The Biology of Revival: Mechanistic Insights into Drought Tolerance in Resurrection Plants

G. P. Darshan[1*], Uday Kumar B. V.[2] and Chethankumar M.[3]
[1] Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India- 110012
[2] School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana, India- 141004
[3] Division of Crop Protection, ICAR-Indian Institute of Horticultural Research, Bengaluru, India- 560089
Corresponding Author: darshangp18@gmail.com

Introduction

As climate change intensifies, droughts are becoming longer, more frequent, and more unpredictable. According to the UN, by 2050, over half of global agricultural land could be affected by periodic water scarcity. The impact of drought extends beyond immediate yield losses. It threatens food security, rural livelihoods, and the stability of entire agricultural economies. Crops like wheat, maize, and rice—our food staples—are often ill-equipped to cope with such stress, especially under conventional high-yield farming systems prioritizing productivity over resilience. But plants are far from passive victims. Over evolutionary time, many species have fine-tuned molecular systems that allow them to endure drought, prepare for it, respond to it, and recover from it. Among the most fascinating of these drought-adapted species are the so-called "resurrection plants"—rare and remarkable plants that can survive near-total desiccation.

The Science Behind Resurrection Plants

Resurrection plants represent a unique and highly specialized group of species capable of surviving extreme dehydration by entering a state of metabolic dormancy. These plants can lose up to 95% of their water content without irreversible damage, only to revive and resume normal metabolic functions once water availability is restored. The term "resurrection" evokes the idea of revival after death, and comes from the Latin word "resurrectio", meaning "a rising again" or "to rise again". Examples of resurrection plants include *Craterostigma plantagineum*, *Xerophyta viscosa*, *Haberlea rhodopensis*, *Myrothamnus flabellifolia*, *Selaginella lepidophylla* (Rose of Jericho), and *Selaginella bryopteris* (Sanjeevani). Without water, *Craterostigma* species of the Scrophulariaceae family can survive for at least two years and most likely much longer. Resurrection plants are often can be classified into two categories: those which lose chlorophyll during dehydration (poikilochlorophyllous plants) which include *Xerophyta viscosa,* and *Myrothamnus flabellifolia,* and those that retain (homoiochlorophyllous plants), which include *Craterostigma plantagineum and H. rhodopensis*. During drought stress, one of the earliest physiological responses in plants is stomatal closure to reduce water loss. However, this adaptive response also restricts the uptake of carbon dioxide, thereby limiting the Calvin cycle's activity. Despite this, chlorophyll continues to absorb light energy, and the light-dependent reactions of photosynthesis remain active. This imbalance between light energy absorption and its utilization for carbon fixation leads to the over-reduction of the photosynthetic electron transport chain. As a result, excess energy is transferred to molecular oxygen, generating reactive oxygen species (ROS) such as superoxide anion, hydrogen peroxide, and singlet oxygen. These ROS can cause significant oxidative damage to cellular membranes, proteins, and nucleic acids. To prevent this photodamage, plants initiate chlorophyll degradation as a protective mechanism, effectively reducing light absorption and minimizing the generation of harmful ROS under drought conditions as seen in poikilochlorophyllous plants. Further, the ROS production is counteracted by upregulation of ROS scavenging genes and other antioxidants. But unlike this, homoiochlorophyllous plants retain their photosynthetic capacity, but at a reduced rate and adopt various mechanisms like leaf folding to reduce absorbed radiation or/and accumulation of anthocyanins and other phenolic compounds to protect against solar radiation, thereby reducing ROS accumulation. When it comes to antioxidant system in resurrection plants, they maintain their antioxidant system, including antioxidant metabolites and enzymes at high capacity throughout all kinds of environmental conditions, protecting themselves against adverse fluctuations in water content. This is a unique feature of the resurrection plant antioxidant machinery, as desiccation-sensitive species do not appear to maintain functional antioxidant systems during extreme drought. Along with this, biochemical changes were seen including the accumulation of sugars like sucrose, trehalose, raffinose, and stachyose, which helps in osmoprotection, protein stabilization, and vitrification. Some proteins like Hydrophilins and LEA proteins in particular, are ubiquitous proteins rapidly synthesized during desiccation in vegetative tissues and seeds of plants. Many of these proteins and metabolites are produced by all plants during stress, but the difference is that the expression of certain genes, like desiccation-responsive LEA genes and catalase genes in *H. rhodopensis* and small heat shock proteins in *C. plantagineum* is constitutive i.e., expressed even under normal growth conditions. Further studies on these resurrection plants by using transcriptome analysis revealed that protein phosphatases were the most abundantly induced among all in *H. rhodopensis,* which indicates the importance of phosphorylation and dephosphorylation in dessication tolerance. Along with this, ELIPs, Early Light-Induced Proteins, are key components of the photoprotective system in resurrection plants. ELIPs are believed to act as transient chlorophyll-binding proteins that prevent the formation of free chlorophyll, which can act as a photosensitizer and generate harmful reactive oxygen species (ROS) in the presence of light. By binding free chlorophyll and possibly other tetrapyrroles, ELIPs reduce the risk of photodamage during the desiccated state when the energy dissipation mechanisms are compromised.

Conclusion

In short, what makes resurrection plants different than sensitive plants includes the constitutive expression of some drought-responsive genes, a manifold increase in metabolites like GABA and sugars. However, this extraordinary resilience comes at a physiological cost. The metabolic investment required for maintaining desiccation tolerance, such as the constant readiness to halt and resume cellular function, slows overall growth and reproductive output. As a result, resurrection plants typically exhibit slow growth rates and limited biomass accumulation under normal conditions. This trade-off highlights the evolutionary balance between survival and productivity, where stress endurance is prioritized over rapid development. A deeper understanding of the complex molecular mechanisms underlying desiccation tolerance in resurrection plants, including the identification of unique protective genes, opens new avenues for crop improvement. These plants exhibit remarkable genetic uniqueness, for instance, 41% of *H. rhodopensis* genes, are exclusive to the species. By characterizing the function of these genes and their regulation, it becomes possible to selectively incorporate them into crops using advanced genetic tools, and by coupling these genes with drought-inducible promoters, their expression can be restricted to stress conditions, thereby avoiding the yield penalty typically associated with constitutive stress responses.

References

Djilianov, D., Ivanov, S., Moyankova, D., Miteva, L., Kirova, E., Alexieva, V., ... & Van den Ende, W. (2011). Sugar ratios, glutathione redox status, and phenols in the resurrection species *Haberlea rhodopensis* and the closely related non-resurrection species *Chirita eberhardtii*. *Plant Biology*, *13*(5), 767-776.

Gechev, T. S., Dinakar, C., Benina, M., Toneva, V., & Bartels, D. (2012). Molecular mechanisms of desiccation tolerance in resurrection plants. *Cellular and Molecular Life Sciences*, *69*, 3175-3186.

Rodriguez, M. C. S., Edsgärd, D., Hussain, S. S., Alquezar, D., Rasmussen, M., Gilbert, T., ... & Mundy, J. (2010). Transcriptomes of the desiccation-tolerant resurrection plant *Craterostigma plantagineum*. *The Plant Journal*, *63*(2), 212-228.

* * * * * * * * *