Plant responses to ambient temperature fluctuations and water-limiting conditions: A proteome-wide perspective ☆

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A B S T R A C T

Background: Every year, environmental stresses such as limited water and nutrient availability, salinity, and temperature fluctuations inflict significant losses on crop yields across the globe. Recently, developments in analytical techniques, e.g. mass spectrometry, have led to great advances towards understanding how plants respond to environmental stresses. These processes are mediated by many molecular pathways and, at least partially, via proteome-environment interactions.
Scope of review: This review focuses on the current state of knowledge about interactions between the plant proteome and the environment, with a special focus on drought and temperature responses of plant proteome dynamics, and subcellular and organ-specific compartmentalization, in *Arabidopsis thaliana* and crop species.
Major conclusions: Correct plant development under non-optimal conditions requires complex self-protection mechanisms, many of them common to different abiotic stresses. Proteome analyses of plant responses to temperature and drought stresses have revealed an intriguing interplay of modifications, mainly affecting the photosynthetic machinery, carbohydrate metabolism, and ROS activation and scavenging. Imbalances between transcript-level and protein-level regulation observed during adaptation to abiotic stresses suggest that many of the regulatory processes are controlled at translational and post-translational levels; proteomics is thus essential in revealing important regulatory networks.
General significance: Because information from proteomic data extends far beyond what can be deduced from transcriptome analysis, the results of proteome studies have substantially deepened our understanding of stress adaptation in plants; this is clearly a prerequisite for designing strategies to improve the yield and quality of crops grown under unfavorable conditions brought about by ongoing climatic change.
This article is part of a Special Issue entitled: Plant Proteomics — a bridge between fundamental processes and crop production, edited by Dr. Hans-Peter Mock.

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1. Introduction

Plants, as sessile organisms, have evolved a wide range of response mechanisms conferring upon them stress tolerance that facilitates their survival under rapidly changing environments. Environmental stresses can affect almost all aspects of plant growth and development, resulting in profound changes in plant morphology and physiology. Consequently, specific signaling pathways are triggered which have serious impacts on gene expression and plant metabolism. Plant response to stress is a highly dynamic process dependent on many factors. For instance, plants exposed to different levels of drought exhibit distinct responses described as mild stress avoidance and strong stress tolerance [1–4]. Plants always maintain a balance between survival and maintenance of growth, a balance which will depend on the severity and duration of specific stress stimuli, as well as on the fitness and preparedness of the plant itself and on its developmental stage [1]. The adaptation of plants to their living conditions therefore requires many unique pathways, underlining the complexity of plant–environment interactions.

Due to ongoing global climate change, plants are experiencing non-optimal growth conditions more frequently and severely than ever before. Abiotic stresses, particularly drought and temperature fluctuations, are considered to be the major factors limiting crop productivity, and it has been estimated that approximately 70% of yield losses are due to unfavorable environmental conditions, as has been reported for many socioeconomically important crop species such as maize, wheat, and rice [5–7].

In order to obtain an overview of the current status of scientific research regarding the most common plant environmental stresses, the UniProt database [8], and open-access articles from PubMed Central
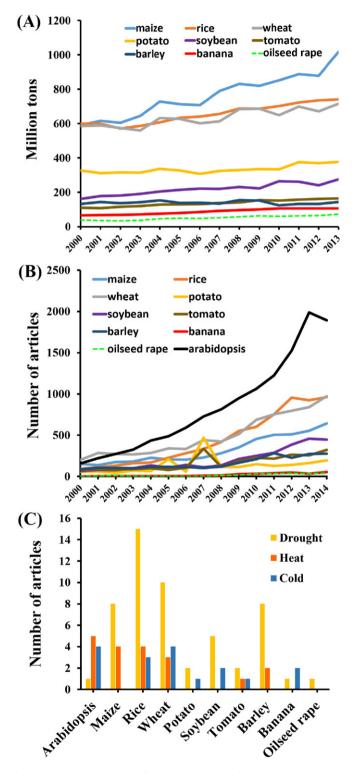
[9] and the Web of Science database (http://isiknowledge.com/wos), were scanned for keywords related to heat, cold and drought stress (also termed water deprivation) in specific plant species, with a focus on proteome-based articles (Fig. 1). Worldwide production figures for the most highly investigated crops were added from the Food and Agriculture Organization Corporate Statistical Database (FAOSTAT), in order to reflect global research interests in the area of agronomic aspects of yield production (Fig. 1A). It is no surprise that most abiotic stress-related studies are performed using the model organism *Arabidopsis thaliana* (Fig. 1B). *Arabidopsis* is widely, though not universally, accepted as an optimal model organism, which is used as an example of how plants respond to stress, and thus applying an *Arabidopsis* model to crop plants has become a prime step of engineering stress tolerance has become an important step in the process of engineering stress tolerance [10]. Unfortunately, differences in stress responses between monocots (maize, wheat, rice, etc.) and dicots complicate the translation of results obtained in *Arabidopsis* directly into crop improvement [11,12]. For instance, many crops are halophyte monocots which have greater tolerance to abiotic stress compared to *Arabidopsis* which, as a dicotyledonous glycophyte, exhibits very limited adaptation to drought [13,14]. Because of this, much effort has been devoted to the analysis of particular responses to abiotic stimuli in various crop species (Fig. 1C). As a result, there are many studies focusing on the proteomes of various crops (e.g. wheat, maize, rice, soybean) in response to conditions of water limitation and extreme temperatures [15–17]. Furthermore, the frequent coexistence of multiple stresses under field conditions has stimulated investigation into responses to the combined action of several stressors [18–22].

To counteract the adverse effects of environmental stress on cellular metabolism, plants respond to changes in their ambient temperature and to water-limiting conditions by reprogramming their transcriptome, proteome, metabolome and lipidome [23]. The proteome of a living organism is a dynamic system controlling and maintaining most of the key processes underlying its growth and development. Because proteins are stable only over limited temperature ranges, and because their assembly is sensitive to osmotic pressure, it is more than likely that the main components of stress-related signaling pathways will have an impact on the plant proteome [24]. Proteomic analysis is a powerful approach which allows the large-scale study of proteins, key components of cell metabolic pathways. One of the major advantages of proteome research is that it makes it possible to establish whether the information stored in an organism's genome, and expressed in its transcriptome, is actually utilized. Because the presence of the mRNA encoding a protein does not necessarily mean that the protein is synthesized by the cell, confirmation that the gene is translated into its functional protein product can only be obtained through proteomic analysis [25,26].

Progress in proteomic approaches has reached the point where they have the accuracy to analyze complex plant samples from different crop species in order to uncover the basis of molecular and biological processes that occur in response to abiotic stress [27]. Proteomic research recruits modern gel-based or gel-free techniques, enabling fast and accurate identification of large proportions of the proteins from specific plant organs, tissues, cells, and subcellular compartments [28]. Separation and identification of proteins can be achieved by 2-DE followed by MALDI-MS, or by a combination of tandem mass spectrometry with liquid chromatography based on, among others, strong cation exchange resins or octadecyl carbon chain (C18)-bonded silica reverse-phase packings. Label-free approaches, such as precursor signal intensity or spectral counting, facilitate the relative quantification of samples that have been analyzed separately by comparing their MS spectra in order to determine peptide abundance in one sample relative to another. Label-based relative quantification methods include stable isobaric labeling techniques such as tandem mass tags (TMT) and isotope-coded affinity tags (ICAT) [29]. For absolute proteomic quantification, several label-based methods are utilized, such as selected reaction monitoring (SRM) or isobaric tags for relative and absolute quantification (iTRAQ) [30,31]. The high-resolution power of mass analysers makes it possible to improve the extraction of peptide signals and obtain high precision mass spectra; such methods include Fourier transform ion cyclotron resonance (FTICR) and Orbitrap mass analyzer [32,33]. Advances in

Fig. 1. (A) Worldwide production of individual commodities from 2000 to 2013 according to FAOSTAT (www.faostat3.fao.org). (B) The total number of articles found in PubMed central and the Web of Knowledge database regarding abiotic stress responses (drought, heat and cold) in crop species with completely sequenced genomes, and the model plant Arabidopsis (09/2015). (C) Number of articles dealing with plant proteomes in relation to abiotic stress (09/2015).