

Plant Immunity: An Enigma during Biotic and Abiotic Stress

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The paradox of plant immune system has continued to inspire phytologists with great fascination. Plants combat biological attack by pathogens with the help of a two tier innate immune system including a first layer with pattern-triggered immunity (PTI) and the second one with effector-triggered immunity (ETI). This total phenomena involves some conserved molecules like microbes/pathogen associated molecular patterns (MAMPs/PAMPs) and various receptors like nucleotide-binding site/leucine-rich repeat (NLR) proteins [1]. Plants trigger a number of integrated immune responses which are applied both locally at the infection site and systemically at distant unaffected sites. The field of 'plant defence and immunity' is moving ahead not only because of its evolutionary significance but also for its dual-faced role in biotic and abiotic stresses. Many secondary metabolites, anti-feedants, protease inhibitors act as bullets triggered by plants to encounter the pathogenic attack. Moreover, defence system invokes a diverse array of immune responses such as reactive oxygen species (ROS) generation, cellular Ca^{2+} spikes, MAP kinase (MAPK) activation, production of phytohormones, and downstream reprogramming [2]. There are clinching evidences to prove that because of the sessile lifestyle and lack of an adaptive immune system several parallel transcription factors (TF) are particularly recruited to regulate plant immune responses. Among those, APETALA2/ETHYLENE-RESPONSE ELEMENT BINDING FACTOR (AP2/ERF), BASIC-HELIX-LOOP-HELIX (bHLH), BASIC DOMAIN LEUCINE ZIPPER (bZIP) are well known families of TFs. Along with this, a signalling loop is always at work being a part of plant immunity and induced by receptor mediated recognition of invading pathogens. The signal transduction is a result of interaction between various molecules such as nitric oxide, ROS intermediates, salicylic acid and several growth regulators like jasmonic acid and ethylene [3]. Some recent studies also bring light to the fact that plasma membrane, working as a great mediator of the plant pathogen interaction, shows changing proteome involved in calcium and lipid signalling, transport, redox homeostasis and vesicle trafficking at the time of immune signaling [4]. The expression of these optimal responses are not always stress specific but a partially overlapping set of responses are also activated for combined biotic and abiotic stresses (Figure 1). There are several commonalities in the biotic and abiotic stress responses in plants [5]. A good number of field study explain that the outcome of this abiotic and pathogen interaction varies depending on the severity of each stress. Severe abiotic stresses cause leakage of cellular nutrients into apoplast which facilitates successful pathogen infection [6]. On the contrary, early exposure of environmental stresses stimulates ROS and various phytohormones which in turn suppress the effect of pathogens. In the case of second story, pathogen infected plant evolves abiotic stress resistance by various mechanisms [6]. Even pathogen-derived molecules show great potentiality to induce plant immune responses and can also help in coinciding simultaneous stress treatment. These interactions between biotic and abiotic stresses are bound to increase in future because of ever changing climatic factors effecting abiotic stresses and expanding host range of pathogens with increased virulent strain development. Till date, molecular mechanisms involved in separate biotic and abiotic stresses are revealed independently whereas molecular and genetic basis of convergence point between both the stresses remain rudimentary.

Though the interaction between abiotic and biotic factors in plants were enlightened through reckoning of information from specific single stress responses, yet the 'omic' approaches exposed to a combination of both stresses simultaneously remain elusive. Plants have adapted tailored strategies to fight various abiotic stresses along with pathogen attack and, it is expected that integrated signal transduction events including hormone signals, receptors and transcription factors play a significant role in it. But knowledge on role of these signalling mechanisms under stress combination is very little till date. Therefore, such studies on simultaneous stresses are the need of the hour to understand these phenomena aided by transcriptome, metabolome and proteomic approaches. It is also reported that some kind of abiotic stresses regulate photosynthetic efficiency too which in turn regulates susceptibility of pathogen attacks [7]. Gupta et al. have recently discussed that molecules like polyamines having a proclaimed role in plant growth and development, also have distinct contribution in both abiotic and biotic stresses [8]. Moreover, generation of ROS, one of the principle incident, is common in case of biotic and abiotic stress responses. Emerging data resulting from transcriptome analysis with DNA microarray technology strongly support not only the existence of such crosstalk between signalling network but also give evidences of presence of overlapping suites of genes involved in it [9]. Narusaka et al. showed that heavy metal ($CuSO_4$) stress and incompatible necrotrophic pathogen infection reveal significant overlap between biotic and abiotic stresses [10]. Mitogen activated protein kinase (MAPK/MPK) cascades also play a crucial role in stress signaling crosstalk and in hormone responses that include ROS signalling [11].

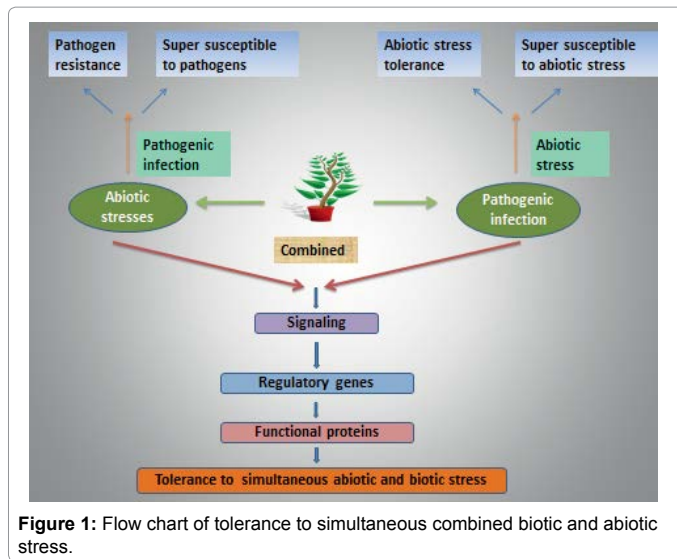
Hence an anticipation of having a significant role of above mentioned molecules and pathways in combined stress condition opens a gate of broad research area. A number of biochemical approaches along with the study of gene expression can be done to decipher the role of various signalling molecules (such as ROS) and to identify the genes and metabolic pathways involved in it. A functional genomic approach such as virus-induced gene silencing in association with high throughput stress effect quantification methods in plants can also put a remarkable acceleration to this study [12]. Especially in this post-genomic era, studies on novel mechanism involving micro RNA, chromatin remodelling and genomic DNA modification are like icing on the cake revealing the complex and sophisticated regulation of gene

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Received April 25, 2015; Accepted May 05, 2015; Published May 10, 2015

Citation: Gupta B, Bhaumik U, Sengupta A, Chakraborty M, Saha J et al. (2015) Plant Immunity: An Enigma during Biotic and Abiotic Stress. J Plant Biochem Physiol 3: e128. doi:10.4172/2329-9029.1000e128

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expression in different stress conditions. So the discussion ends with the conclusion that simultaneous occurrence of abiotic and biotic stresses rather than a single condition is more lethal to crops causing low yield. This knowledge is leading the world of plant science to a great start and is aimed at developing transgenic crops and plants with enhanced tolerance to naturally occurring combined environmental conditions.

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