



Stress Response in Rice

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A large proportion of world's population depends on rice for food. Rice contributes to human nutrition up to 20% of the calories consumed worldwide. Asia, with 145 millions ha yielding more than 650 million tonnes, is the main world rice producer accounting for 90% of the total. Europe contribution is limited to 4,3 million tonnes that result from a cultivated area of about 700.000 ha.

Rice is grown in a wide range of environments characterized by different temperatures, climates and soil-water conditions. It can grow in areas ill-suited for other crops.

Nonetheless, adverse environmental conditions seriously threaten rice production causing enormous losses in large areas of the world, even in the most productive irrigated lands. In fact, abiotic and biotic stresses often prevent the achievements of optimum yields, limiting the attainment of the maximum potential of growth.

Abiotic stresses, such as drought, high salinity, high or low temperatures, flooding, high light, ozone, low nutrient availability, mineral deficiency, heavy metals, pollutants, wind and mechanical injury, all represent a serious threat to sustainable rice production. Among them, drought and high salinity are the two main causes of yield losses worldwide [1]. Biotic stresses, brought about by biological agents such as viruses, bacteria, fungi, nematodes, insects or herbivores, further reduce rice productivity. Blast disease, provoked by the fungus *Magnaporthe oryzae*, and bacterial blight, caused by the bacterium *Xanthomonas oryzae* pv. *oryzae*, represent two of the most serious and destructive diseases of this crop [2]. Over the past decades, the mechanisms of response to abiotic and biotic stresses in rice have been extensively investigated at physiological, biochemical, genetic and molecular levels.

More recently, the availability of high-throughput techniques has offered unprecedented opportunities for the dissection of the complex signalling pathways and the regulatory gene networks involved in such responses, providing new tools for the targeted manipulation of stress-related traits. In fact, "omics" platforms allow for whole genome transcriptome analyses (including a global survey of small RNAs), proteomic analyses (including the identification of post-translational modifications) and metabolomic analyses, providing a comprehensive profile of all metabolites accumulated under any given condition. Metabolites may play a dual role since they may act either as effectors or as signalling molecules capable of modulating gene expression.

Omics approaches applied to stress in rice should carefully consider the dynamics of the response by monitoring the different time points during stress exposure. In this way, dataset integration can provide a more informative picture of the whole response, not just single snapshots. Integrative data are actually starting to accumulate in rice as reported in the following few examples. By a combined transcriptomics and proteomics approach, the role of jasmonic acid in controlling RNA and protein expression in rice shoots and roots has been dissected [3]. A combined transcriptomics and metabolomics analysis performed on rice response to bacterial blight has identified some corresponding changes, although a coherent interpretation of the global results is still far to be attained [4]. Moreover, an integrated transcriptomics,

proteomics, and metabolomics approach has surveyed the molecular response to ozone exposure in the leaves of rice seedlings [5].

These combinatorial, wide-spectrum approaches can undoubtedly take advantage on the wealth of genetic and genomic information available for rice, since long considered an ideal model system for monocotyledonous species. These include high-quality genome sequences, high-density genetic and SNP maps, large germplasm collections, mutant collections for loss- or gain-of-function analyses, well-established protocols for genetic transformation. In addition, several publicly available databases have been created that are constantly implemented. All these resources can support both the basic and applied aspects of rice research on stress response, in the attempt of unravelling the molecular mechanisms as well as engineering stress tolerant plants.

Numerous rice lines exhibiting tolerance to abiotic and/or biotic stresses have been reported, so far. They are obtained either by molecular-assisted breeding or transgenic approaches. These latter typically suffer from the lack of field trials that should demonstrate the positive effects of the transgenes under realistic field-stress conditions. Researches are more often focused on the identification and the functional analysis of candidate genes than on the production and field validation of new, stress tolerant, resource-use efficient, and highly productive rice varieties. The great expectations raised by the huge amount of dataset available have thus gone largely neglected.

In rice, as in other plant species, the vast majority of the stress-related studies has primarily been focused on single stresses, either abiotic or biotic, and this approach, despite the undeniable progress in the whole area, offers an oversimplified and unrealistic picture. In fact, out in the field, plants are actually exposed to combinations of different stresses that can occur either simultaneously or successively. Therefore, plants must have developed the ability to detect and respond to different combinations of multiple external signals. Under this view, developing stress tolerant plants and testing their performance against individually imposed stresses may reveal to be an inadequate strategy. More so, since it is now well established that plants subjected to multiple stresses activate a unique response that is not simply additive but results from synergistic and/or antagonistic interactions leading to effects that are unpredictable when considering each individual stress [6]. In accordance, the presence of a second stress can either exacerbate the negative effects of the first or, on the contrary, contribute to a positive

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response. These interactions might depend not only on the nature of each stress, but also on its severity, timing and duration. For example, it has been observed that virus infection delays the appearance of drought symptoms, and this kind of protection appears to be related to the increased level of osmoprotectants and antioxidants that is induced by the virus. Again, the effect on plant growth and development of a combined nematode and drought stress, is different depending on the specific nematode. The nematode parasitic infection can either mitigate the severity of the drought stress, or increase drought-related losses [6]. Of recent, systems biology approaches have also begun to address the many questions raised by these complex crosstalks by identifying overlapping steps of the different signalling pathways. Through the integration of large transcriptomics and proteomics datasets, these genome-scale approaches are facilitating the recognition of key genes/proteins that constitute the regulatory nodes/hubs in charge of orchestrating the crosstalk between abiotic and biotic stresses.

Epigenetic modifications may also play a key role in plant stress response and adaptation [7]. Destabilization of epigenetic regulation has been shown to lead to novel epialleles and transposon mobility which, in turn, can broaden plant phenotypic variation. Genome-wide epigenomic information has been accumulated in rice and epigenetic changes have been shown to lead to inheritable phenotypic variation, the extent of which is not known. Both abiotic and biotic stresses are sources of epigenetic variation and these environmentally induced epigenetic effects can be transmitted to the progeny. In rice, inheritable DNA methylation changes have been observed under salt and nitrogen deficiency stresses. Significantly, artificially induced demethylation of the promoter region of the Xa21G gene, that confers resistance to *Xanthomonas (X.) oryzae pv. oryzae*, abolishes its constitutive silencing, caused by hypermethylation, thus resulting in acquisition of disease resistance [8]. Both hypomethylation and disease resistant traits were faithfully maintained for at least ten generations. Identification of the phenotypic consequences due to epigenomic variations and the characterization of the epialleles involved in the adaptive responses to environmental cues can be regarded as an attractive novel strategy to ameliorate agronomically favorable traits in rice.

Ultimately, we like to mention some intriguing studies done in the spaceflight environment, a quite unique stress factor, the effects of which have been investigated in rice and in few other plant species [9]. Uniqueness lies in the fact that unusual, multiple external stimuli, such as

microgravity, space magnetic fields and cosmic radiations are involved. Several studies have reported that the spaceflight environment can be quite effective in generating changes at both genetic and epigenetic level. Extensive alteration in both DNA methylation pattern and transposable elements activity were observed in rice plants germinated from space-flown seeds and some of these changes can be heritable, thus causing transgenerational effects. This unusual mutagenic source is regarded as a unique tool to generate useful mutants with beneficial traits of potential use in plant breeding.

In conclusion, we can state that studying stress response in rice remains a vivid, rewarding and stimulating argument of research, with important consequences at both environmental and social levels in consideration of the ongoing global climate change and the predicted increase of the world population.

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