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HEAT SHOCK PROTEINS: CLASSIFICATION, FUNCTIONS AND EXPRESSIONS IN PLANTS DURING ENVIRONMENTAL STRESSES

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ABSTRACT

Heat shock proteins assist in folding proteins that is a basic cellular constituent responsible for various crucial functions including protein assembly, transportation, folding in normal conditions and denaturation of proteins in stress and in other cellular function. Abiotic factors like increased temperature, drought and salinity negatively affect reproduction and survival of plants. Plants (HSPs), as chaperones, have crucial part in conversing biotic and abiotic stress tolerance. Plants react towards critical changes through biochemical, growth, and physiological mechanisms included expression of stress-reactive proteins, which are regulated by interconnected signaling cascades of transcription factors including heat stress TFs.

Keywords: HSPs, heat shock factors, stress response, resistance proteins, PCD.

INTRODUCTION

HSPs proteins are found mostly in every cell from prokaryotes to eukaryotes. HSPs have been comprehensively studied in animals and humans. Recently their role in plants was thoroughly studied. HSPs were described as a result of heat shock conditions, but now get activate by various stresses like Ultraviolet light, cold, wound healing, drought, salinity and pathogenic infections (Lindquist et al., 1988). The term “heat shock protein” is now incorrect because HSPs are not expressed only under high temperature, also expressed under other stresses. HSPs are essential in maintaining balanced cell internal conditions under optimum and damaged growth conditions about in all living cells (Wang et al., 2004). Many types of HSPs are function as chaperon proteins that assist in folding upon folding of three dimensional proteins or proteins that get denatured by stress within the cell. Therefore many folding proteins are considered as HSPs due to their folding nature in response to stress (Wang et al., 2004). It also functions in the stability of cellular proteins and have role in protein refolding under diverse environmental conditions (Huttner et al., 2012). HSPs that respond to stresses mainly located in cytoplasm. It is suggested that HSPs have dynamic and diversified role in protein homeostasis because of its ubiquitous nature in living cell. HSPs are generally found in fungi plants and animals, HSP transcripts expression were upregulate at extreme temperature (Lindquist et al., 1986). Under normal physiological conditions HSPs are localized in the cytoplasm but translocate to the nucleus under stresses.

Structure and Classification of Plant HSFs and HSPs

Expression level of HSPs regulated specifically by transcription factors called heat shock factors. HSFs usually occur as inactive proteins and share a preserved structure. The

basic structural domain of HSF consists of N-terminal binding site of DNA (DBD) that is characterized by central helical motif binds to heat shock elements. HSE at the target promoter thus sequentially initiates gene transcription under stress conditions (Scharf et al., 2012).

In comparison with other vertebrates, plants HSF consist of a large amount of HSF members originated from a complex plant-specific superfamily and are found in a wide range of species. HSFs are characterized into three classes, *HsfA*, *B*, and *C* in plants (Kotak et al., 2004). The HRA/B regions of *HsfBs* have dense region associated or same as all told non-plant. However category Hsf A associated C have an extended HRA/B region that consists of twenty one and seven (*HsfCs*) because of an insertion of organic compound residues between the HR-A and HR-B components respectively (Scharf et al., 2012). The carboxyl end activation domains of HSFs are represented by short amide motifs (AHA motifs) that are essentials because the accelerator in several studies (Döring et al., 2000).

Various types of HSPs have been studied in almost all living cells (Bharti et al., 2002). All HSPs have some distinct characteristics including the presence of heat-shock domain at C-terminal. Plant Hsps are classified into five types on basis of approximate molecular weights. Generally plant HSPs consist of N and C-terminal end that is nuclear binding domain region –I,-II and a middle one which is characterized by an amino end and followed by carboxyl-end.

HSP90

This type is one of highly expressed proteins in the plant cells, where its content is 1–2% of total protein levels in cytoplasm (Prasinos et al., 2005) described that HSPs are cytosolic proteins in eukaryotes having conserved amino acid sequences. The basic eukaryotic molecule *HSP90* assist the proper folding and maturation of other protein substrates, various among them are main activators of biological circuits. *HSP90s* has central position in numerous pathways regulating growth, so it is a concern of study in various fields (García-Cardena et al., 1998).

HSP90 consists of three domains: N terminal with ATP-binding motif, middle and C-terminal end. CTD is responsible for HSP90 dimer formation. HSP90 function as chaperones in dimers regulated by ATP (Wayne et al., 2011). HSP90 participate with HSP70 and act by interacting with unit of chaperons, that includes *Hip* (interacting proteins) and *Hop* (organizing proteins). *Hsp90s* act as mediator in plant abiotic stress signal pathways (Liu et al., 2006) but the mechanisms still are unclear.

HSP70s

HSP70 is the most widely studied member found in all plants and animals (Boorstein et al., 1994). HSP70 called as on basis of molecular weight 70kDa and act as molecular chaperons. HSP70 perform necessary functions in various life forms and its homolog located in cell component such as chloroplast, endoplasmic reticulum, mitochondria and cytosol. HSP70 function as basic chaperon that it assists in folding of regulatory proteins prevent aggregation of denatured proteins (Tompa et al., 2010).

When exposed to elevated temperature it triggers cellular response which is evident in almost all kingdoms of life. This causes the enhanced expression of multigene members that can encode molecular chaperones (Hartl et al., 2009). HSP70 respond by binding to hydrophobic region on surface of semi folded proteins and maintain low protein concentration (Mayer et al., 2005). While *HSP70s* assembled during heat shock, their essential cognates (HSC70) were expressed due to their involvement in maintaining proteostasis.

Small Heat Shock Proteins (SHSPs)

The sHSPs are unique and evolutionally preserved having molecular weight ranging from 12 to 42 k Dalton. HSP20 named so as MW are in the range of 15–22 kDa. Members of this family have distinct 80–100 long amino acid sequences which are not found in other proteins of HSP family. Their function does not depend on ATP and bind to the foreign protein substrates in a co-operative manner. These proteins have several characteristics including the degradation of the proteins that do not have ability to refold (Reddy et al., 2015). The sHSPs cannot refold foreign proteins, but they can bind to semi folded or damaged substrate part thus prevents unfolding of stable protein accumulation (Sun et al., 2002). On basis of cellular location, functions and sequence similarity, sHSP established a more diverse family in comparison to other HSPs. The studies showed sHSP to be localized in the nucleus and other cellular organelles (Waters et al., 2013). The protective role of sHSP against a wide variety of stresses has been rapidly studied in different crop species including *Oryza sativa*, *Solanum lycopersicum* (Yu et al., 2016), *Glycine max* (LopesCaitar et al., 2013), *Triticum aestivum* (Muthusamy et al., 2017), *Zea mays* (Hu et al., 2010).

Regulation of HSPs

In the plant genome, approximately 7% of the coding regions comprise TFs and mostly are large gene families as compared to animals and yeasts, such as Hsfs (Udvardi et al., 2007). In various critical conditions like high temperature, heat shock factors get activated and move in the cytosol thus undergo trimer formation. These HSF are phosphorylated in signaling cascades and transfer to nucleus where they bind with corresponding cis-elements which is present in upstream part of HSP gene. The mRNA is translated into protein thus increased expressions of HSPs in the cytoplasm (Fig. 1) (Young et al., 2010). The HSR in plants and mammals is coordinated by a set of highly conserved proteins known as HSPs, and expression of this protein is controlled by HSFs (Snyman et al., 2008). Increased number of HSFs in plants helps them to tolerate various forms of external changes during their lifespan. There are almost fifteen known and studied HSFs in *Arabidopsis thaliana* and greater than 21 in tomato (Sly) and all are thought to perform significant functions in stress responses. In Sly two *Hsf* A2 and B1, are heat inducible but the expression of HsFA2 and HsFB1 is controlled by HsFA1, which is regarded as the key activator of the HSR (Mishra et al., 2002). HsFA2 called as “**work horse**” in stress response and is the major HSF during a plant exposed to increase temperature (Mishra et al., 2002).

Abiotic Stress: Signaling Pathways

Plants are subjected to various biotic and abiotic factors, which adversely affect its survival and growth (Mittler et al., 2006). To cope with these conditions, plants have evolved various defense signal strategies that are anatomical (Banon et al., 2004), physical (Wahid et al., 2007) and physiological (Morales et al., 2003). Plants also respond to stress situations by controlling gene expression at the molecular level, enable plants to ensure their existence in critical situations. At molecular and cellular levels, abiotic stress response is directed through signaling pathways that consists of primary and secondary messengers. When exposed to stress the signals get initiated that sequentially activate signaling pathways and phosphorylate transcription factors in signaling pathways (Vij et al., 2007). As cell exposed to stress, receptors like kinases, G-protein-coupled receptors, and regulatory molecules receive those signals which then activates the secondary molecules like calcium thus leads to activation of signaling pathways e-g MAP, CDP, SOS3/protein kinases, TF and stress responsive genes. Components of MAP kinase cascades are the converging molecules in abiotic stress signaling

pathways. Several plants are genetically engineered with stress tolerance traits for proper insights and studies of signaling pathways (Akpinar et al., 2012). The significant regulation and the developments succeeding sections briefly describes the salient components like ROS, Ca⁺ and MAP kinase in signaling cascades in plants (Gong et al., 2013).

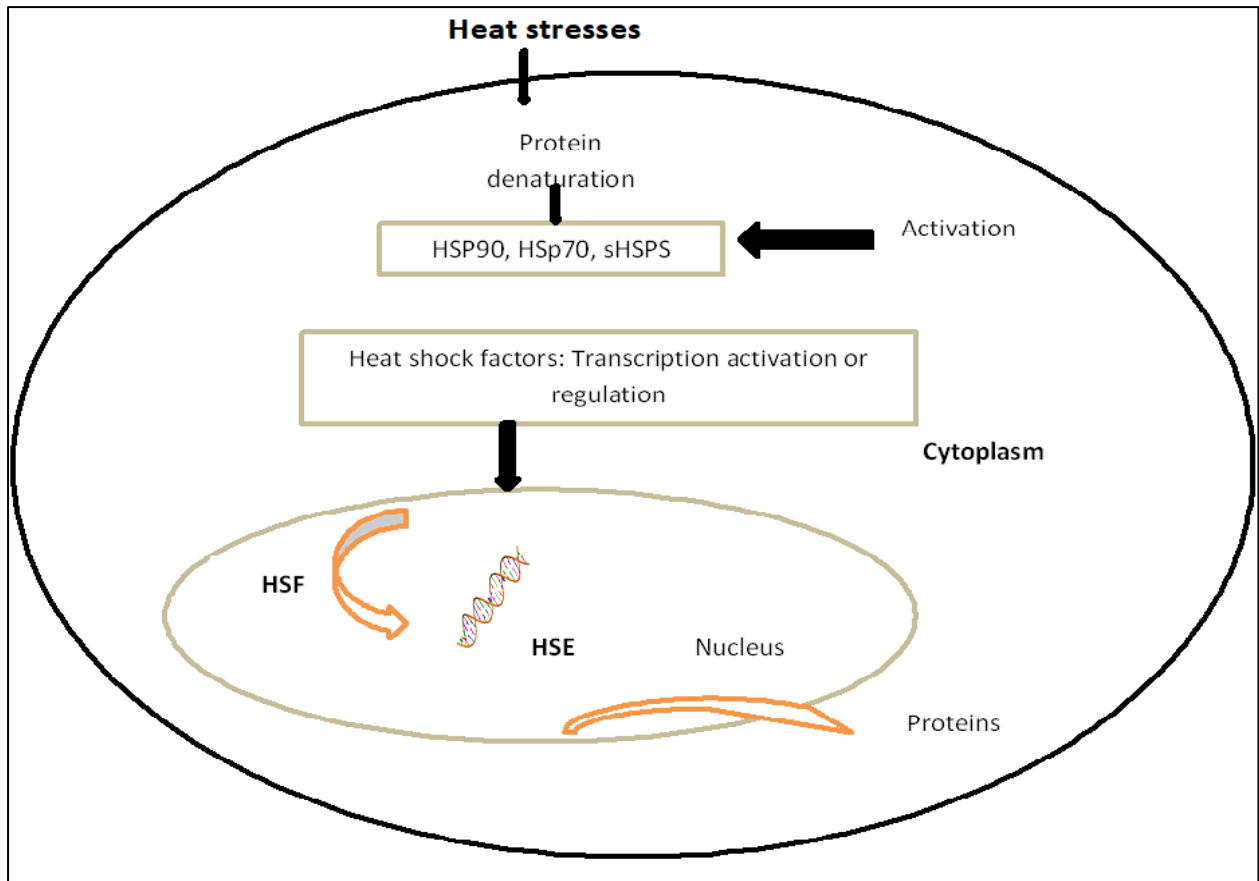


Figure 1: Regulation of HSP in plant cells.

Functional Role of HSPs in Abiotic and Biotic Stress

Abiotic Stress

Abiotic stresses are critical changes like extreme temperatures, drought, ionic imbalance due to salinity, which hinder plants growth, existence, and quality. Nowadays environmental changes have further worsened the situation. The population of world by the year 2050 will be expected ~ 9 billion (Reguera, M et al., 2012), so in such conditions stress

resistance plants should be cultivated by using transgenic and omics methods. A number of studies conducted by various scientists reveal the role of HSPs under different stresses in several plant species, such as *Arabidopsis*, *Oryza sativa*, *Glycine max*, *Populus* and *Vitis vinifera* and exact functional mechanisms of HSPs in plant stress response have recently become study of concern (Yer et al., 2016).

Drought is the mostly studied adverse environmental factor that produces drastic affects on growth of many crops in climatic change conditions. It negatively influences plant

morphology, physiology and molecular mechanisms. This also causes decline in photosynthetic rate, transport of mineral nutrient leading to starvation, imbalance of ion and hormones. Water deficiency affects the quantity and quality of proteins synthesis and as a result, HSPs also get influenced. The expression pattern of HSPs was studied at genome level in the seedling of upland rice plants. expression of HSP70 was elevated during drought condition (Reddy et al., 2014). HSP gene exhibited upregulation in transgenic *Arabidopsis* and *Saccharum officinarum* during drought condition (Yer et al., 2016). Effects of combined stress conditions were studied in both irrigated and non-irrigated cotton and showed that transcripts of HSP accumulated in non-irrigated type. HSP genes expressed at higher rate in drought-tolerant plants in comparison to sensitive as *Cicer arietinum*. The same expression observed in *Populus* plants (Xu et al., 2010). HSP17.7 showed drought tolerance in genetically engineered rice crops (Agrawal et al., 2016).

Nearly 50% half of the world irrigated land, is affected by salinity. Studies showed that many HSPs were induced and up-regulated under salinity like *HSP70* in rice seedlings (Ngara et al., 2014) and *HSP70*, their subtypes -9,-12,-33 in *Populus* (Manaa et al., 2011). Furthermore, *HSP40* in *Oryza sativa* (Wang et al., 2018) and in poplar almost all types of HSPs were up-regulated against salinity (Manaa et al., 2011). Different HSPs in *Arabidopsis* like *HSP 90* (Xu, J et al., 2013), *HSP100* and small HSPs in *Oryza sativa* (Muthusamy et al., 2016) showed tolerance against salinity. Thus studies exhibited that response of HSPs towards salinity stress is also genotype and specie dependent.

High environmental temperature affects almost all organisms and especially plants, because they are sessile and more exposed to change in climatic conditions (Bita et al., 2013). Temperature stress is most widely studied and affected among plants. Increased temperature has affected the protein folding, arrangements and cause denaturation. As a result of high temperature production of free radicals that is taken as secondary stress (Fragkoste fanakis et al., 2015). Free radicals or ROS act as stress signal in plants and produce HSR and other stress responsive proteins. The interactions between HSPs and ROS have been widely studied in many plant species (Driedonks et al., 2015).

A number of studies have identified the activation of heat stress genes under high temperature stress. Hsps of different molecular weight showed diverse expressions under heat stress conditions. *HSP90.1* has been reported in *Oryza sativa* and *Arabidopsis* (Prasad et al., 2010) and its all classes (A, B, and C) in *Glycine max* (Xu et al., 2013). Under normal conditions, regulation levels of all HSPs were monitored and it negatively regulates HSF (Yamada et al., 2007). Under heat effects the mostly reported types are *HSP70* and *HSP60* chaperonin families, which keep protein in proper folding positions using ATP as a source of energy (Hartl et al., 2011). *HSP70* located in cytosol was involved in heat tolerance in *Arabidopsis* (Jungkunz et al., 2011).

High expression of *HSP70s* have been investigated under high temperature in a number of plant crops; such as cotton (Song et al., 2018), vegetables like, tomato, potato; ornamental (Huang et al., 2019) (Liu et al., 2018) grain such as wheat (Wu et al., 2018). In normal condition as well as under high-temperature and drought situations (combine effect) different studies have demonstrated the expression of *HSP60* present in chloroplast. It has a role in Rubisco assembly, chloroplast development and protection (Xu et al., 2010). sHSPs and *HSP40* were up-regulated under high-temperature in many plant species (Huang et al., 2019). Different types of HSPs respond to abiotic stresses in different ways and their expression pattern were studied in different species with the help of biomolecular techniques illustrated in table 1. The activation of plant *HSP20* during stress is directly related to cellular Ca^{2+} concentration. Elevated level of Ca^{2+} activates calmodulins and/or MAP kinases and followed basic signal pathway. This activation could help to identify certain regulatroy elements present in the promoter region, inducing its expression level (Swindell et al., 2007).

Biotic Stress

Recently sHSPs have been studied in plant biotic stresses. HSP20s known as stress responsive proteins, and generally functions are same as chaperons. Their participation has been reported to against the crop pathogens most important among them are viruses, bacteria and nematodes. Some genetic basis has explained that these folding proteins play a crucial role in plant defense syste. One hypothesis is that these chaperones are involved in accumulation of various resistance proteins, and so for the defense signal cascade coordination. However there is still need the better explanation of HSP20 cascade mechanism and function in plants biotic stress (Lopes-Caitar et al., 2016). Biotic factors like pathogens that are viruses, bacteria, fungi and other micro-organisms also affects plant quality, growth and development. These microorganisms attack their hosts and deprive of their nutrition that in severe cases death of plants. They cause huge pre- and post-harvest losses of crop plants. In comparison with plants animals have their adaptive defense mechanism which helps them to cope with critical changes such as foreign particles and can recognized the past infections, while plants have only innate immunity. Still plants try to adopt advanced strategies against these stresses (Singla et al., 2016). These defense strategies are incorporated in the plant's genome, which can code a large number of resistance genes. This is one of the adaptive mechanism plants adapt through regulation of HSPs.

Plant productivity got affected by the pathogenic bacteria, one of the important factors among biotic stresses. Bacteria harm their host by entering xylem vessel blocking supply of water and other nutrients resulting in wilting and browning of plants. Plants react to pathogenic bacteria by using their first line defense pattern pathogen-associated resistance. Plants also have evolved innate immunity that is Effector-triggered immunity. When pathogenic bacteria attacks plants this immunity get triggers R-protein that translate through resistance gene, R protein can identify the pathogen effectors thus effective mechanism initiate against the invaders specially bacteria as explained in Fig.2 (Dodds et al., 2010).

HSPs have role against virulent bacteria strains as studied in different species of plants against some bacterial infections. *Ralstonia solanacearum* causes infection against *Nicotiana tabaccum* sHSP class *HSP17* was initiated and accumulated in virulent strain (Maimbo et al., 2007). Pathogenesis related protein expressed highly after infection even in avirulent state. HSP20 show down-regulation in presence of PR proteins even in virulent state of non-pathogenic bacteria. In contrast, HSP90 has a positive interaction with above mentioned pathogen in tobacco. In Arabidopsis, small HSPs classes were studied and their expression pattern was down-regulated (Bricchi et al., 2012).

Later studies have explored the downregulated expression in Arabidopsis was due to hormone that is salicylic acid as it also get affected by pathogens to cause infection (Pavlova et al., 2009). Viruses need living machinery of plants or neighboring cell for the spread of their infection (Rybicki et al., 2015).

The expressions of HSP depend on the pathogen strains as well as on the time after inoculation.

In some cases, viruses target the expression of HSPs and their subcellular targeting in cell to develop an infection in plants. Viruses infect the rice plants through pathogen Rice strip virus (RSV) that is source of other diseases that cause rigidity in various plant organs like stem and leaves along with strips along veins. Various investigations revealed the relation of HSP20 with pathogen Rice strip virus in which virus cause host infectivity at cellular level. Some heat shock proteins including HSP70 have positive interaction with RSV, mean if HSP70 silenced it lowers the viral infection (Bolhassani et al., 2019).

Table 1: Expressions of different types of HSPs in abiotic stresses.

Plants (Different species)	Types of HSPs	Stresses	Expression level	References
<i>Arabidopsis</i>	HSP70	Cold, heat, drought stress	upregulated	(Yer et al., 2018; Kim et al., 2013)
	HSP90	Salinity, heat stress		(Mishra et al., 2016; Xu et al., 2010)
	HSP17.6	Oxidative stress		(Scarpeci et al., 2008)
Cotton <i>Gossypium Hirsutum</i>	All Hsps	Drought stress	upregulated	(Augustine et al., 2015)
Wheat <i>Triticum</i>	HSP70	Heat, cold stress	Upregulated	(Id, H.W et al., 2018)
	All HSPs	Salt stress		(Sobhanian et al., 2011; Wang et al., 2008)
	HSP 90	Cold stress	Down regulated upregulated	Hlavackova et al., 2013) (Chauhan et al., 2012)
	sHSPs HSp21 HSP26	Cold stress Heat stress		
Rice <i>Oryza sativa</i>	HSP70	Salinity and drought stress	upregulated	(Ngara et al., 2016)
Tobacco <i>Nicotiana tabacum</i>	HSP70	cold, drought stress	Upregulated	(Jin, Y et al., 2011; Ono, K et al., 2001)
Maize <i>Zea mays</i>	HSP26	Drought stress	Upregulated	(Benesova et al., 2012)
Tomato <i>Solanum lycopersicum</i>	HSP70	Heat, cold stress	UpRegulated	(Duck et al., 1994)
	HSP20	heat	Up/downregulated	(Yu, J et al., 2016)
Potato <i>Solanum tuberosum</i>	HSP70	Heat stress	upregulated	(Liu, J et al., 2018)

In previous studies, interesting report had pointed out another pathogen virus “Tomato Yellow leaf curl Virus have role in regulating programmed cell death by deactivating SlyHSF2. As a result of this inactivation, HSP90 gene is silenced which reduced the programmed cell death and plant remain in healthy conditions for long time after viral replication and infection.

Furthermore, the “Root knot nematode” coat protein localization from the cytoplasm to the nucleus was linked with *HSP70* of *S. lycopersicum*. The expression of *HSP70* get silenced in the *Solanum lycopersicum* to control virus attack. Contrarily to this *HSP90* downregulation promoted viral infection (Gorovits et al., 2017). Latest study on Potato virus Y in potato heat-tolerant and sensitive plants exhibited that HSPs expression get induce in

both extreme temperature conditions. Similarly, the expression of PR (pathogen related) proteins was also highly suppressed the viral infection (Makarova et al., 2018). Resistance was developed against viral infection in *Cytosin peptidemycin* for controlling Rice Black Streaked Dwarf Virus". various inhibitory enzymes, defense genes and HSP also upregulate to control the virus infection (Yu L et al., 2018).

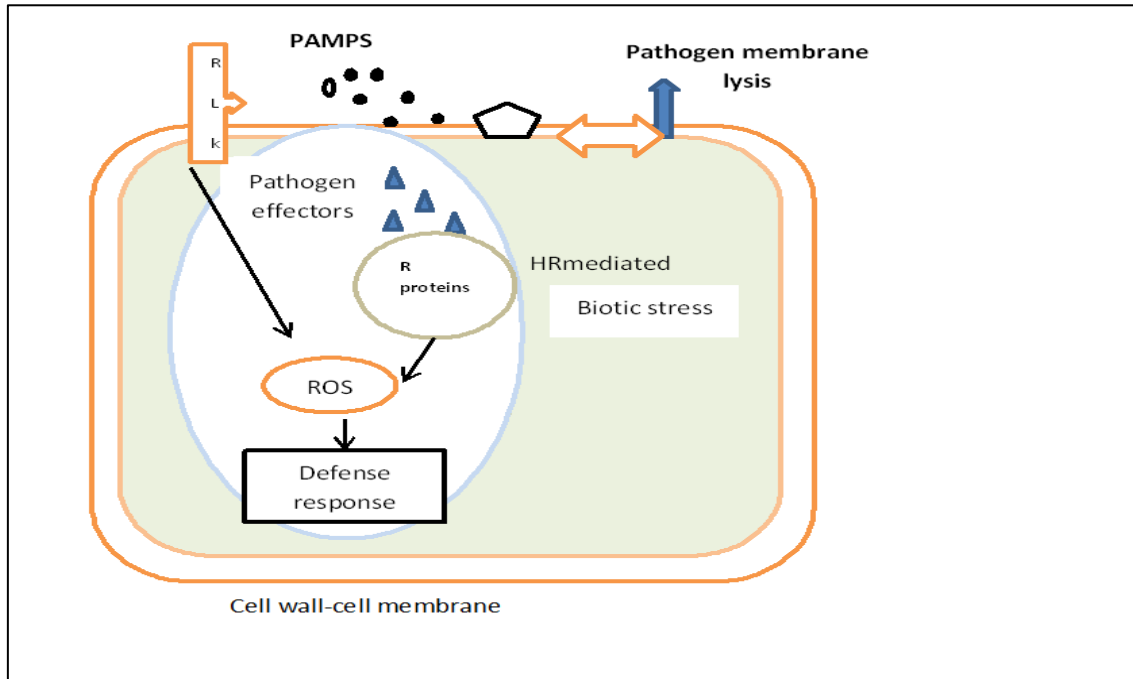


Figure 2: HR mediated biotic stress, representation of hypersensitive response. Plants respond to pathogen by triggering pathogen-associated molecular patterns (PAMPs).

Nematodes species such as the root-knot nematode cyst nematodes and root-lesion nematode cause more harm to agriculture. HSPs are involved in resistance to phyto-nematodes (Li et al., 2015). Studies analyzed the sequenced data of *Gossypium* after pathogen *Rotylenchulus reniformis* attack at interval of 3 to almost 12 days. About 23 HSPs and 41 HSPs were induced in susceptible genotypes and resistant genotypes respectively. Pathogens attack the plants causing root necrosis, nutrients and water deficiency. In response to biotic stress position of cis-acting elements in the upstream area of Hsp gene got activated but it depends on the distance from the site of transcription. HSP17.7, in exogenously produced tobacco showed that HSE were activated within 83 base pairs (bp) but the expression upregulates beyond 83 bp (Escobar et al., 2003). This was further confirmed by study in HSP17.6 and HSP18.6, where they expressed within 108 and 49 bps respectively (Barcala et al., 2008). The research shows that the HSE and other regulatory motif regions that also interact with TFs and influenced the expression of sHSP in biotic stresses. HSP90 down regulated in tomatoes showed tolerance to nematodes infection (Bhattarai et al., 2007). On the other hand, HSP90, stimulate the infection caused by nematodes.

CONCLUSION

HSPs have ubiquitous nature and role in maintaining the protein homeostasis and stability of cell. HSPs have different types in plants and other species that perform different functions. Due to climate change when cell exposed to biotic and abiotic stresses, they affect plants growth and development or eventually leads to death. When expose to stress plants

HSPs respond in different ways. Heat stress initially acts on the quaternary structure of protein thus affecting its folding and denatured protein. Different functional genomic studies have been performed that identified various components under different stresses. Plants respond to stress after transcription regulation of HSPs at molecular level. Different signaling passages get activated in response to stress which phosphorylates other transcription factors and also heat shock factors that transcribed into proteins thus express under stress in different ways. Multiple number of genes affected under stress conditions thus it imply there is not a single marker that get functional against stress. HSPs have crucial role in reaction of stress and can be used in development of transgenic plant. In controlled experimental conditions in laboratory HSPs studies were performed on model plants. HSPs have widely distributed types and each of them have significant role across different interconnected pathways. The response of HSP is genotypical specifically at tissue level. The expression study analysis of HSP types in various stresses were up and down regulated. There is a crosstalk study between various hormonal pathways, but its exact nature during simultaneous biotic and abiotic stress still need to be identified. There is no definite set of marker get identified that will predict the tolerance mechanism against stress Researchers should identified exact markers with a definite degree of confirmation. There is need to understand the exact mechanism how HSPs participate in sensing stress signals transduction, and transcriptional regulations of several stress genes. Although much work has been conducted on plant abiotic stress and its relation with signaling pathways still there is need of efforts in modern molecular proteomics and transcriptomic tools, to get more perceptions about molecular mechanism(s) of basic various signaling pathways.

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