Heat stress response in plants: a complex game with chaperones and more than twenty heat stress transcription factors

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Compared to the overall multiplicity of more than 20 plant Hsfs, detailed analyses are mainly restricted to tomato and Arabidopsis and to three important representatives of the family (Hsfs A1, A2 and B1). The three Hsfs represent examples of striking functional diversification specialized for the three phases of the heat stress (hs) response (triggering, maintenance and recovery). This is best illustrated for the tomato Hsf system: (i) HsfA1a is the master regulator responsible for hs-induced gene expression including synthesis of HsfA2 and HsfB1. It is indispensable for the development of thermotolerance. (ii) Although functionally equivalent to HsfA1a, HsfA2 is exclusively found after hs induction and represents the dominant Hsf, the “working horse” of the hs response in plants subjected to repeated cycles of hs and recovery in a hot summer period. Tomato HsfA2 is tightly integrated into a network of interacting proteins (HsfA1a, Hsp17-CII, Hsp17-CI) influencing its activity and intracellular distribution. (iii) Because of structural peculiarities, HsfB1 acts as coregulator enhancing the activity of HsfA1a and/or HsfA2. But in addition, it cooperates with yet to be identified other transcription factors in maintaining and/or restoring housekeeping gene expression.


1. Introduction

1.1 Plant stress response

During evolution, the origin of terrestrial plants (about 400 million years ago) required special adaptations to rapidly changing environmental conditions (Levitt 1980). Examples for these organismic adaptations are:

- The predominant role of the sporophyte in the life cycle of plants with the sensitive gametophyte being enclosed.

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Abbreviations used: CBP, CREB binding protein; CS, cosuppression; HAT, histone acetyl transferase; hs, heat stress; HSE, heat stress promoter elements; HSG, heat stress granules; HSP, heat stress protein; NES, nuclear export signal; NLS, nuclear localization signal; OE, overexpression; WT, wild type.

The organization of leaves as photosynthetic organs with the active cells inside, a protective outer layer of the epidermis and cuticle and, intimately connected with this organization, the necessary gas exchange proceeding through tightly controlled apertures (stomata).

The formation of stress resistant dormant forms (seeds) for propagation and survival of unfavourable conditions.

The development of a mechanically stabilized chomophyte allowing the generation of long-lived and very big plants with systems for long-distance nutrient and water transport.

But in addition to this, plants also became specialized to grow and propagate under extreme environmental conditions, e.g. under conditions of low or high temperatures, of high salt or heavy metal stress or of extreme water deficiency. As sessile organisms they developed remarkable capabilities to rapidly respond to multiple environmental changes from which they cannot escape. A network of interconnected cellular stress response systems is a prerequisite for plant survival and productivity (Nover et al. 1989a; Cherry 1994; Brunold et al. 1996).

1.2 The molecular cell biology of the heat stress response

Although stress responses of plants were studied experimentally since the middle of the 19th century (Sachs 1864; Müller-Thurgau 1980), a milestone for the analysis of cellular stress response systems was the pioneering work of the Italian developmental biologist F Ritossa working with the fruitfly Drosophila melanogaster. After a fortuitous increase of the temperature of the incubator, he observed striking changes of the puffing patterns, i.e. gene activity patterns of the polytene chromosomes in larval salivary glands (Ritossa 1962, 1996). Surprisingly enough, the same reprogramming of transcription was also observed after addition of chemical stressors like salicylate, 2,4-dinitrophenol and azide. About 10 years later A Tissieres and co-workers (Tissieres et al. 1974) identified the newly formed heat stress proteins (Hsps).

Soon, the rapidly developing field of heat stress biology included investigations in other eukaryotic organisms and bacteria. In fact, Ritossa had discovered the central parts of a general stress response system conserved throughout the living world including all prokaryotes and eukaryotes investigated so far (Nover et al. 1989a; Nover 1991; Forreiter and Nover 1998; Scharf et al. 1998a; Bhati and Nover 2002).

To present an overview of a more than 40 years of molecular cell biology research in this field, we will use a hypothetical eukaryotic cell under stress (figure 1). The essential elements of this model can be summarized as follows (Wu 1995; Scharf et al. 1998a; Morimoto 1998):

- Besides heat stress (hs), a large number of chemical stressors and various states of mammalian diseases cause activation of heat stress genes.
- Very likely, the stress sensing system in cells are deviations of protein homeostasis, i.e. of the equilibrium between new synthesis, folding, intracellular targeting, biological function and degradation of proteins. Proteins are shown in two states: (i) proteins in the native state (squares); and (ii) partially denatured proteins (stars) bound to chaperones.
- Heat stress proteins (Hsps) and constitutively expressed members of the conserved Hsp families are molecular chaperones essential for maintenance and/or restoration of protein homeostasis (see part 3 of this overview). Denaturation of proteins and problems in the processing of newly synthesized proteins during stress are assumed to result in a decrease of the pool of free chaperones.
- The transcription of Hsp encoding genes is controlled by regulatory proteins called heat stress transcription factors (Hsfs). They exist as inactive proteins mostly found in the cytoplasm. In figure 1, this is exemplified for the master regulator, HsfA1a, of the hs response in tomato (see below). Stress causes activation with oligomerization and, eventually, recompartmentation to the nucleus, where it binds to its target sequences (HSE) present in the promoter of hs genes (steps 1 and 2 of the Hsf cycle, on the left of figure 1).
- New synthesis of Hsps is assumed to replenish the pool of free chaperones. There is good evidence that in a kind of autorepression, some of the chaperones, e.g. Hsp17-CII, Hsp70, Hsp90 (Guo et al. 2001; Kim and Schöffl 2002; Port et al. 2004), are involved in the second part of the Hsf cycle leading to the restoration of the inactive state of hsfs in plants and animals (steps 3 to 5 of the Hsf cycle).

A peculiarity of plants is the unique complexity of the Hsf family with more than 20 members and the existence of hs-induced forms of Hsfs, which may play a major part in the modulation of transcription in the course of a long-term hs response. The complexity of the Hsf families is exemplified in figure 2 for three plants, i.e. for Arabidopsis and rice, whose genomes were sequenced (The Arabidopsis Genome Initiative 2000; Goff et al. 2002; Yu et al. 2002), as well as for tomato with the best studied Hsf system (Scharf et al. 1990, 1998b; Treuter et al. 1993; Boscheinen et al. 1997; Bhati et al. 2000, 2004; Döring et al. 2000; Heerklotz et al. 2001; Mishra et al. 2002; Port et al. 2004; see reviews by Nover et al. 2001; Bhati and Nover 2002).

Much information about the tomato Hsf system stems from the expressed sequence tag (EST) databases. References to the sequences used for the evolutionary tree in figure 2 can be found in table 1 and the following homepage (http://www.unifrankfurt.de/fb15/botanik/nover.html).