

# Ribosomal Proteins and their Extra Ribosomal Functions in Abiotic Stress Tolerance of Plants

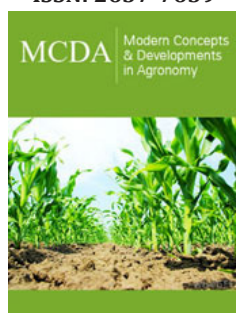
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## Opinion

Ribosomal proteins (RPs) that include both small (RPS) and large subunit (RPL) proteins have been known to be involved in several very important functions in ribosome assembly, protein synthesis and other basic cellular functions in association with several other components [1]. The composition of ribosomal protein subunits that are involved in ribosome assembly is heterogeneous [2] indicating clearly that individual subunit protein components have other functions apart from the basic cellular functions they are associated with. Although each RP gene has multiple paralogs, the expression of all of them appears to be differentially regulated for normal development with some of them functioning in spatio-temporal and signal-induced manner while others exhibit binding properties. The expression of ribosomal proteins has been shown to be regulated by various environmental cues and treatments with signaling molecules [3,4]. The involvement of ribosomal proteins in extra ribosomal functions in animal systems has also been well documented [5].

The extra ribosomal functions of RPs in plants have also started coming to the fore in environmental stresses [6,7]. Several RPL and RPS genes are upregulated in rice at an early stage under salt stress [8]. A mutation in RPL24, which is an important translation initiation factor resulted in defective gynoecium development, reduced ovary size and elongated gynophore in the pistils of Arabidopsis [9]. Thus, the roles of Ribosomal Proteins in extra ribosomal functions are being slowly appreciated in plants. Water use efficiency (WUE) is an agronomically important trait in rice as it is well known that this crop requires large quantities of water to sustain its yield and productivity. It is also a well-known fact that this crop receives maximum attention in terms of allocation of water for its cultivation leaving the other crops thronging for optimal water supplies. Water saved in rice cultivation through enhanced water use efficiency can be reallocated to other crops for enhancing their productivity limits, which is important for food sustainability. In this direction, an activation tagged rice mutant population was developed and screened for identification of activation tagged mutants for enhanced water use efficiency and this analysis has revealed that two out of the five potential mutants that exhibited enhanced water use efficiency as estimated using  $\Delta^{13}\text{C}$  analysis demonstrated the activation of two ribosomal protein large subunit genes, *RPL6* and *RPL23A* associated with significantly enhanced water use efficiency [10]. Subsequent interesting analyses by Moin et al. [4] and Saha et al. [11] in a genome wide survey and characterization of RPL and RPS genes in rice showed that these genes are differentially regulated in various abiotic and biotic stress treatments and in response to the treatments with different signaling molecules. These analyses also validated the differential expression of *RPL6* and *RPL23A* identified in the activation tagging experiments on rice water use efficiency. The involvement of *RPL23A* in abiotic stress tolerance was further demonstrated by its constitutive overexpression in the native system, rice [12]. The ribosomal proteins also appear to be under the modulatory control of a Serine/ Threonine Protein Kinase-the Target of Rapamycin (TOR). It has been demonstrated that one of the downstream targets of TOR is another kinase, p70 kDa, S6 kinase1 (S6K1), which phosphorylates the Ribosomal Protein Small Subunit, *RPS6* [13] for translational activation in eliciting a cascade of signaling events ensuring plant development and survival.

TOR inactivation resulted in reduced growth and ribosome biogenesis by coordinated downregulation of transcription and translation of plastidic ribosomal proteins and rRNA in Arabidopsis plants [14-16]. Ectopic overexpression of *Arabidopsis thaliana* TOR in rice was also associated with significantly enhanced expression of the Ribosomal Protein genes, which was also associated with enhanced water use efficiency and high photosynthetic efficiency [17] corroborating the earlier observations on enhanced expression of RP genes in stress conditions. All these findings provided a secure basis for the extra-ribosomal activities of RPs. The targeted overexpression of selected RP genes can be exploited in crop systems to ameliorate abiotic stress and improve plant performance. However, the important link between TOR activity, RP phosphorylation, ribosome biogenesis and translation efficiency to impact protein synthesis under environmental stresses in plants has not yet been properly elucidated. In essence, the ribosomal proteins are also involved in extra ribosomal functions in addition to the routine basic housekeeping functions in the cell. The literature on their extra ribosomal functions is slowly accumulating in various systems including plants. To comprehensively summarize the extra ribosomal functions of the Ribosomal Proteins in various systems, a special issue has been launched on the Journal "Frontiers in Bioscience", which is scheduled for the year 2021 and contributions in all formats are welcome for inclusion in that issue.

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