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Signal Perception and Transduction in Plants

Abdul Razaque Memon* Camil Durakovic

International University of Sarajevo, Sarajevo, Bosnia andHerzegovina

*Corresponding author
Email: amemon@ius.edu.ba

Abstract

Plants are sessile organisms and are not able to move away from adverse environmental conditions and must response to an array of environmental and developmental cues. They heavily rely on high sensitivity detection and adaptation mechanisms to environmental perturbations. Signal transduction, the means whereby cells construct response to a signal, is a recently defined focus of research in plant biology. Over the past decade our understanding of plant signaling pathways has increased greatly, in part due to the use of molecular genetics and biochemical tools in model plants for example Arabidopsis thaliana and Medicago truncatula. This has assisted us in the identification of components of many signal transduction pathways in diverse physiological systems for example hormonal, developmental and environmental signal transduction pathways and cross-talk between them.During the last 15 years the number of known plant hormones has grown from five to at least ten. Furthermore, many of the proteins involved in plant hormone signaling pathways have been identified, including receptors for many of the major hormones. In addition, recent studies confirm that hormone signaling is integrated at several levels during plant growth and development.

In this review paper we have covered recent work in signaling pathway in plants especially how plants sense biotic and abiotic stresses and the potential mechanisms by which different chemical molecules and their downstream signaling components modulates stress tolerance.

Keywords: Plant signaling, plant hormones, phytochrome signaling, receptor kinases, G protein coupled receptors

1. Introduction

The signaling networks that have evolved to generate appropriate cellular responses are varied and are normally composed of elements that include a sequence of receptors, non-protein messengers, enzymes and transcription factors. Receptors are normally highly specific for the physiological stimulus, and therefore are disparate in their identities. Likewise enzymes and transcription factors tend toward specificity, and this fact is reflected in abundance at the genome level. The Arabidopsis genome, for example, potentially encodes in the region of 1000 protein kinases, 300 protein phosphatases, and 1500 transcription factors [1-3]. By contrast, non-protein messengers are relatively few. They include calcium [4], nucleotides [5], hydrogen ions [6], active oxygen species and lipids [7, 8]. Among stimuli- both external and internal- that convey information to plants are light, mineral nutrients, organic metabolites, gravity, water status, turgor, soil quality, mechanical tensions, wind, heat, cold, freezing, growth regulators and hormones, pH, gases (CO_2, O_2 and C_2H_4), wounding and diseases, and electrical flux.

Plant responses to stimulus are modulated by developmental age, previous environmental experience, and internal clocks that specify the time of year and the time of day. For mature plant cells, the response can be physiological and biochemical; for growing cells, it can be morphological and developmental. Integration of various forms of signaling information is usually crucial to determining the final response. In a seed, for example, the decision to germinate can be irreversible and, if timed inappropriately, could be fatal. This clearly reflects the presence of complex system for signal recognition and transduction in this germination process.

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2. Over view of Signal transduction

The signal transduction pathway uses a network of interactions within cells, among cells, and throughout plant[9]. The external signals that affect plant growth and development include many aspects of the plant's physical, chemical, and biological environments. Some external signals come from other plants. Apart from gravitropic signals, all other signals vary in intensity, often from minute to minute [10]. Many signals interact cooperatively and synergistically with each other to produce the final response. Signal combinations that induce such complex plant responses include red and blue light, gravity and light, growth regulators and mineral nutrients [11].

For example the overall regulation of seed germination involves control by both external factors and internal signals. The involvement of gibberellin acid in the initiation of seed germination is well known [12]. Peptides and lipo-chitooligosaccharides are another class of signaling molecule that is currently attracting considerable interest and generating much excitement [13], [14]. The emerging information is the peptides are ubiquitous signaling molecules in plants, and that they appear to operate via receptor serine/threonine kinases. With more than 340 genes in the Arabidopsis genome encoding putative proteins in this class, it is likely that more peptide-based signaling systems will be identified in plants in the near future. Lipo-chitooligosaccharides [15] produced by rhizobia are a class of signaling molecules that mediate recognition and nodule organogenesis in the legume-rhizobia symbiosis. Their synthesis is specified by the nodulation genes of rhizobia and hence they are commonly known as Nod factors. Studies using plant and rhizobial mutants and purified molecules suggest that Nod factors are recognized by more than one receptor. Genetic approaches have been initiated to identify specific genes involved in Nod factor signal perception and transduction [16]. The major advance in our understanding of LCO perception requires the cloning of genes encoding Nod factor receptors. Genetic and biochemical approaches appear to be the most promising strategies. All of the signal mentioned above including hydrogen peroxide and nitric oxide mediated signaling is believed to operate at or near the plasma membrane. The extracellular matrix (ECM), which was once mistakenly thought to be inert as far as signal transduction was concerned, is also a very important repository of signaling information in plants [17, 18]. The possibility that plants might signal through heterotrimeric G proteins and small G proteins has also created much excitement since their discovery in yeast and animal systems [19],[9]. Over the years, a considerable body of evidence has amassed by studies involving pharmacological intervention that suggests that these proteins are involved in numerous signaling pathways in plants. Phospholipase D is a possible targets for G proteins in plants [20-22] and emerging as one of the important components of cellular signaling in plant cells. Other intracellular signaling components, which are certainly involved in cross-talk/signal integration, are the mitogen-activated protein (MAP) kinases (MAP-kinase module). The emerging story of MAP kinase reveals a highly flexible signaling module that is involved in a large number of signaling pathways. Plant hormones are other small organic signaling molecules which can influence so many aspects of growth and development. The concept of cross-talk between hormones has attracted much attention, with the idea that hormone signaling pathways make up a complex interacting web of informational transfer that allows a variety of stimuli to cause a plethora of overlapping responses [23].

RNA-mediated regulation of genes responsible for signaling in plants is also a recent and exciting discovery. A decade ago, the existence of a double-stranded RNA (dsRNA)-directed RNA degradation and DNA methylation mechanism was discovered in plants and animals, and identified as defense system against viruses and transposons. It now seems that components of this mechanism not only generate short interfering RNAs (siRNAs) that direct the defense system, but also short temporal RNAs (stRNAs) or microRNAs (miRNAs), from endogenous, developmentally expressed, partially self-complementary RNA transcripts [24],[25]. The stRNAs regulate the expression of target genes by inhibiting the translation of their mRNAs, and large numbers of miRNAs are being found in a wide range of organisms. The discovery of miRNAs probably heralds the start of investigations into a very important, but previously unsuspected, part of gene regulation in signal transduction. Another part of gene regulation in signal transduction is through RNA binding proteins which affect RNA stability and controls the translational initiation [26][27]. RNA binding proteins are involved at all stages in the life of an RNA molecule, from transcription through to degradation, and are central to the cell's maintenance and development.

3. Signals from the Environment

Numerous environmental factors influence plant development. Temperature, light, touch, water, and gravity are among the stimuli that serve as signals for the activation of endogenous developmental programs. Of these, light has an especially important role, not only as an energy source for photosynthesis, but also as a stimulus for many developmental processes throughout the life cycle of plants, from seed germination through flowering. In plants, light-dependent responses are

controlled by a series of photoreceptors that can be classified into three known groups-the phytochromes, Phytochromes are red-light/far-red-light (R/FR) photoreceptors that perceive light through a tetrapyrrole chromophore that is bound covalently to their amino-terminal photo sensory domain. The carboxy-terminal domain contains two PAS (for period circadian protein, Ah receptor nuclear translocator protein and single-minded protein) repeats, which initiate a signaling cascade by mediating direct interactions with molecules such as the basic-helix-loop-helix transcription factor PIF3, and a histidine-kinase-related domain (HKRD), which might phosphorylate direct targets such as cryptochromes and phototropins [28-30].

phytochrome kinase substrate 1 (a protein that negatively regulates phytochrome signaling. The light-labile phytochrome (phy)A is more active in far-red light (FR), whereas phyB and other light-stable phytochromes are more active in red light (R). Light stability of these phytochromes depends on their specific properties which regulates There are several properties of phytochromes which affects the differential response of these phytochromes.This difference is due in part to their differential light-stability, but also to other properties that are specific to the phyA domain (see Fig1, [31]).

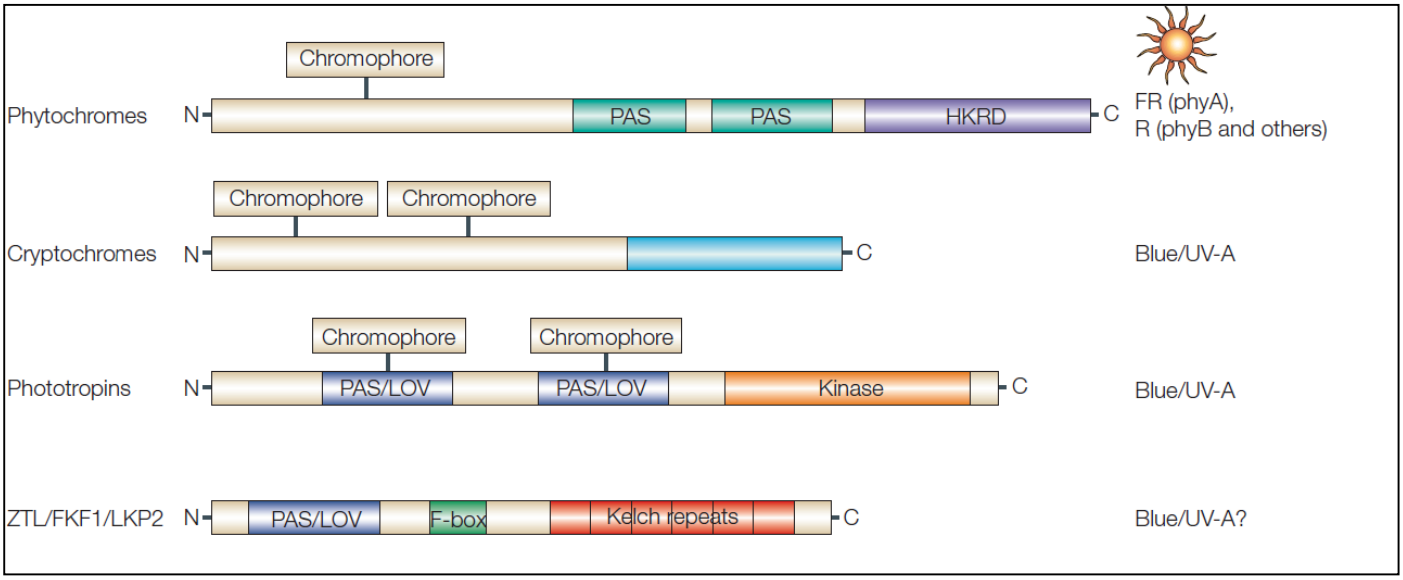

Figure 1. The plant photoreceptors involved in signal transduction.

Cryptochromes are blue/UV-A photoreceptors that bind pterin (5,10-methenyltetrahydropteroyl polygultamate) and flavin chromophores at their amino-terminal domain. Blue-light activation of cryptochromes initiates a signalling cascade through their carboxy-terminal domain. This signaling cascade operates in part through the direct inactivation of constitutive photomorphogenic 1 (COP1), which is a general repressor of photomorphogenic responses [30]. Phototropins have two PAS/LOV domains that bind a flavin mononucleotide (FMN) chromophore. The absorption of blue light triggers the formation of covalent adducts between FMN and cysteine residues in the PAS/LOV domains, which induce a conformational change that is thought to initiate a signalling cascade through activation of the serine/threonine kinase activity at the carboxy-terminal domain [30].Zeitlupe (ZTL), flavin-binding kelch repeat F-box 1 (FKF1) and LOV kelch protein 2 (LKP2) share a unique combination of motifs, which includes an amino-terminal PAS/LOV domain, an F-box domain that probably recruits proteins for ubiquitylation and subsequent degradation, and six kelch repeats that mediate protein–protein interactions [32],[33],[34],[35]. The PAS/LOV domain of this family of proteins might bind FMN, allowing these molecules to target specific proteins for degradation in a light-dependent manner [30].

Phytochromes are typically encoded by small˜multigene families,e,g. PHYA-PHYE in Arabidopsis [36]Quail 2002 a, b). Each forms a homodimer of ~ 240 kDa and light sensitivity is conferred by the presence of a tetrapyrrole chromophore covalently bound to the N-terminal half of each monomer ((Montgomery, 2002 #208)Montgomery and Lagarias, 2002). Dimerization domains are located within the C-terminal half of the proteins, as are other domains involved in the activation of signal transduction [37]Quail 2002a). Each phytochrome can exit in two photoinconvertable confirmations, denoted Pr (a red light-absorbing form) and Pfr (a far red light-absorbing form). Because sunlight is enriched in red light (compared with far red light), phytochrome is predominantly in the Pfr form in the light, and this can convert back to the Pr form during periods of darkness by a process known as dark reversion. Photo conversion back to Pfr can also be mediated by pulses of far red light.

The primary mechanism of phytochrome regulation of gene expression centre on two strikingly different hypotheses (Fig. 2). In one, it is considered to be a kinase that act on multiple substrates thereby regulating the expression of genes differentially. The other is that phytochromes interacts with one or more specific reaction partners that direct signal transduction towards the selective control of gene expression (Fig 2) [37].

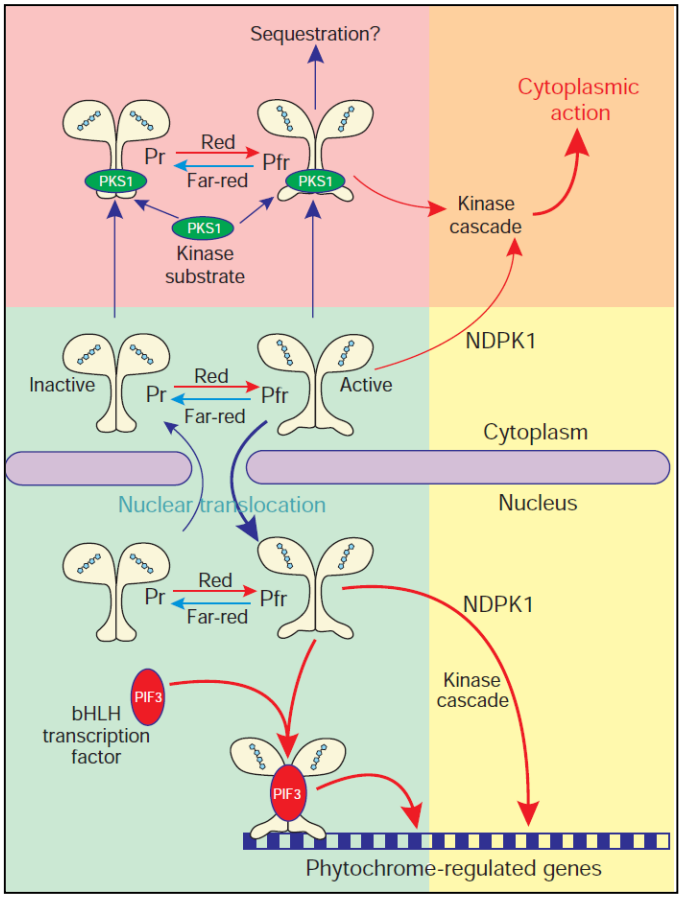

Fig 2. Diagram shows the phytochrome action and the mechanism of phytochrome mediated gene regulation.

Phytochromes undergo photoconversionfrom the biologically inactive form (Pr) to the active form (Pfr). Pr and Pfr are shown asdimers in the cell. The Pr–Pfr conversions are initiated by photon absorption in thechromophore leading to steric changes, causing the holoprotein to `open up' andfacilitating interaction with putative reaction partners. The Fig 2 shows the threemajor theories for the subsequent actions of the phytochromes, although Pfr mayregulate growth and development by other processes. Pink area: both Pr and Pfrinteract with PKS1, the phytochrome kinase substrate, in the cytosol. This may be thefirst step in a kinase cascade (orange area) culminating in action within the cytoplasm. Alternatively, interaction with PKS1 may result in sequestration ofphytochrome in the cytosol, preventing translocation to the nucleus. Yellow area: Pfr interacts with NDPK1, a nucleoside diphosphate kinase, which is located both in thecytoplasm and the nucleus. Again, this interaction may initiate a kinase cascade(orange) leading to ultimate action within the cytoplasm and/or nucleus. Green area:Pfr translocates to the nucleus and Pr is translocated back to the cytoplasm. Theweights of the arrow emphasize the differential rates of import and export. Within thenucleus, Pfr binds with PIF3 (phytochrome interacting factor 3) which is locatedexclusively within the nucleus. PIF3 is a basic helix–loop–helix transcription factorthat binds to the promoters of selected light-regulated genes in combination with Pfr and initiates or enhances transcription.In principle, the gene expression and regulationcould emanate from the kinase activity of phytochrome *per se*, and/or activation of NDPK1 [38].
Phytochrome localization to the nucleus is highly significant finding given that many phytochrome responses are dependent upon changes in gene expression. However, it should be noted that phytochrome translocation is rather slow, except for phyA, and that the majority of the intracellular Prf pool is not translocated to the nucleus [39]. These and other observations suggest that phytochromes may activate signaling pathways in both the cytoplasm and the nucleus. Using phyB truncated protein for localization studies have shown that the carboxy- terminal domain of phyB localizes to discrete sub nuclear foci even in the dark, whereas the amino-terminal domain remains mostly in the cytoplasm [11].

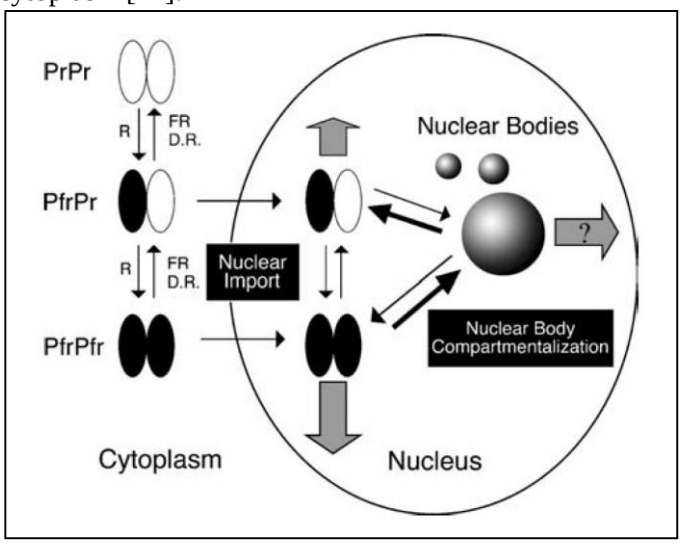

Fig 3. A schematic illustration shows the localization of phytochrome using phyB as a model [11].
Translocation of phytochromes after light activation has been shown in two steps. Nuclear import and localization in nuclear bodies.At least one molecule of phytochrome in the Pfr form(phytochrome dimer) is required for nuclear import. In the nucleus, PfrPfrhomodimers are more likely to compartmentalize to nuclear bodies. Shaded arrowsrepresent phyB signaling function. D.R., dark reversion.

Genetic approaches have implicated a range of nuclear-localized proteins downstream of phytochrome and its physically-interacting partners that are involved in phytochrome signaling. Some of these are now quite well characterized, most notably the COP9 signalosome, COP1, and HY5 [40]. The COP1 and COP10 proteins are not intrinsically associated with the COP9 signalosome but also appear to play a role in regulating protein degradation[41-43]. COP10 resembles a ubiquitin-conjugating E2 enzymes [42-44], whereas COP1 has been proposed to be an E3 ubiquitin ligase containing several recognizable domains, such as RING-finger zinc-binding domain, a coiled-coil domain and a WD-40 repeat motif [40][45][46].

4. Receptors

To initiate transduction, a signal must first be sensed by a receptor. Most known receptors are present in the plasma membrane, although some are located in the cytosol or other cellular compartments. Three classes of membrane-located receptors have been identified in animal cells and they are as follows: 1. G protein-linked recptors: when activated, they convey information to a protein that binds GTP as the first stage in transduction. The G-protein α-subunit is usually released from the β/γ-subunits into the cytoplasm, where it can activate other enzymes.2. Enzyme-linked receptors are commonly protein kinases. Binding of the ligand causes the receptor to dimerize, leading to intermolecular phosphorylation with activation of the receptor. 3. Ion-channel-linked receptors may be coupled directly to important cell surface channels that open when the receptor is occupied[19, 47, 48].

5. Receptor-like kinases in plants

Development of multicellular organisms relies on coordinated cell proliferation and differentiation. In animals, growth factor receptor kinases play key roles in cell differentiation and development, either by stimulating or inhibiting cell growth. Recent studies revealed that higher plants also possess genes coding for putative receptor kinases [49-52]. Recent studies revealed that the receptor serine/threonine kinases comprise the largest and most diverse class of receptor proteins in plants. For instance, a completely sequenced Arabidopsis genome contains over 500 genes encoding RLKs, suggesting that higher plants, like animals, use receptor kinase signaling commonly and broadly in responding to vast arrays of stimuli to modulate gene expression. Although only a handful of RLks thus far are shown to have defined biological functions, their roles in development, self-incompatibility response, and defense against pathogens illustrate important and versatile function of the RLK super family. However, given that only a few RLKs have been shown to regulate developmental processes, it is far from being understood how receptor-kinase signaling control cell proliferation in plants. A common feature of these putative receptor kinases (RLKs),is that each has an N-terminal signal sequence, an extracellular domain that varies in structure, a single membrane-spanning region, and a cytoplasmic protein kinase catalytic domain (see Fig 4). Unlike animals, where a majority of the receptor kinases possess tyrosine kinase activity, all of the plant RLKs thus far are shown to phosphorylate serine-threonine residue, except one that displays dual specificity in vitro [50, 53, 54]. Plants RLKs are classified into 7 sub-families based on the structural feature of the extracelluar domain, which is thought to act as aligand-binding site.

S-domain class: S_RLKs possess an extracellular S-domain homologous to the self-incompatibility-locus glycoproteins (SLG) of Brassica oleracea . The S-domain consists of 12 conserved cysteine residues (ten of which are conserved). In addition, the S-domain possesses the PTDT-box, which has a conserved WQSFDXPTDΦL sequence (x, non conserved amino acid; Φ, aliphatic amino acid). In Brassica, the S-RLK gene is physically linked to the S locus [51]. It has been shown that the S-RLK primarily functions as a receptor for the pollen-derived ligand, SCR (S-locus cysteine rich protein) during the self-incompatibility recognition process between pollen and stigma. The SLG protein is required for a full manifestation of the self-incompatiblity response. However, isolation of several S-RLK genes from self-compatible plant species and their expression in vegetative tissues indicate that S-RLKs may play a developmental role in addition to self-compatibility. In addition, one of the S-RLKs of BrassicaI is implicated in plant defense response [55, 56]. LRR class:The leucine-rich-repeat class is the largest family, comprising more than 170 genes in Arabidopsis. LRRs are tandem repeats of approximately 24 amino acids conserved leucines. LRRs have been found in a variety of proteins with diverse functions, from yeast, flies, humans, and plants, and are implicated in protein-protein interactions. Several LRR-RLKs have been shown to play critical roles in development. Those include ERECTA which regulates organ shape, CLAVATA1 which controls cell differentiation at the shoot meristem, HAESA, which regulates floral abscission process, and BRI1, which is involved in brassinosteroid perception [57][58][59][60]. On the other hand, rice gene Xa21 confers resistance to Xanthomonas oryzae pv oryzae [61]. Therefore, LRR-RLKs also play a role in disease resistance. Interestingly, the tomato Cf disease resistance gene products, which confer a race-specific resistance to Cladosprium fulvum, contain extracellular LRR domains but lack the cytoplasmic protein kinase domain. Because LRR domains typically mediate protein-protein interactions [62-64], the ligands of these receptors are expected to include peptides.

TNFR class: The maize CRINKLY4 (CR4) gene product possess TNFR (tumor-necrosis factor receptor)-like repeats, that has a conserved arrangement of six cysteines, and seven repeats of ~39 amino acids that display a weak similarity to the RCC GTPase [65][66][67]. CR4 is required for a normal cell differentiation of the epidermis [68]. The Arabidopsis genome contains several genes related to CR4 [67, 69].

EGF class: The cell wall associated receptor kinases (WAKs) represent the EGF (edpidermal growth factor) class. The EGF=like repeat motif is characterized by a conserved arrangement of six cysteines. The EGF-like repeats are found in variety of animal extracytoplasmic receptor domains and are known to play a role in protein-protein interactions. In Arabdopsis, four WAKs (WAK1 to WAK4) have been identified, and all of them have extracellular EGF-like repeats [70]. Reverse-genetic experiments suggest that WAKs may be involved in pathogenic responses.

PR class: The Arabidopsis PR5K (PR5-like receptor kinase) is the known example of this class. The extracellular domain of PR5K exhibits sequence similarity to PR5 (pathogenesis related protein 5), whose expression is induced upon pathogen attack [21, 71, 72]. The structural similarity between the PR5K receptor domain and PR5 suggests a role for PR5K in pathogenesis response.

Lectin class: The Arabidopsis LecRK1 gene product possesses an extracellular domain homologous to carbohydrate-binding proteins of the legume family. Although biological function of LecRK1 is yet known, its structure feature suggests that LecRK1 may be involved in a perception of oligosaccharide-mediated signal transduction. The Arabidopsis genome contains >30 genes belonging to Lectin-RLKs several genes coding for Lectin-RLKs [73].

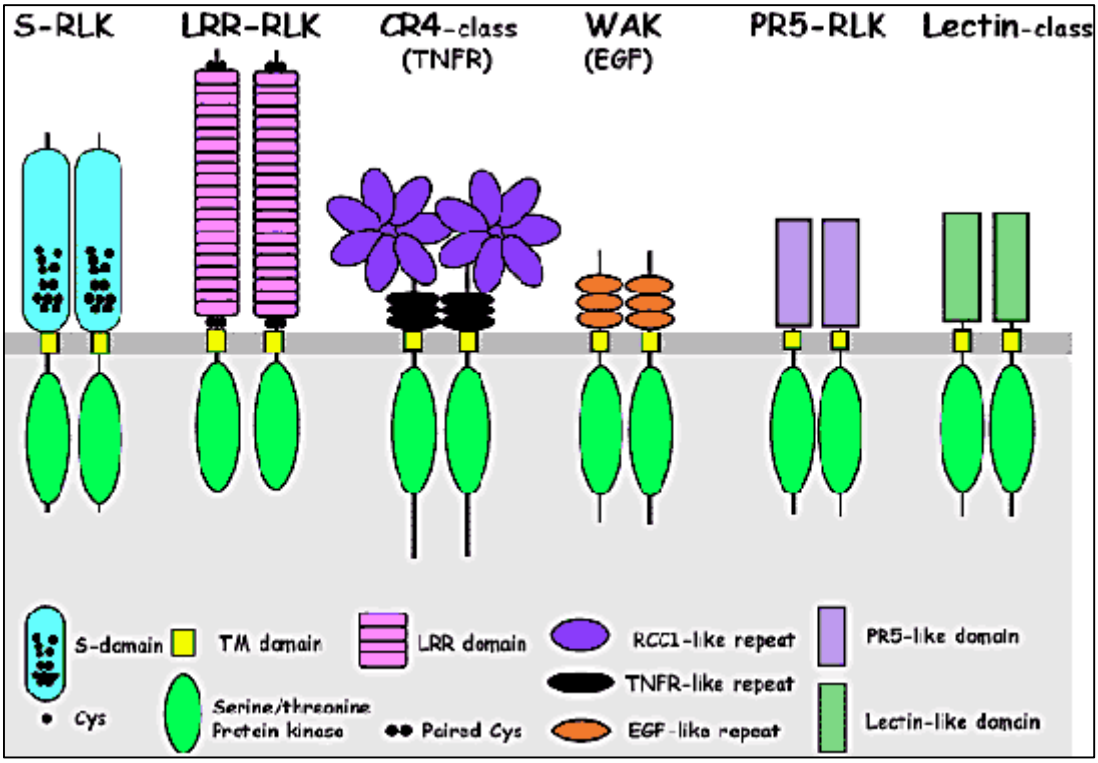

Fig 4. Structural families of Receptor S/T Protein Kinases in Plants

Six major families of plant receptor kinases are classified by their putative extracellular domains. Approximate gene numbers for each family in *Arabidopsis* are indicated. Where known, genetically defined functions for members of each family are listed in the text. The S-type and LRR-, CR4-receptors [74][75-77]; WAK type (Wall-Associated Kinase) [78]; PR type (pathogenesis related); lectin type[79]

6. Signaling in Plant Development

All higher plants possess several classes of photoreceptors. Phytochromes (phyA-phyE) sense red and far-red light. Three distinct photoreceptor families as mentioned in above setion: for example phototropins (phot1 & phot2), cryptochromes (cry1 & cry2) and the Zeitlupes (ZTL, FKF1 & LKP2) sense UVA/blue light. UVB-receptors are currently unknown. These photoreceptors allow plants to sense the intensity, quality, periodicity (day-length) and direction of light. These photoreceptors control important developmental transitions (e.g. the induction of flowering). Cryptochrome and phytochromes also determine whether a seedling will adopt an etiolated development (after germination in the dark) or a photomorphogenic development when the seedling develops in the light. The etiolated mode of development allows the seedling to rapidly emerge from the soil into the light. Shade avoidance and phototropism are two important adaptive responses, which allow seedlings to optimize photosynthetic light capture. The list of Arabidopsis photoreceptors is presented in Fig. 5.

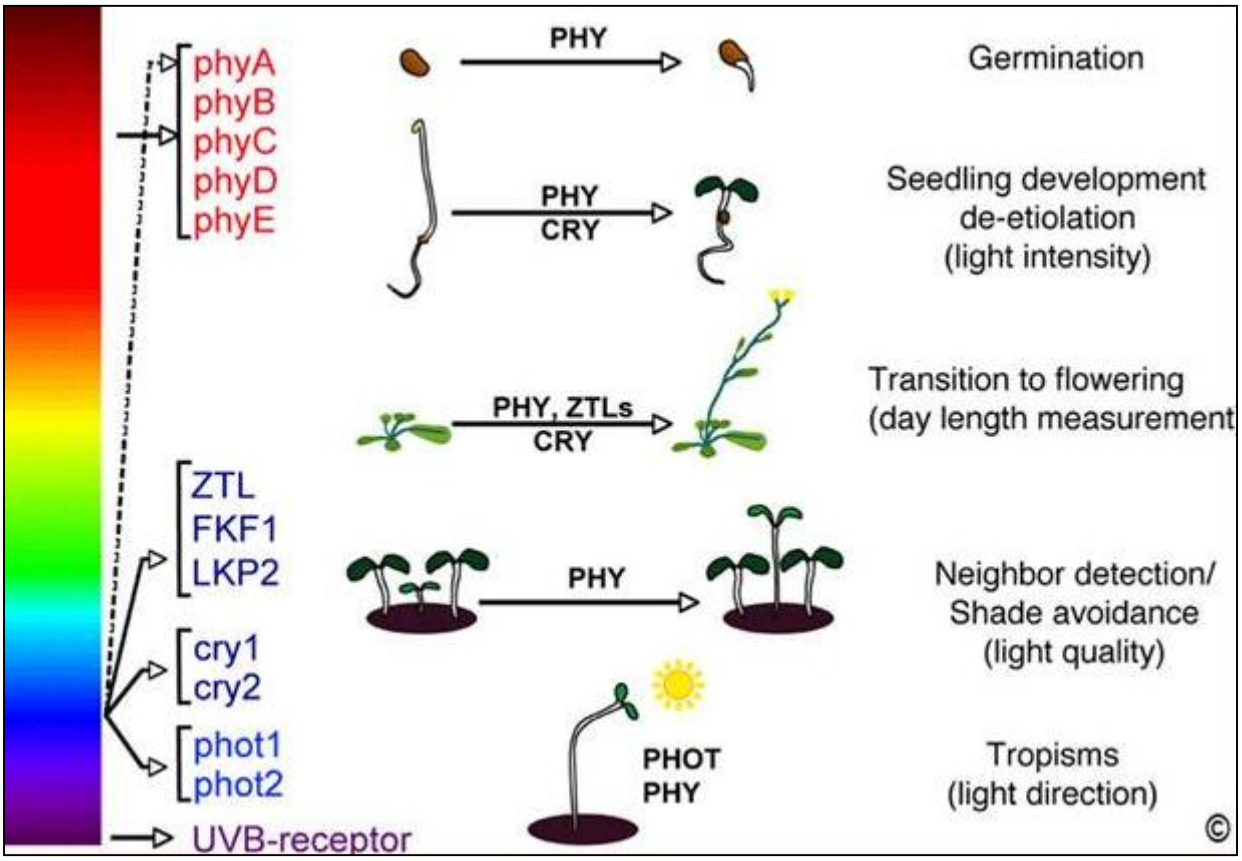

Fig 5. The effect of light on plant growth and development[1]

At the level of biological function, there is substantial evidence that key elements of signaling pathways related to stress [80-82], defense [83], sugar [84, 85], and osmotic responses [86, 87] are at least partially conserved in plants, animals, and fungi. These conserved pathways regulate processes that are basic to unicellular as well as multicellular organisms. For example, sugar sensing provides a mechanism for long-distance communication between plant organs [84, 85]. In contrast, the signaling pathways that underlie much of multi-cellular development and pattering are, as far as we can tell, highly novel in plants. The Ras, Wnt, and hedgehog signaling pathways that are central to animal development [88] are not detected in plants. Although auxin signaling is mediated by a highly conserved ubiquitin mediated proteolysis apparatus; the downstream targets of the auxin-regulated SCFTIR1 complex are highly novel and plant specific.The generalization that developmental pathways are less conserved than responses common to unicellular organisms is consistent with the hypothesis that multi-cellular development occurred independently in plants and animal lineages.

[1] http://www.unil.ch/cig/en/home/menuinst/research/research-groups/prof-fankhauser.html

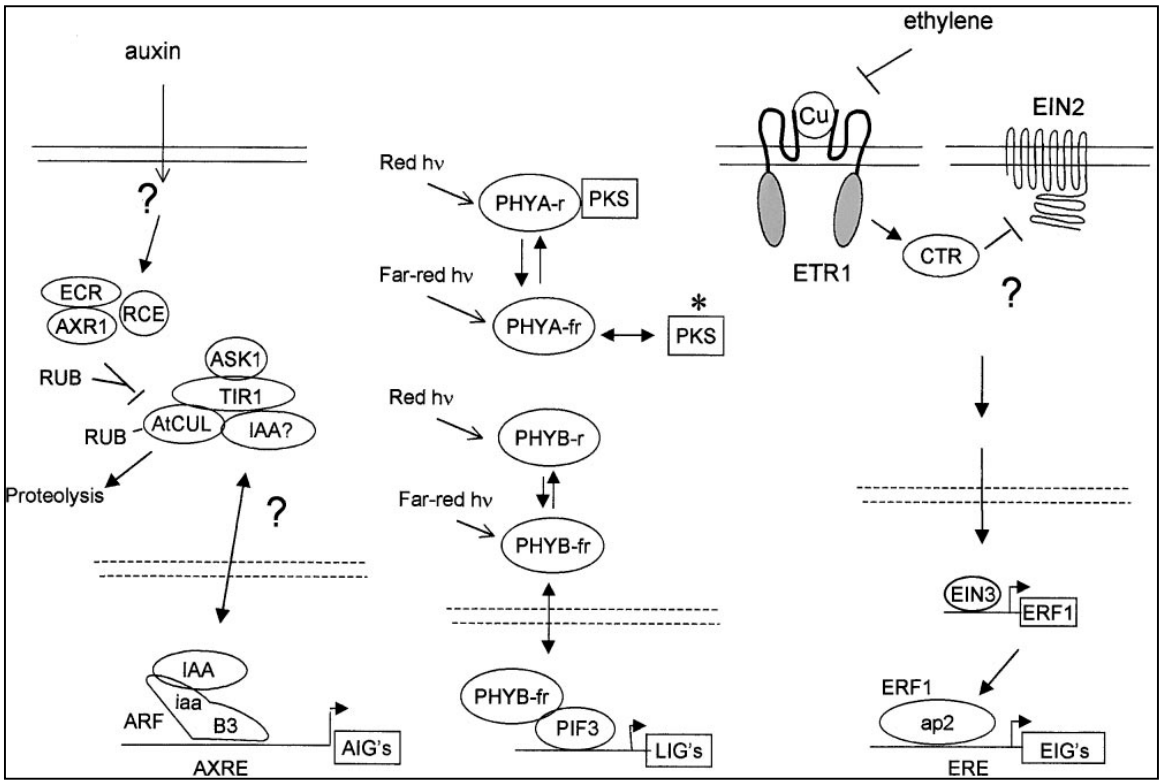

Fig 6. A simplified diagram for key signal transduction pathways for auxin, red, and far red light and ethylene in Plants. Two defined activities of PHY-fr are shown. PHYA-fr phosphorylates PKS1 localized in the cytosol Nuclear localized PHYB-fr interacts specifically with the PIF3 transcription factor, effecting regulation of one class of light-induced genes (LIGs). The ERF transcription factors contain AP2 DNA binding domains specific for the ethylene response elements in promoters of ethylene induced genes (EIGs). AIG, auxin induced gene. Cell membranes are represented by paired horizontal lines, dashed lines represent the nuclear envelope (see[89]).

The hormone pathways-auxin, cytokinin, abscisic acid, gibberellin, and ethylene, brassinosteroid-appear to be very important in many contexts in plant development (see Fig 6).Recently, the concept of cross-talk between hormones has attracted much attention with the idea that hormone signaling pathways make up a complex interacting web of informational transfer that allows a variety of stimuli to cause a plethora of overlapping responses [23]. Much of the evidence for signaling cross-talk in hormone biology comes from genetic studies using the model plant Arabidopsis thaliana. A number of molecular mechanisms have been identified that explain the interactions between hormones. Genetic perturbations of one hormone response can cause changes in the synthesis or degradation of another hormone [90]. Alternatively, hormone signaling pathways can share signaling components so that both pathways are disrupted by a single mutation [91]. In this review one of our aims is to update the knowledge related to the growing relationship between hormone signaling and developmental studies with the intention of demonstrating that developmental context is required for a full understanding of how a hormone functions.

Auxin (indole acetic acid) regulates many aspects of plant growth and development and plays a pivotal role in many processes throughout the plant life cycle. These include embryogenesis, lateral root development, vascular differentiation, apical dominance, tropic responses and flower development [92]. In spite of the tremendous amount of information that has accumulated, the auxin signaling pathways have not been fully elucidated. The known primary auxin responsive genes include three gene families called the AUX/IAA, GH3 (growth hormone) and SAUR (small auxin-up RNA) families [93]. The AUX/IAA proteins are short –lived nuclear proteins that function as transcription regulators.These proteins do not interact directly with DNA but exert their regulatory activity through another group of proteins called auxin responsive factors (ARFs). There are at least 29 AUX/IAA genes in the Arabidopsis genome. Most of the AUX/IAA proteins share four conserved domains, designated domains I to IV. Domains III and IV are located in the C-terminal half of the protein and are involved in homo- and heterodimerization with other AUX/IAA proteins and heterodimerziation with ARFs that also share domains III and IV (also called the CTD or C-terminal domain). Additionally, ARFs contain an N-terminal DNA binding domain (DBD) . There are 23 ARF genes in the Arabidopsis genome and all but two (ARF3/ETTIN) and ARF17) contain the CTD region [94][95].

ARFs bind to conserved DNA sequences (TGTCTC) called auxin-responsive elements (AXRE) in the promoter regions of primary/early auxin response genes [95]. ARFs can act as either transcriptional activators or repressors

depending on the nature of their middle region (MR) domain. The ARFs with a Q-rich MR function as activators, whereas other RFs with a P/S/T-rich MR function as transcriptional repressors [94]. The half-life of these proteins in wild-type Arabidopsis seedlings ranges from ~10 min to ~80 min, depending on the protein [96][97][98]. This short half-life can be extended several fold by treatment with proteosome inhibitors such as MG115 and MG132, indicating that the degradation of the AUX/IAA proteins is associated with the proteosome pathway [98].

This auxin signaling is mediated by a highly conserved ubiquitin ligase complex (Ubiquitin-proteosome pathway) [92][99-104]. The pathway is defined by the AXR (AUXIN RESISTANT) and TIR (AUXIN TRANSPORT INHIBITOR RESISTANT) mutants of A. thaliana. AXR1 and a partner protein, ECR1, comprise a RUB (related to ubiquitin)-activating enzyme analogus to E1 of the ubiquitin pathway [99, 101-104]. These proteins together with a RUB-conjugating enzyme, RCE1, RUB-modify AtCUL, a cullin homolog [92]. AtCUL is a component of an SCF (SKP-culin-F-box) ubiquitin ligase complex that includes TIR1, the F-box protein, and ASK1, a homolog of yeast SKP1 [96, 105]. Mutation in TIR1 and ASK1 inhibit the auxin response, suggesting that the SCFTIR1 complex regulates turnover of a repressor. Possible downstream targets of the SCFTIR1 comple include IAA domain proteins such as those defined by the dominant auxin insensitive mutants, AXR2 and AXR3 [106, 107]. The IAA homology domain is conserved in a large family of auxin induced proteins in plants. Dominant muatations in the IAA domain that confer insensitivity to auxin also strongly inhibit turnover of IAA proteins [108]. Protein-protein interactions mediated by the IAA domains are proposed to modify activity of the ARF (auxin responsive factor) transcription factors bound to auxin response elements (AXRE) of auxin induced genes [94, 106]. Key components of ethylene signal transduction pathway include ETR1 (ETHYLENE TRIPLE RESPONSE-1), the ethylene receptor; CTR1 (CONSTITUTIVE ETHYLENE RESPONSE-1), a raf-like protein kinase; EIN2 (ETHYLENE INSENSITIVE-2), a membrane protein related to mammalian NRAMP proteins; and EIN3 (ETHYLENE INSENSITIVE-3), a novel transcription factor. In the absence of ethylene, ETR1 and related receptors actively inhibit the ethylene response. The inhibitory action of ETR1 requires the CTR1 kinase. Hence, ethylene binding to ETR1 is proposed to cause inactivation of CTR. Inactivation of CTR1 potentiates signaling mediated by the C-terminal cytoplasmic domain of EIN2 [91]. ENI2 signaling leads to activation of the ENI3 transcription factor in the nucleus. ENI3 is a direct activator of the ETHYLENE RESPONSE FACTOR [109] genes. ERF transcription factors in turn bind to ethylene response elements of downstream ethylene induced genes.

Abscisic acid (ABA) was discovered independently by several groups in early 1960s. Originally believed to be involved in the abscission of fruit and dormancy of woody plants, the role of ABA in these processes is still not clear. ABA is, however, necessary for seed development, adaptation to several abiotic stresses, and sugar sensing. The regulation of these processes is in large partly mediated by changes in de novo synthesis of ABA.

Our understanding of the function and synthesis of ABA has been greatly enhanced by the identification and characterization of ABA-deficient mutants [110]. The ABA–deficient mutants have been identified by the following phenotypes: precocious germination, susceptibility to wilting, an increase in stomatal conductance, and an ability to germinate and grow on media containing a high concentration of sucrose or salt. Several genes involved in ABA signaling pathways have been isolated from Arabidopsis. These include genes for protein phospahtases (ABI1 and ABI2) and for putative transcription factors (ABI3-5). One of the well studied ABA signaling pathways is the closure of the stomatal pore in response to ABA [111]. ABA application is known to cause elevation in guard cell cytosolic (Ca^{2+}) ion levels, and oscillation in cytosolic (Ca^{2+}) are necessary for stomatal closure [111].

The pH and redox status of the cell are crucial factors in mediating or regulating ABA signal transduction. Cytosolic increases in both H2O2 and NO concentrations occur in guard cells before (exogenous) ABA-induced stomatal closure [112][113, 114]. Interestingly, both of these secondary messengers are associated with pathogen interactions and with Ca^{2+}cyt increases that are indicative of the convergence of different pathways at the level of Ca^{2+} oscillation [115].

The growing list of ABA-response regulators comprises G proteins; protein phosphatases, such as PP2Cs; and protein kinases of the calcium-dependent protein kinase (CDPK) and SUCROSE NON-FERMENTING PROTEIN-1 (SNF-1) - like groups [116].

Analysis of GPA1 (Gα subunit of a heterotrimeric G protein) implies a role for heterotrimeric G proteins in modulating ABA responses [71, 72, 117], and there is strong evidence that small G proteins also regulate ABA responses [118][119]. The Rho-like small G protein ROP10 negatively regulates ABA-mediated stomatal closure, germination and growth inhibition [119]. The recruitment of ROP10 to the plasmamembrane requires a functional farnesylation site and is a prerequisite for altering ABA responses. Hence, the role of ROP10 in ABA responses is reminiscent of the role of the small G protein RAS in the mitogenic response of mammals. Interestingly, ROP proteins are also associated with increased H2O2 production because of their activation of NADPH oxidases and, together with H2O2-induced ROP deactivators, are part of redox rheostat [120]. ROP2 and ROP6/AtRac1

contain a putative geranylgeranylation motif, and the expression of dominant –negative and constitutively active forms of both of these small G proteins characterized them as peliotropic negative modulators of ABA responses [118][121, 122]. The roles of ROP2 and ROP6/AtRac1 were linked to reorganization of the actin skeleton and to vesicle transport, which are required for both stomatal closure and tip growth [118][121, 122]. In this context, a syntaxin deficiency in osmotic stress-sensitive mutant (asm1) gave rise to impaired vesicle transport or fusion and resulted in ABA-insensitive stomatal regulation [86]. Transcriptome analyses have shown that ABA dramatically alters genomic expression [123][3]. More than 1300 ABA-regulated genes were identified by random massive sequencing of Arabidopsis transcripts, of which half showed decreased expression in response to ABA [123]. ABA regulation of the majority of the1300 genes (more than 90%) was impaired in abi1-1, emphasizing the central role of this locus in ABA signal transduction.

The control of ABA on gene expression and on the proteome includes posttranscriptional processes, such as mRNA maturation and control of the stability of transcripts and proteins. ABA strongly down regulates the expression of ribosomal proteins and concomitantly up regulates the genes that are involved in proteolysis [123]. In addition to ABA-mediated control of TFs, the regulation of RNA polymerase II (RNAP II) has been identified as a novel control point in plant stress signaling [86].

Plants utilize a variety of metabolites as signaling molecules, including many that have analogs in other eukaryotes. Hormones derived from aromatic amino acid, steroid, apo-carotenoid, and fatty acid derivatives mirror major classes of animal hormones.

The brassinosteroid (BR) and abscisic acid (ABA) hormones are analogs of steroid and retinoid hormones of animals, respectively [124]. Key steps in plant and animal steroid biosynthetic pathways are highly conserved. The human steroid 5α-reductase type I or type II genes, for example, rescue the Arabidopsis det2 mutant, which is deficient in the synthesis of the steroid hormone brassinolide [124]. The apo-carotenoid, retinoic acid and abscisic acid, are derived from oxidative cleavage of plant carotenoids. The biochemical mechanism of apo-carotenoid synthesis was illuminated by analysis of viviparous14, an ABA-deficient mutant of maize [110]. VP14 defines a new class of dioxygenases that catalyze specific oxidative cleavage of carotenoids. Related genes are found in genomes of animals and bacteria that synthesize apo-carotenoids [110], suggesting that this mechanism is broadly conserved in nature.

Brassinosteroids (BRs) are steroidal plant hormones that are essential for growth and development. They are essential factors for cell and stem elongation, unrolling of grass leaves, bending of grass leaves at the sheath/blade joints, xylogenesis, and ethylene production. BR biosynthesis and sensitivity mutants show dwarfism and, when grown in the dark, share some characteristic with light grown plants [125]. The identification of components of the BR signal transduction pathway revealed different modes of transcriptional control in animal and plants. Steroid signaling in plants appear to be perceived at the plasma membrane through a leucine-rich-repeat (LRR)-receptor ser/thr kinases BRI1 and BAK1 [49]. Localization of these receptor kinases on the plasma membrane suggest that BR signaling is initiated on the cell surface [49]. Moreover, the extracellular domain of BRI1 confers BR responsiveness to heterologous cells [77]. The possibility that membrane–bound steroid receptors exist in animals remains; however, LRR receptor S/T kinases related to BRI1 are not found in animal genomes. BR signaling is reminiscent of growth factor and TGF-B signal transduction in animals. It is possible that the use of steroid signals is ancient and that the signal transduction mechanisms have diverged radically in plants and animal lineages. The phosphorylation cascade could be a basis of extensive cross-talk and thereby explain the complexity of BR response [126-130].

Jasmonic acid (JA) and related octadecanoid compounds are cyclic products of lipid oxidation and are structurally related to prostaglandins, autacoidal hormones that have a variety of physiological activities in mammals. Both JA and prostaglandins are derived from fatty acids. JA signal pathway involves several signal transduction events: the perception of primary wound or stress stimulus and transduction of the signal locally and systemically; the perception of this signal and induction of JA biosynthesis; the perception of JA and induction of responses; and finally, integration of JA signaling with outputs from the salicylic acid, ethylene, and other signaling pathways [131][132].

Salicylic acid (SA) is a central signaling molecule responsible for the coordinated expression of pathogenesis related (PR) genes and the onset of systemic acquired resistance [133]. SA-mediated responses appear to involve multiple steps including early oxidative signaling, which helps to establish the reducing conditions that are necessary for a key regulator, the NONEXPRESSOR OF PR GENES 1 (NPR1) monomer, to enter the nucleus. Multiple and redundant TGA transcription factors cooperate with nuclear NPR1 to activate the expression of late PR genes. Mutations in the Cys residues of NPR1 and some of TGA confirm that protein translocation and transcription activation are modulated by cellular redox states. New evidence also supports the concept that a single NPR1 protein has multiple functions in different subcellular locales, which presumably rely on interactions with distinct or overlapping partners. New transcription factors that are involved in NPR1-independent SA regulation of gene expression have also emerged.

7. Conclusions

Signal transduction is an actively expanding topic of research in plant biology. Signals, which include a wide array of external and internal stimuli, are amplified and communicated by complex signal transduction networks, most of which initiate with the activation of receptor proteins. Bacterial receptor and transduction systems provide models for plant receptors, including proteins that sense ethylene and phytochrome. Among the various plant signal transduction pathways that have been identified many of the components are common to many signal transduction networks in animals, such as GTPases and phospholipids derivatives. Investigations into the roles of GTPases in plant signal transduction has been progressed considerably and several small GTP binding proteins have been implicated in these processes. Cyclic nucleotides also appear to act as a second messengers in plant cells and most likely interact with another second messenger, cytosolic calcium. Calcium channels and other calcium transporters form the basis of a complex Ca^{2+} signaling network in plants. Protein kinases are the most common transduction components interpreting signal in plant cells. Various classes of protein kinase act in concert with protein phosphatases to mediate plant cell signaling and control metabolism. Plant hormones are important elements in controlling plant growth and development, and progress is being made in understanding how cell transduce these signals. . Photoreceptor induced signaling mechanism influence numerous aspects of plant development; however, our understanding related to the the photorecptor mediated plant development at molecular level is limited. Inspite of the considerable progress in elucidating the molecular events underlying in photomorphogenesis, there are still a large number of unresolved issues. Advances in signal transduction research are rapidly expanding our understanding of how plant cells communicate and cooperate.

This should explore the significance of the results of the work, not repeat them. A combined Results and Discussion section is often appropriate. Avoid extensive citations and discussion of published literature.

8. References

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