



Proteomics: State of the art to study Mediterranean woody species under stress



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ARTICLE INFO

Keywords:

Abiotic stress

Blast2GO analysis

Woody plant proteomics

Systemic review

ABSTRACT

Mediterranean woody species are vulnerable to multiple stresses that negatively affect plant survival and productivity. Drought and heat are increasing threats to the agricultural and forestry systems, making it urgently necessary to determine the mechanisms of plant adaptation and survival. Proteomics allows for the characterisation of a large number of proteins in a given tissue/organ, providing an integrated picture of the molecular events involved in stress responses. In this paper, we have evaluated the contribution of proteomics for the identification of stress-responsive proteins and tolerance/adaptation mechanisms in woody plants of agronomic importance in the Mediterranean basin. A systematic review was performed (Web of Knowledge, 5th March 2013) on the relevant genera for this region: *Quercus* sp., *Pinus* sp., *Eucalyptus* sp., *Vitis* sp., *Olive* sp., and *Citrus* sp. The term Rosaceae was also included in the search due to the relevance of fruit tree crops of this family in the Mediterranean region. This systematic review highlighted the lack of extensive and comprehensive proteomic analyses for Mediterranean plants under stress. The approach retrieved 19 and 38 papers concerning the assessment of abiotic and biotic stresses, respectively, at the proteome level, and 20 and 46 papers, respectively, concerning analyses at the transcriptomics level. With regard to abiotic stress, gel-based proteomic methodologies (15 papers) enabled the identification and quantification of 395 stress-responsive proteins. These results revealed metabolic adjustments to stress, with major alterations in carbon, nitrogen, and amino acid metabolisms. The most consistently represented stress-responsive proteins were RuBisCO, RuBisCO activase, heat shock proteins, chlorophyll *a/b* binding protein, and proteins from the oxygen-evolving complex. We concluded that gel-based proteomics revealed key proteins and metabolic pathways important for the ability of plants to adjustment to environmental fluctuations. The integration of this information with physiological, agronomic, and technological performance (e.g. survival, productivity, and food and technological quality) is essential for the sustainable development of the Mediterranean regions.

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1. Introduction

The Mediterranean basin is one of the richest regions in the world in terms of plant diversity (Myers et al., 2000) and is also one of the areas most vulnerable to abiotic and biotic stresses. The Mediterranean climate is characterised by dry and hot summers, rainy and mild winters, with high inter- and intra-annual rainfall variability. Drought coupled with extreme temperatures is an abiotic stress that most adversely affects the survival, growth, development, and productivity of Mediterranean woody species (Mooney, 1983; Ogaya and Penuelas, 2003). These environmental

constraints are predicted to become even more severe in the near future because of global climate change (Planton et al., 2012; Sanchez-Gomez et al., 2011).

Mediterranean forests are the repository of a great bulk of terrestrial biodiversity and they support multiple wood and non-wood industries (Scarascia-Mugnozza et al., 2000). Pine trees are an important source of wood and nuts. *Eucalyptus* species are the basis for the pulp and paper industry due to their fast-growth. Oak woodlands are natural ecosystems with productive (i.e. cork, wood, cattle, and hunting) and environmental (i.e. biodiversity, soil protection, and water regulation) value. Fruit woody crops (e.g. *Olive* sp., *Vitis* sp., *Citrus* sp.) make up the basis of the Mediterranean diet and many also represent critical regional food products that are in worldwide demand (Sofó et al., 2012). Therefore, stress is a threat to food and feed productions and endangers forest ecosystems (David et al., 2007; Mantri et al., 2012; Sofó et al.,

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2012). Understanding how plants acclimate to different stressors can contribute to mitigating the impact of stress.

Depending on the degree of species-specific plasticity, as well as stress intensity and progression rate, plants undergo a series of physiological and biochemical adjustments to avoid or tolerate different stresses (Macedo, 2012). Current state of the art proteomics may help unravel the mechanisms activated by Mediterranean plants in order to cope with and recover from adverse environmental events. Proteomics is a powerful tool for studying stress tolerance, enabling the identification and quantification of stress tolerance-associated proteins (Abril et al., 2011; Agrawal et al., 2012), thus providing the missing link between the transcriptome and the metabolome (Afroz et al., 2011). Two dimensional polyacrylamide gel electrophoresis (2-DE) and mass spectrometry (MS) are still the most widely used analytical techniques for the profiling, identification, and quantitative assessment of protein expression in plant species, particularly when little is known about their genome sequence (Abril et al., 2011; Afroz et al., 2011). Understanding the dynamics of stress tolerance-associated proteins expression, and gaining insight into their function is essential for breeding and/or engineering stress-tolerant crops with novel traits through marker selection and transgenic strategies (Agrawal et al., 2012). In the Mediterranean context important issues that need to be addressed are:

1. The impact of drought, heat, and salinity on plant growth and survival, as well as fruit quantity and quality (Rowley and Mockler, 2011). Responses at the level of leaf shedding (Ogaya and Penuelas, 2006) and modification of root architecture (Vilagrosa et al., 2012) can provide useful information about genotype plasticity and adaptation to the environment. Additionally, the impact on wood and cork growth and quality need to be evaluated.
2. The impact of air pollutants, which originate from anthropogenic activities or forest fires, on seed germination capacity and plant regeneration, growth, and ability to cope with other stresses (Fares et al., 2013; Vallejo et al., 2012).
3. Multiple stresses effects, namely the study of the interactions between abiotic and biotic stresses (Syvertsen and Garcia-Sanchez, 2014).

The mechanisms underlying responses to environmental fluctuations and understanding how such mechanisms relate to plant performance will provide powerful tools for agricultural and forest management, as well as for genotype selection.

In this report, we review the current literature concerning the effects of abiotic stresses on Mediterranean woody crops and trees at the proteome level. Our goal was to list the stress-responsive proteins for functional annotation, thereby revealing metabolic pathways associated with stress, and to compile quantitative data for meta-analysis (Gurevitch and Hedges, 1999). It should be noted that the data in the pertinent literature are fragmented and, therefore, a comprehensive understanding of the mechanisms activated or deactivated during stressful conditions is needed (Cramer et al., 2011; Pinheiro and Chaves, 2011).

2. Criteria for the systematic review

Bibliographic data available from the Web of Knowledge (<http://apps.webofknowledge.com>, 5th March 2013) were considered for the systematic review of proteomic information. We selected specific genera (*Quercus* sp., *Vitis* sp., *Eucalyptus* sp., *Olive* sp., *Citrus* sp., *Pinus* sp. and *Prunus* sp.), that were relevant to social, environmental, and economic factors. The term “Rosacea” was also included in the search since it includes many fruit trees.

Additionally, for comparison purposes, the search term “Arabidopsis” was also included. The bibliographic review was complemented with a parallel search for related transcriptomic data using the same search terms.

This survey identified less than 450 papers that used proteomics methodologies in the study of Mediterranean woody species, which represents only 6–7% of papers available for *Arabidopsis* (Table 1). This number was further reduced by considering only peer reviewed original research articles and with the removal of duplicate records. However, when stress related studies were considered, the lack of proteomic data on Mediterranean woody species is fully revealed: there were only 19 papers on abiotic stress and 38 on biotic stress. A similar dearth of research was found with regard to the use of transcriptomic methodologies: there were only 20 and 46 papers that addressed abiotic and biotic stresses (Table 1), respectively. Only two papers reported both protein and transcript data (Grimplet et al., 2009; Jellouli et al., 2010). In two other cases, protein and mRNA data extracted from the same sets of experiments were published as two separate papers: *Citrus* (Tanou et al., 2009, 2012) and *Quercus* (Sergeant et al., 2011; Spiess et al., 2012).

In this report, an “abiotic-stress” paper was defined as original research on the effects of stress on the plant proteome, and in which stress-responsive proteins were identified and the stress effects on protein abundance was quantified. By applying this filter, a total of 15 proteomics papers on abiotic stress were considered for inclusion in the quantitative analysis, thus revealing the genuine scarcity of available data.

3. Data extraction for meta-analysis

Proteomic studies on Mediterranean woody species under abiotic stress are available for drought ($n=10$), salinity ($n=4$), acid rain ($n=1$), and low temperature ($n=1$). No data are available for high temperature, UV-radiation, or multiple stress effects on the plant proteome. The papers that met the criteria defined in this review (Table 2) used 2-DE-based proteomics, and mostly involved analysis of leaves.

Meta-analysis requires quantitative data (i.e. average values, standard deviation, and sample size) (Gurevitch and Hedges, 1999; Walker et al., 2008); it was only possible to extract these data from five papers (Bedon et al., 2012; Echevarria-Zomeno et al., 2009; Jellouli et al., 2010; Macarasin et al., 2009; Tanou et al., 2009). In all the other cases, authors were contacted and asked whether they would make their data available. Several authors replied but only two sent the necessary quantitative information (Jorge et al., 2006; Renaut et al., 2008). Thus, the limited number of studies available did not support the application of meta-analysis methodologies.

Alternatively, information on proteins identified as abiotic stress-responsive was collected from the 15 available papers (Table 2). Most of the papers documented studies on leaves/needles under drought stress (seven papers), except for work on *Vitis*, for which other organs were also analysed (Table 2; Supplemental table S1). The number of identified protein spots per paper ranges considerably (i.e. from 1 to 77 spots; Table 2), mainly as a result of the following: the primary objective of the analysis, methodological limitations at the time of the investigation (e.g. genome availability), different mass spectrometry techniques (i.e. peptide mass fingerprinting versus tandem mass spectrometry), and available budget for mass spectrometry (MS). Our methodological approach compiled 494 proteins, corresponding to 356 unique UniProtKB accessions. These were the stress-responsive proteins for which we then carried out further functional categorisation on the basis of biological processes, molecular function(s), and the cellular components/organelles with which they are associated.

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