Journal of King Saud University – Science (2011) **23**, 139–150

King Saud University
Journal of King Saud University – Science
www.ksu.edu.sa
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ORIGINAL ARTICLE

Plant heat-shock proteins: A mini review

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Received 21 April 2010; accepted 29 June 2010

KEYWORDS
Higher plants;
Crop plants;
Chaperones;
Heat-shock proteins;
Transcription factors;
Stress;
Heat stress;
Heat tolerance

Abstract Plants as sessile organisms are exposed to persistently changing stress factors. The primary stresses such as drought, salinity, cold and hot temperatures and chemicals are interconnected in their effects on plants. These factors cause damage to the plant cell and lead to secondary stresses such as osmotic and oxidative stresses. Plants cannot avoid the exposure to these factors but adapt morphologically and physiologically by some other mechanisms. Almost all stresses induce the production of a group of proteins called heat-shock proteins (Hsps) or stress-induced proteins. The induction of transcription of these proteins is a common phenomenon in all living things. These proteins are grouped in plants into five classes according to their approximate molecular weight: (1) Hsp100, (2) Hsp90, (3) Hsp70, (4) Hsp60 and (5) small heat-shock proteins (sHsps). Higher plants have at least 20 sHsps and there might be 40 kinds of these sHsps in one plant species. It is believed that this diversification of these proteins reflects an adaptation to tolerate the heat stress. Transcription of heat-shock protein genes is controlled by regulatory proteins called heat stress transcription factors (Hsfs). Plants show at least 21 Hsfs with each one having its role in regulation, but they also cooperate in all phases of periodical heat stress responses (triggering, maintenance and recovery). There are more than 52 plant species (including crop ones) that have been genetically engineered for different traits such as yield, herbicide and insecticide resistance and some metabolic changes.

In conclusion, major heat-shock proteins have some kind of related roles in solving the problem of misfolding and aggregation, as well as their role as chaperones.

1. Introduction

Plants interact with not only climatic factors (such as irradiation, temperature, and drought) but also soil factors (such as salinity) and biotic factors (such as herbivores and pathogens). All these factors put the plant under interrelated stresses (Levitt, 1980). Moreover, daily sudden changes in the temperature and the presence of heavy metals, toxins, and oxidants due to human activities could result in extra stresses on plants (Vierling, 1991).

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Peer review under responsibility of King Saud University.
doi:10.1016/j.jksus.2010.06.022

Production and hosting by Elsevier

Basic Stresses such as drought, salinity, temperature, and chemical pollutants are simultaneously acting on the plants causing cell injury and producing secondary stresses such as osmotic and oxidative ones (Wang et al., 2003). Plants could not change their sites to avoid such stresses, but have different ways and morphological adaptations to tolerate these stresses. Some of these are, the dominance of sporophyte that embraces the sensitive gametophyte, the presence of epidermis with stomata for gases exchange, the formation of dormant organs, and the presence of conducting tissues for long distant transport. Other ways of defense at the molecular level are very important for the survival and growth of plants. Plants show a series of molecular responses to these stresses. The physiological processing basis for these molecular responses will not be covered here as it has been reviewed in depth lately (Shao et al., 2007a).

Heat stress as well as other stresses can trigger some mechanisms of defense such as the obvious gene expression that was not expressed under "normal" conditions (Morimoto, 1993; Feder, 2006). In fact, this response to stresses on the molecular level is found in all living things, especially the sudden changes in genotypic expression resulting in an increase in the synthesis of protein groups. These groups are called "heat-shock proteins" (Hsps), "Stress-induced proteins" or "Stress proteins" (Lindquist and Crig, 1988; Morimoto et al., 1994; Gupta et al., 2010). Almost all kinds of stresses induce gene expression and synthesis of heat-shock proteins in cells that are subjected to stress (Feige et al., 1996; De Maio, 1999). In *Arabidopsis* and some other plant species low temperature, osmotic, salinity, oxidative, desiccation, high intensity irradiations, wounding, and heavy metals stresses were found to induce the synthesis of Hsps (Swindell et al., 2007). However, stressing agents lead to an immediate block of every important metabolic process, including DNA replication, transcription, mRNA export, and translation, until the cells recover (Biamonti and Caceres, 2009).

It was known a long time ago that the most damage to crop plants in fields occurs when two or more stresses are prevailing (Mittler, 2006). Hence, in order to study the plant tolerance, it is very necessary to mimic the natural conditions in a specific area. Most recent studies indicate that the plant responses to two or more factors are unique and differ from the response to one factor only. For example, subjecting the plants to drought only leads to high content of proline, but subjecting the same species to drought combined with high temperature leads to high content of sucrose and other sugars, but not proline (Rizhsky et al., 2004). Hence, Mittler (2006) studying all prevailing abiotic factor;[s has suggested to treat this situation as a new stress condition that he called "Stress combination". The mechanisms of plant tolerance to a combination of diverse stress conditions, particularly those that mimic the field environment, have gained interest particularly for the biotechnologists (Chen and Zhu, 2004; Al-Babili and Beyer, 2005; Luo et al., 2005; Munns, 2005; Shao et al., 2007b).

Heat stress – high temperature – affects the metabolism and structure of plants, especially cell membranes and many basic physiological processes such as photosynthesis, respiration, and water relations (Wahid et al., 2007). On the molecular level, this effect of heat stress reflects the temperature dependence of Michaelis–Menton constant (K_m) of every enzyme participating in the process (Mitra and Bhatia, 2008). Plants must cope with heat stress for survival, so they developed different mechanisms including the maintenance of cell membrane stability, capturing the reactive oxygen species (ROS), synthesis of antioxidants, accumulation and osmoregulation of osmoticum, induction of some kinases that respond to stress, Ca-dependent kinase proteins, and enhancing the transcription and signal transfer of chaperones (Wahid et al., 2007).

The induction and synthesis of heat-shock proteins due to high temperature exposure are common phenomena in all living organisms from bacteria to human beings (Parsell and Lindquist, 1993; Vierling, 1991; Gupta et al., 2010). It seems that the synthesis of these proteins is costly energy wise that is reflected on the yield of the organism.

2. Heat-shock proteins classification

Historically, the observation of the Italian Scientist R. Ritossa on gene expression of the puffing in the chromosomes of *Drosophila melanogaster* after exposure to heat was the start of discovering the heat-shock proteins. The result was an increase in protein synthesis that occurred also by the use of other stress factors such as azide, 2,4-dinitrophenol, and salicylate (Ritossa, 1962). After that report, these proteins were identified and named as heat-shock protein (Hsp) (Tissieres et al., 1974). Researchers started studying the relationship of the synthesis of these proteins with the tolerance of stresses. On the other hand, it was reported that the induction of Hsp synthesis in *Glycine max* var. Wayne seedlings is accompanied by the reduction of other proteins synthesis after the exposure of such seedlings to heat shock (from 28 to 45 °C) for 10 min (longer periods killed the seedlings). Moreover, subjecting the seedlings to flashes of heat at 40 °C before exposing them to higher temperatures (45 °C) protects the seedlings (Lin et al., 1984).

Many types of Hsps have been identified in almost all organisms (Bharti and Nover, 2002). All Hsps are characterized by the presence of a carboxylic terminal called heat-shock domain (Helm et al., 1993). Heat-shock proteins having molecular weights ranging from 10 to 200 KD are characterized as chaperones where they participate in the induction of the signal during heat stress (Schöffl et al. 1999). Some researchers concluded that although there are some evidences for the genetic expression phenomenon in some specific cases, there are no final and conclusive evidence that this is what is happening in natural environment (Feder and Hofmann, 1999).

Heat-shock proteins of archaea have been classified on the basis of their approximate molecular weight into: (1) Heat-shock proteins 100 KD, i.e. Hsp100, (2) Hsp90, (3) Hsp70, (4) Hsp60, and small heat-shock proteins (sHsps) where the molecular weight ranges from 15 to 42 KD (Trent, 1996). These sHsps are usually a complex of small subunits where the molecular weight ranges from 200 to 800 KD (Kim et al., 1998).

In eukaryotic organisms, one of the reviews concluded that the principle heat-shock proteins of human beings do not differ from those of bacteria except for the presence of Hsp33 (Schlesinger, 1990). Later, the Hsps of human beings were grouped into five families (Kregel, 2002) as in Table 1.

In plants, general reviews (Schlesinger, 1990; Schöffl et al., 1998; Kotak et al., 2007) suggested five principal classes of Hsps characterized by their activities as molecular chaperones according to their approximate molecular weight: (1) Hsp100, (2) Hsp90, (3) Hsp70, (4) Hsp60, and (5) small heat-shock