



Edited by  
Girdhar K. Pandey

# Protein Kinases *and* Stress Signaling *in* Plants

Functional Genomic Perspective

WILEY Blackwell



## **Protein Kinases and Stress Signaling in Plants**



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Functional Genomic Perspective

*Edited by*

*Girdhar K. Pandey*

*University of Delhi*

*New Delhi*

*India*

**WILEY** Blackwell

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## Editor Biography



*Source:* Girdhar K. Pandey

**Girdhar K. Pandey** received his BSc (Hon.) in Biochemistry from Delhi University in 1992 and MSc in Biotechnology in the year 1994 from Banaras Hindu University (BHU). Subsequently, he joined Ph.D. in the School of Life Sciences, Jawaharlal Nehru University (JNU) and worked in the field of calcium signal transduction under abiotic stresses in plants. He was awarded the Ph.D. degree in the year 1999 and then pursued postdoctoral career at Department of Plant and Microbial Biology, University of California at Berkeley in the year 2000. There, he extended his work in the field of calcium-mediated signaling in *Arabidopsis* by studying CBL-CIPKs, phosphatases, channels/transporters, and transcription factors involved in abiotic

stresses. Currently, he is working as Professor in the Department of Plant Molecular Biology, Delhi University South Campus.

Pandey's research interests involve detailed mechanistic interplay of signal transduction networks in plant under mineral nutrient deficiency (mostly potassium, calcium, and nitrate) and abiotic stresses such as drought, salinity, and oxidative stresses induced by heavy metals. His laboratory is working on the coding and decoding of mineral nutrient deficiency and abiotic stress signals by studying several signaling components such as calcium sensors such as calcineurin B-like (CBL) and CBL-interacting protein kinases (CIPK), phosphatases (mainly PP2C and DSP), transcription factors (AP2-domain containing or ERF, WRKY), transporters and channels proteins (potassium and calcium channels/transporters) in both *Arabidopsis* and rice. The long-term goal of his research group is to establish the mechanistic interplay and crosstalk of mineral nutrient-deficient conditions

and different abiotic stress signaling cascades in Arabidopsis and rice model system by using the advance tools of bio-informatics, genetics, cell biology, biochemistry, and physiology with greater emphasis on functional genomics approaches.

See Pandey's web page for further information about his lab and research work: <https://sites.google.com/site/gkplab/home>; <https://www.dpmb.ac.in/index.php?page=girdhar-pandey>.

## Preface

Agriculture is one of the primary determinants of a healthy economy both at the micro- as well as macro level. The global population dynamics in the face of climate change as well as challenges posed by various abiotic and biotic stresses influence crop productivity. The scientific community is expected to be ahead of times, to provide a solution to such issues and more often than not, by envisioning the challenges that lie ahead. In this regard, plant biologists hold a larger role to overcome these challenges by discovering novel methods. The development of high yielding and tolerant cultivars through continuous selection and breeding along with latest technologies pertaining to cultivation, harvesting, and extension are a significant improvement. However, the advent of -omic approaches have heralded a golden era for crop improvement. The functional clues from model systems have paved the way for plant biologists to engineer stress tolerance through an integrated approach involving genetic manipulation, gene editing, and breeding.

The availability of crop genomes in public domains, and understanding of functional genomic approaches, has enabled the identification of function of plant gene(s) and gene families in relation to the whole genome(s). The role of gene(s) in the regulation of the plant phenotype/behavior under various physiological or developmental conditions can be established with the tools of genomics and functional genomics. The functional genomics approach has enabled plant biologists to develop a systematic approach where interplay of one or more genes in regulating the phenotype can be deciphered. The identification of critical trait-determining protein(s) will lead to the development of road maps of complete regulatory and metabolic pathways involved in physiological and developmental processes.

Plants have a highly evolved surveillance system to enable them to overcome the challenges posed by various stress factors. Plants utilize a highly efficient signaling system through several sensory and transducing components as well as effector molecules to bring about a response. Signals are perceived by receptors, followed by a transduction process that amplifies the signals via generation of second messengers (such as  $\text{Ca}^{2+}$ , lipids, cNMP, etc.). The final response is regulated through the effector molecules. Signaling responses are either fast (occur within seconds to minute) or slow (may take minutes to hours). They occur as direct physiological changes or through the regulation of gene and protein expression. Although both prokaryotes and eukaryotes exhibit a high degree of conservation in several component pathways, plants and animals do exhibit unique or distinct signaling components. The complex interplay and coordination between one or more signaling pathways occurs through crosstalk/overlap and/or specificity in generation of final response.



Signaling pathways are also considered the neuronal circuitry of a cell, primarily responsible for sensing, communicating, and maintaining homeostasis of biological processes. There are several regulatory controls in signaling pathways which turn the cellular processes “on or off,” thus, acting as molecular switches. Protein phosphorylation–dephosphorylation, a post-translation modification, is a well-studied molecular switch. This reversible process is catalyzed by two important enzymes, Kinases and Phosphatases. Phosphorylation is the covalent attachment of a phosphate group to the target protein that causes conformational alterations in the protein resulting in modulation of either activity or function. Kinases phosphorylate substrate proteins while phosphatases dephosphorylate a phosphorylated protein, thereby, forming a molecular switch to trigger the activation or inactivation of diverse cellular processes. Protein kinases transfer the terminal phosphate groups from nucleoside triphosphates such as ATPs to the hydroxyl group or nucleophilic centers of other functional groups belonging to specific phosphosites in a protein. In the living organisms, nine amino acids (tyrosine, serine, threonine, cysteine, arginine, lysine, aspartate, glutamate, and histidine) are reported to be phosphorylated. However, three amino acids, i.e. serine (Ser), threonine (Thr), and tyrosine (Tyr) were found to be majorly phosphorylated in eukaryotic cells and have profound implications in the signaling pathways. In eukaryotes, protein kinases are subdivided into two major classes, i.e. Ser/Thr and Tyr kinases. In addition, there are certain kinases which can phosphorylate both Ser/Thre as well as Tyr residues and are known as dual specificity protein kinases (DsPTKs). Based on the “kinome” analysis of plants and animals, it has been observed that in comparison to animals, plants have almost no typical Tyr kinase, but, a large repertoire of Ser/Thr kinases.

Protein kinases are the key components of the signaling pathway and are primarily responsible for phosphorylating the target proteins that could be a metabolic enzyme, cytoskeletal protein, transporters/channels or a transcription factor. Protein kinases also act as components of signaling cascade, such as MAP kinase cascade in transducing the signal downstream. Many of these kinases also act as nodal points to converge or diverge one or multiple signaling pathways and also responsible for generating specificity and overlap/crosstalk in the signaling pathways. Their ability to act as an integrator or modulator of signaling pathway(s) and fine-tune the final output or response in the stimulus–response-coupling process is well appreciated.

This book on “*Protein Kinases and Stress Signaling in plants: Functional Genomic Perspective*” comprises of 22 chapters contributed by several well-known plant biologists working in the field of “Protein kinases and stress signaling” with a special emphasis on “Functional Genomics aspect.” It presents a state-of-the-art and timely contribution of knowledge to develop a better and holistic understanding of stress perception, its signal transduction and finally generation of responses against one or multiple stress signals.

The first chapter focuses on the role of Two-component system (TCS) in plant stress signaling. It is a predominant form of signaling involved in bacteria (prokaryote) relying on histidine and aspartate-based phosphotransfer to response regulators, which ultimately regulate the stress response. Interestingly, TCS is absent in animal and fungi but is observed in hormonal (cytokinin and ethylene) and stress signaling in plant systems. Plant TCS is a multistep system comprising of three partners: histidine kinases (HKs) that act as receptors, histidine containing phosphotransfer proteins (HPTs) that serve as shuttle proteins

and response regulators (RRs) that act as output proteins. A comparative account of this circuitry among the monocot and dicot plant species is discussed in detail.

Plant genomes encode a large number of Ser/Thr receptor like kinases known as Receptor-like protein kinases (RLKs) that regulate a diverse array of signaling processes. Arabidopsis is reported to encode ~610 RLKs. Lectin receptor like kinases (LecRLKs), a subclass of RLKs, are not reported in humans and yeast. They are plant-specific and are involved in the regulation of diverse cues such as biotic and abiotic stresses, hormonal, symbiosis as well as plant growth and development. Chapter 2 describes the cellular functions of LecRLKs and their implication in development of stress-tolerant crops.

In photosynthetic organisms, light perception generally involves various photoreceptors, i.e. Phytochromes (PHYs; red and far-red light sensing), Cryptochromes (CRYs; blue light sensing), Phytotropins (PHOTs; blue light sensing), Rhodopsins (blue to red light sensing), and UVR8 (UV-B light sensing). Some photoreceptors coupled with kinases (Histidine or Ser/Thr) are termed “photo-activated kinases (PAPKs).” These photoreceptors possess light sensing domains coupled with effector domains, which are responsible for a variety of physiological functions. Chapter 3 elaborates the role of PAPKs in green algae under abiotic stresses including varying light conditions.

Glycogen Synthase Kinase 3 (GSK3) known as SHAGGY in *Drosophila* is a non-receptor Ser/Thr protein kinase that is highly conserved in all eukaryotes. Originally known to be a key regulator in glycogen metabolism, it has been implicated in multiple signaling pathways and conditions like inflammation, Type II diabetes, cancer, Alzheimer’s disease, and bipolar disorder. Chapter 4 gives a detailed account of GSK3-like kinases in plants in the context of their versatility as well as physiological and biochemical relevance in cellular signaling. AMPK (5’ AMP-activated protein kinase) or SNF1 (Sucrose Non-Fermenting 1) Ser/Thr protein kinases are involved in the maintenance of cellular energy homeostasis in animals and yeast whereas plants have the homologs of AMPK and SNF1 protein kinases, known as SNF1-related kinases (SnRKs). These are classified into three subclasses, i.e. SnRK1, SnRK2, and SnRK3. Chapter 5 presents the role of SnRK1 and TOR (Target Of Rapamycin; another Ser/Thr kinase involved in energy and growth homeostasis) in balancing growth and defense signaling. The TOR-SnRK1-regulated growth-defense trade-offs and stress mitigation as well as the potential for the utilization of these pathways for crop improvement are discussed. Chapter 6 elaborates the pivotal role of SnRK2 in the early events of ABA signaling from the perspective of functional genomics. Chapter 7 details the role of several lipid-activated kinases in signaling pathways in plants regulating myriad physiological and developmental processes.

Calcium ( $\text{Ca}^{2+}$ ) has been recognized as one of the key molecules involved in the regulation of diverse biological processes, including the adaptative and defense machinery of an organism. It serves as a ubiquitous second messenger in all eukaryotic organisms. Various physiological and environmental cues trigger a spatiotemporal increase in intracellular  $\text{Ca}^{2+}$  concentration also known as “Calcium signature.” This  $\text{Ca}^{2+}$  signature is sensed and transduced downstream to  $\text{Ca}^{2+}$  sensors, kinases/phosphatases and other effector proteins. Chapters 8–12 describe the different facets of  $\text{Ca}^{2+}$  signaling where different  $\text{Ca}^{2+}$  sensors are involved in the execution of the signaling process under different conditions in plants. Chapters 8 and 9 specifically emphasize the role of  $\text{Ca}^{2+}$ -dependent protein kinases (CDPKs) as “ $\text{Ca}^{2+}$  sensor and responder” in plant growth, development, and stress

management. The role of one of the most important  $\text{Ca}^{2+}$  sensors, calmodulin (CaM) and its association with CaM binding kinases under stress conditions, is elaborated in Chapters 10 and 11. Besides, CDPK and CaM, plants also have another important class of  $\text{Ca}^{2+}$  sensors known as Calcineurin B-like protein (CBL), which associate with SnRK3 subclass of proteins known as CBL-interacting protein kinase (CIPK). Chapter 12 presents a detailed account of CIPKs in regulating diverse stress responses. Chapter 13 uncovers the role of Casein Kinase 2, a conserved pleiotropic enzyme involved in a number of developmental and stress responses. Chapter 14 presents the role of cyclin-dependent kinases (CDKs) in controlling cell division and stress responses in plants in the light of conserved mechanisms of eukaryotic cell division and novel features of cell cycle regulation in plants.

Mitogen-activated protein (MAP) kinase cascade is one of the finest examples of signaling cascades. It comprises of three hierarchical kinases, also known as MAPKKK, MAPKK, and MAPK. It regulates myriad biological processes such as growth, cell differentiation, cell death, hormonal signaling and stress/defense responses in eukaryotes. Chapters 15–18 highlight the role of MAPKs in different abiotic and biotic stresses and their complexity. Chapter 19 discusses the role of protein kinases in the regulation of responses to abiotic and biotic stress stimuli in combination and the development of adaptive or stress tolerance mechanisms.

The role of tyrosine phosphorylation in the regulation of a diverse array of physiological and developmental processes has been extensively studied in animal systems. This process is catalyzed by protein Tyr kinases (PTKs) in animals, whereas the identification and presence of a typical PTK is still a topic of debate in plants. However, Tyr phosphorylation has been reported on the basis of several proteomic and functional analyses, for the obligatory regulation of multiple cellular responses in plants. In Chapter 20, the role of protein Tyr phosphorylation and the presence of noncanonical protein Tyr kinases in plants under stress is discussed. Chapter 21 discusses the kinase-mediated regulation of potassium ( $\text{K}^+$ ) homeostasis, particularly, under salinity and drought stress, from the functional genomics perspective. This assumes importance due to the essentiality of  $\text{K}^+$  macronutrient for the smooth functioning of cellular processes as well as plant growth and development under stress.

The last chapter (Chapter 22) summarizes the role of various kinases involved in the peroxisomal functions including stress management. Peroxisomes are indispensable for the functioning of lipid metabolism, generation of reactive oxygen/nitrogen/sulfur species and detoxification, and synthesis of vitamins and hormones. The regulation of peroxisome biogenesis and functions through the post-translational modifications (PTM), particularly, protein phosphorylation, needs more attention.

A detailed mechanistic understanding of several signal transduction components, especially kinases, will help attain the ultimate goal of developing useful tools to generate crop varieties. This can be achieved by genetic manipulation or genome engineering through gene editing methodologies of key kinases involved in stress signaling pathways, which ultimately leads to augmentation of stress tolerance in crop plants without compromising on crop productivity.

Because of space constraints and several other limitations, not all aspects of protein kinases involved in stress signaling could be discussed here, these may possibly be targeted in future endeavors. I firmly believe that this book will meet the needs of a wide spectrum

of scientific readers including students, scientists, and academicians. This work is only possible because of the significant contributions from several plant biologists and I am indebted to all the contributors. I also express my sincere thanks to Dr. Malathi Bheri and Dr. Sibaji K. Sanyal for critical reading and constructive suggestions related to this book. Moreover, I express my sincere thanks to Delhi University, Department of Biotechnology (DBT), Science and Engineering Research Board (SERB), Council of Scientific and Industrial Research (CSIR), India for supporting the research in my lab.

Girdhar K. Pandey  
(Editor)

## 1

## Two Component Mediated Stress Signaling in Plants

A Comparative Profiling in Monocots and Dicots

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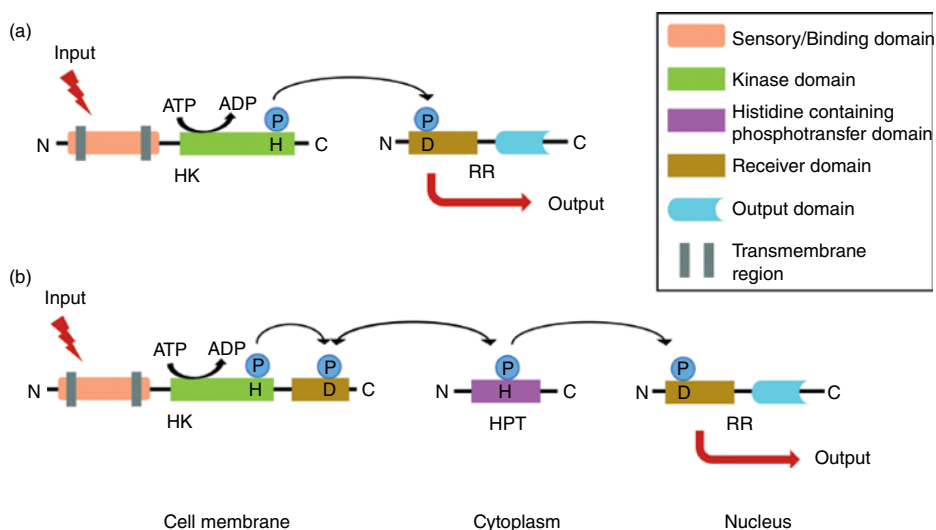
#Equal contribution

### Introduction

Living organisms are constantly exposed to environmental changes. Different organisms adapt and respond differently to the adverse conditions (Bray 1997; Kozlowski 1997; Sakai and Larcher 2012; Bleuven and Landry 2016). One of the key features that distinguish plants from animals is that the former are sessile in nature and require more efficiently governed genetic regulation to cope with unfavorable environmental conditions. Hence, during evolution, plants have developed intricate mechanisms to face these environmental challenges to some extent. Plants' responses toward environmental stresses are multigenic and are governed by complex signaling molecules working in an orchestrated manner (Nongpiur et al. 2012). Various -omics approaches, including genomics, transcriptomics, proteomics and metabolomics, have been utilized to understand the signaling machinery operative under abiotic stresses. These studies reveal that tolerant plants withstand the extremes of environment in an adaptive manner, by re-adjusting the major signaling and metabolic pathways to maintain cellular homeostasis (Ward and Thompson 2012; Ding et al. 2013; Soni et al. 2015). The response toward stresses involves complex molecules, wisely regulated at distinct checkpoints. Environmental changes are perceived by receptors such as histidine kinases (HKs), hormone receptors, G-protein coupled receptors (GPCR), receptor kinases, transporters, antiporters, and tyrosine or serine/threonine kinases (Kacperska 2004; Osakabe et al. 2013; Zargar 2018). These activated receptors trigger downstream cascade by activating signaling molecules like  $Ca^{2+}$ , ROS (reactive oxygen species), and other adapter molecules, which ultimately leads to the initiation of a series of post-translational protein modification events (Nishida and Gotoh 1993; Lee et al. 2007). These modifications can result in the activation of effector proteins, which function directly in the alleviation of the effects of the stress. The modifications can also stimulate the

regulation of transcription factors, which modulates the expression of stress related genes to combat the detrimental effect of the environmental extremes (Jaspers and Kangasjärvi 2010; Sinha et al. 2011; Zhu 2016). Though a certain level of overlap does exist in the responses to different environmental constraints, these responses are usually distinct for each environmental stress (Zhu 2001; Fujita et al. 2006). More than one type of stress can turn “on” similar set of genes and thus participate in the crosstalk for stress signaling (Fujita et al. 2009; Gupta et al. 2016).

The two-component system (TCS) is known to play a significant role in regulating various biological processes in both prokaryotes and eukaryotes, including higher plants. However, in eukaryotes, animals do not possess TCS regulatory system. TCS is a signal transduction pathway, which primarily evolved for the perception and transduction of extracellular signals. This signaling mechanism operates by the His-Asp phosphorelay. As the name suggests, the simplest form of TCS involves two major components for signaling; one membrane bound sensory HK and the other one is its cognate response regulator (RR). Signal is perceived by the HK, which auto-phosphorylates at a conserved histidine residue and then transfers this phosphoryl group to a conserved aspartate residue on the RR, which in turn stimulates a response. This kind of TCS, designated as prototypical TCS, has been identified only in prokaryotes and has been shown to govern distinct cellular processes such as chemotaxis, quorum sensing, and osmotic response (Aizawa et al. 2000; Mitrophanov and Groisman 2008). Schematic diagram, for how the TCS signaling proceeds, is given in Figure 1.1. A more complex form of TCS, designated as the multistep phosphorelay (MSP), is found in both prokaryotes and eukaryotes. The MSP possesses an additional shuttle protein to



**Figure 1.1** Typical structure of TCS signaling machinery. (a) Prototypic TCS signaling machinery operating in a bacterial system, where the signal is perceived through a simple histidine kinase (HK) and transferred to the response regulator (RR). (b) Hybrid type histidine kinase (HHK) largely present in the eukaryotes. In this case, signaling proceeds via His-Asp-His-Asp phosphorelay and signal perceived through HHK is transferred to RR via an intermediate histidine containing phosphotransfer (HPT) protein. Sources: Aizawa et al. (2000); Mitrophanov and Groisman (2008).