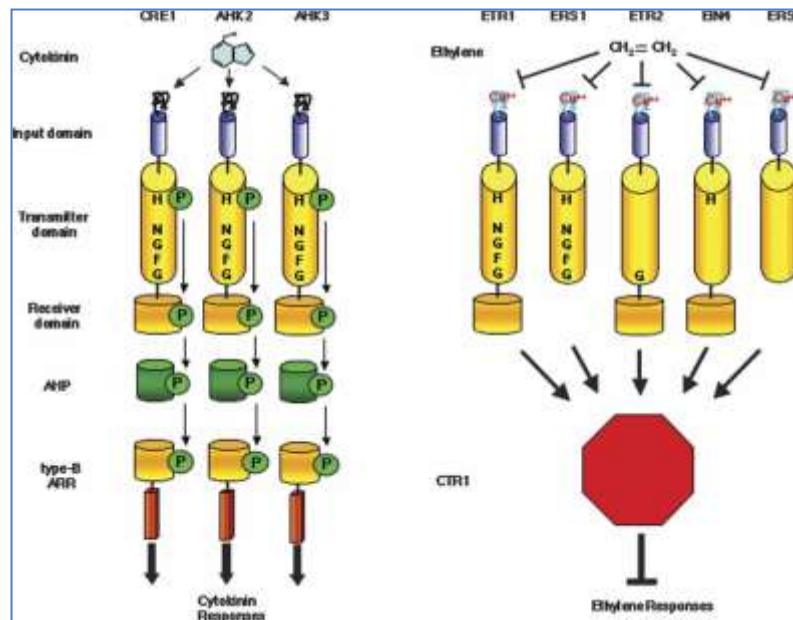


Figure 1: The prototypical two-component system. (A) The two-step system found only in prokaryotes.

B) The derivation of component prokaryotes eukaryotes



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Figure 2: Structural relationships within and between two-component regulators involved in cytokinin and ethylene perception. (A) In *Arabidopsis*, three cytokinin receptors (CRE1, AHR2, and AHR3) all bind cytokinins at their extracellular input domain. (B) Five ethylene receptors (ETR1, ERS1, ETR2, EIN4, and ERS2) exist in *Arabidopsis* that all bind ethylene in their extracellular domain

2.2 Leucine-rich repeat (LRR)-based hormone receptors

In both plants and animals, steroid-based molecules have been identified that act as hormones for directing growth. The LRR is a common protein motif of usually 20–29 residues that is found in a number of proteins with diverse functions throughout all kingdoms. Plant receptors have an extracellular LRR domain that is fused to an intracellular serine/threonine kinase domain. In animals, LRR-based receptors transduce their signals through intracellular protein–protein interactions rather than directly through kinase domains[4].

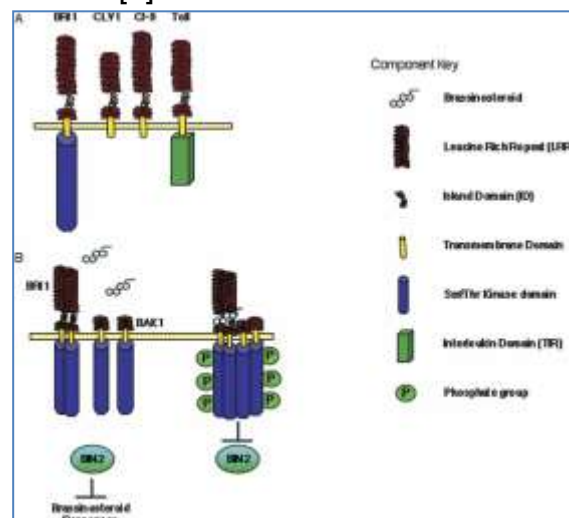


Figure 3: LRR receptors. (A) Comparison of four types of LRR receptors found in plants and animals (B) Mechanism of BR perception.

2.3 Ubiquitination-based hormone receptors

Mutations in Aux/IAA genes that conferred increased resistance to auxin mapped to a common domain shown to be important in protein stability. Hence, decreasing the turnover of an Aux/IAA protein somehow conferred decreased auxin sensitivity.

The SCF complex, which was first identified in yeast, provides a mechanism by which cells can rapidly degrade proteins by targeting them to the 26S proteasome. Briefly, ubiquitin is first activated by an E1 enzyme and then passed to a family of ubiquitin-conjugating E2 enzymes. The E2 enzyme carrying an ubiquitin molecule can interact with the Cullin subunit of the SCF complex. The SKP1 subunit acts as an adaptor protein between Cullin and the F-box so that when the F-box protein captures a protein target it is now in the vicinity of the E2 enzyme and can be ubiquitinated. This process is reiterated until the target protein accumulates more than four ubiquitins, which signal it for degradation via the 26S proteasome [4].

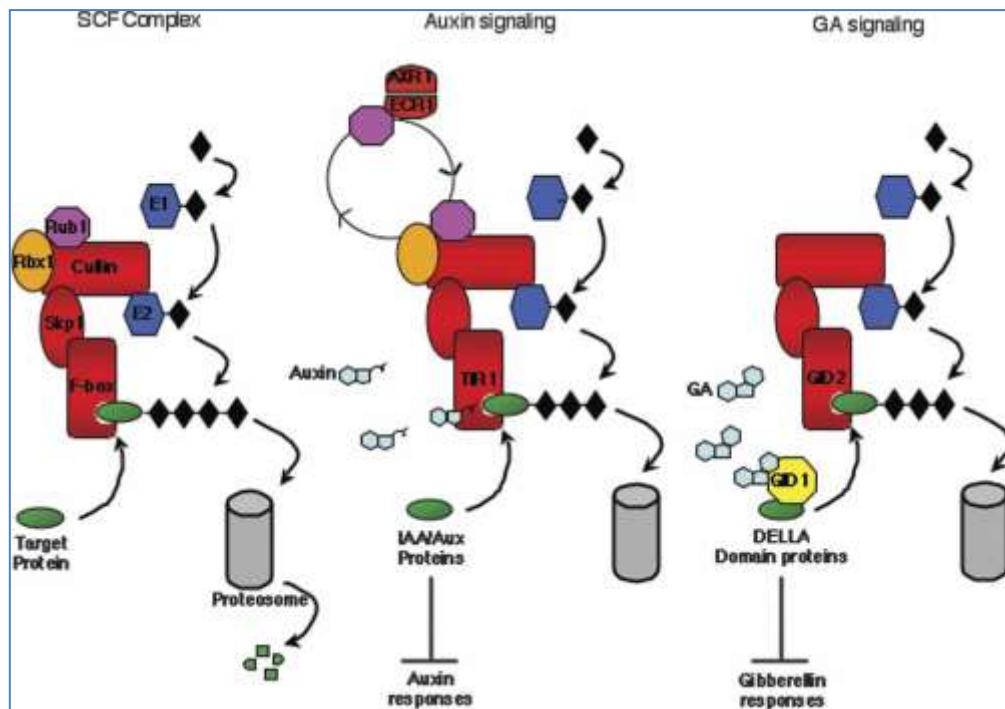


Figure 4: SCF-dependent hormone-regulated ubiquitination of proteins. Key components in a canonical SCF pathway are shown, and related components in the auxin and GA pathways have the same shape

2.4 F-box proteins as receptors

IAA (auxin) regulates an amazingly diverse array of processes in plant growth and development ranging from embryo patterning to growth responses to tropic stimuli. Auxin response involves a large-scale reprogramming of gene expression affecting hundreds of auxin-regulated genes. The *Arabidopsis* TIR1 gene was identified more than a decade ago as a positive regulator of auxin response. TIR1 is one of several hundred F-box proteins encoded in the *Arabidopsis* genome. F-box proteins function as substrate recognition modules for multisubunit Skp1–Cullin1–F-box protein (SCF) ubiquitin ligases. The novelty in the mode of auxin perception raises several exciting possibilities. How widespread is this mechanism? *Arabidopsis* and rice both encode nearly 700 F-box proteins, nearly all of which remain to be characterized [4].

2.5 Absciscic acid: multiple receptors and pathways

Absciscic acid (ABA) regulates a diverse array of processes including seed maturation and dormancy, root growth, leaf senescence, and the transition between vegetative and reproductive growth. It is also a major stress hormone that regulates the adaptation of plants to environmental stresses including cold, drought, and salt by modulating the expression of stress-responsive genes and controlling the aperture of stomata to regulate water content.

The first reported ABA receptor was the 'Flowering time conteol protein A' (FCA), a factor previously implicated in the vegetative-to-reproductive transition. As an RNA-binding protein, FCA defines an entirely new class of hormone receptors. On a very basic level, however, the effects of ABA binding to the FCA receptor are similar to the auxin, jasmonate, and GA receptors. The *Arabidopsis* 'Receptor like kinase 1' (RLK1) protein is localized to the plasma membrane, and mutants exhibit reduced ABA sensitivity, raising the possibility that it may be an extracellular receptor. However, ABA binding has yet to be demonstrated. *Arabidopsis* G-protein mutants have ABA response defects, suggesting that a G-protein-coupled receptor (GPCR) might function as a plasma membrane-localized site of perception.

The identification of three unrelated receptors in three different cellular locales paints a very complicated picture of ABA signaling. Instead of a single receptor acting upstream of a branched signaling pathway, these findings suggest that ABA responses are mediated by partially if not entirely distinct receptor classes and signaling components. Establishing molecular connections between the receptors and the wealth of ABA signaling. Components identified through genetic studies, and identifying potentially common nodes connecting the individual pathways will hopefully begin to clarify this picture in the near future [5].

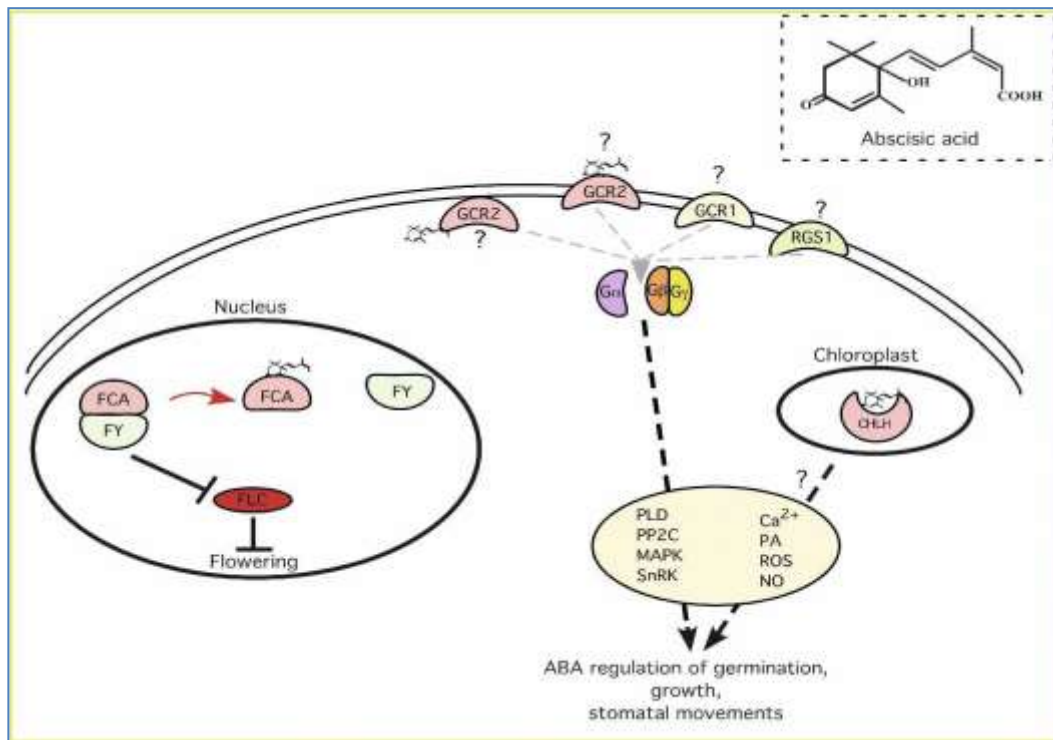


Figure 5: ABA receptors act at different cellular locations. Genetic studies have implicated G-proteins and several potential downstream effectors and secondary messengers in ABA response.

2.6 G protein coupled receptors (GPCR) in plants

Canonical G protein signaling involves a seven transmembrane GPCR that interacts with a heterotrimeric G-protein consisting of α , β , and γ subunits. Upon ligand binding to the receptor, the G α subunit releases GDP and binds GTP, and dissociates from the G $\beta\gamma$ dimer. Furthermore, unlike the hundreds of GPCRs found in animals, *Arabidopsis* encodes many fewer potential GPCRs, most of which are highly divergent and none of which has been assigned a ligand. Plants also appear to lack adenylyl cyclase and phospholipase C β , two of the most common effectors of G-protein signaling pathways in animals. Thus it is unclear at this point whether plants use canonical or a variant form of GPCR-mediated G-protein signaling [5].

2.7 Photoreceptors in plants

Both plants and animals use a variety of light-responsive proteins to sense light of different wavelengths. In plants, these are usually referred to as *photoreceptors*. However, because the term photoreceptor is also used for light-sensitive cells in the animal retina (see p. 867), we shall use the term *photoprotein* instead. All photoproteins sense light by means of a covalently attached light-absorbing chromophore, which changes its shape in response to light and then induces a change in the protein's conformation.

Animals use some of the same photoprotein families used by plants. The most extensively studied animal photoproteins are the rhodopsins, which are membrane-bound, G-protein-linked proteins that regulate ion channels in the light-sensitive cells of the retina, as discussed earlier. The best-known plant photoproteins are the phytochromes, which are present in all plants and in some algae. These are dimeric, cytoplasmic serine/threonine kinases that respond differentially and reversibly to red and far-red light: whereas red light usually activates the kinase activity of the phytochrome, farred light inactivates it.

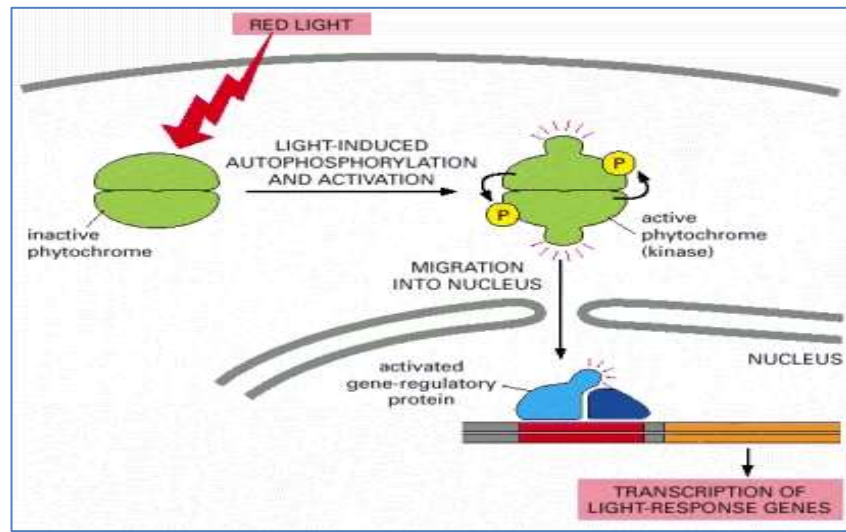


Figure 6: A current view of one way in which phytochromes mediate a light response in plant cells. When activated by light, the phytochrome, which is a dimer, phosphorylates itself and then moves into the nucleus, where it activates gene regulatory proteins to stimulate the transcription of specific genes.

When activated by red light, the phytochrome is thought to phosphorylate itself and then to phosphorylate one or more other proteins in the cell. In some light responses, the activated phytochrome migrates into the nucleus, where it interacts with gene regulatory proteins to alter gene transcription. In other cases, the activated phytochrome activates a gene regulatory protein in the cytoplasm, which then migrates into the nucleus to regulate gene transcription. In still other cases, the photoprotein triggers signaling pathways in the cytosol that alter the cell's behavior without involving the nucleus.