**Exogenous application of spermine and putrescine mitigate adversities of drought stress in wheat by protecting membranes and chloroplast ultra-structure**

* [Nemat Hassan](https://link.springer.com/article/10.1007/s12298-019-00744-7#auth-1),
* [Heba Ebeed](https://link.springer.com/article/10.1007/s12298-019-00744-7#auth-2) &
* [Alshafei Aljaarany](https://link.springer.com/article/10.1007/s12298-019-00744-7#auth-3)

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**Abstract**

Polyamines (PAs) are positively charged molecules known to mitigate drought stress; however, little is known about their mechanism of alleviating drought stress. We investigated the effects of PAs exogenously applied as a seed primer and as a foliar spray on the growth, membrane stability (MS), electrolyte leakage (EL), Na+ and K+ cations, reactive oxygen species (ROS), catalase (CAT; EC 1.11.1.6) and guaiacol peroxidase (GPX; EC 1.11.1.7) activity and chloroplast ultra-structure in wheat (*Triticum aestivum* L.; cv. Sakha-94) under drought stress. Three PA solutions, namely, putrescine, spermine and a mixture of the two (Mix), were each applied at a concentration of 100 µM. Our study demonstrated that the retardation of chlorophyll loss and elevation of Rubisco levels were involved in PA-enhanced growth under drought stress. These relationships were mainly reflected in elevated fresh weight and dry weight in response to foliar spraying with all PA solutions and seed priming with the Mix solution. The elevated growth seemed to be due to increased photosynthetic pigments, protein and Rubisco. In contrast, drought decreased growth, photosynthetic pigments, protein and Rubisco. MS was enhanced by PAs applied as a seed primer or foliar spray, as shown by clear reductions in EL %, malondialdehyde (MDA) content and the Na+/K+ ratio as well as reduced ROS markers and elevated CAT (but not GPX) activity. Further study showed that the Mix solution of PAs, applied either during seed priming or as a foliar spray, improved chloroplast ultra-structure, suggesting that improvements in Rubisco and photosynthetic pigments were involved in PA maintenance of chloroplast stability. Therefore, the present study showed that elevated CAT activity is the main mechanism through which PAs reduce ROS and MDA, thereby improving MS and protecting mesophyll cells structurally and functionally under drought stress in wheat.